CITIZEN SCIENCE BASED BIRD POPULATION STUDIES

PhD thesis

2017

Henning Heldbjerg

AARHUS
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Data sheet

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Preface

This PhD thesis is the result of an Industrial PhD Project award, partly funded by the Innovation Fund Denmark. The PhD was carried out in a collaboration between DOF-Birdlife Denmark (the company partner) and Department of Bioscience, Kalø, Aarhus University (the university partner), with additional funding from 15. Juni Fonden and Aage V Jensen Naturfond.

The overall aim of the project was to improve the scientific use of data from citizen science based bird population studies in Denmark. This was achieved by (i) improving the use of the existing data covering more than 40 years and (ii) describing new ways of a) obtaining the information required to cover more species and b) securing adequately detailed information in the future by extending current schemes. Such information is essential to be able to provide the knowledge base for the optimal management and conservation of vulnerable or declining species.

The PhD was initiated in November 2014 and completed in October 2017. During this period, the mobility requirements of the PhD were met by collaboration with foreign research groups at the Cornell Lab of Ornithology, Cornell University, Ithaca, US, at British Trust of Ornithology (BTO), Thetford, UK and at Sovon, Dutch Centre for Field Ornithology, Nijmegen, The Netherlands.

The thesis consists of two parts. The first part is a short introduction that aims to define the research questions, describe the nature of the data and their collection methods and to present the results of the investigations. It also briefly describes how the work relates to the state-of-the-art work within the field. The last section has intentionally been kept short, because much of this ground is covered in a commentary paper included in the second part of the thesis. The second main part of the thesis consists of nine chapters, each of them written as a scientific paper in varying stages of completion. Seven papers are published already and two are submitted.

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I also like to thank DOF-BirdLife Denmark (DOF) as an organisation for giving me this opportunity. Jan Ejlsted, Michael Grell as well as Steffen Brøgger Jensen, Henrik Wejdling and the other members of DOFs Executive Council, who provided the necessary time for the idea of the PhD project to grow and make the original application. The new management team, Sigrid Andersen and Mark Desholm (my supervisor in DOF) supported the idea and accepted my absence to work only on the PhD. All of the staff at DOF kindly helped with all sorts of things, particularly the staff of the Bio-team from whom I received much help and many fruitful discussions.

None of this work could have been undertaken without the selfless contribution of the very many bird-watchers that during the last almost 50 years have contributed data to the various monitoring projects. I am very grateful to each and every one of you and I sincerely hope that some of you will see the value of your contributions to the results presented in the PhD and that you will continue your invaluable work.

I enjoyed wonderful fieldwork experiences during the springs of 2015-2017. I am grateful for meeting and working with 'Starling-Master' Peder Thellesen, thanks for sharing all your knowledge from a life-long interest in Starlings and thanks to you and Karin for opening your warm, hospital home and letting me invade your farm with videos, cameras, loggers etc. I also thank Michael Fink Jørgensen, Tony Fox, Bjarne Holm, 'Mikkel' Torben Mikkelsen, Iben Hove Sørensen and Martin Vestergaard for various help in the field work, collaboration that I enjoyed greatly.

I had the great opportunity to visit several organisations that I admire for their work based upon Citizen Science bird monitoring. I hand picked those I wanted to visit and was welcomed by the most friendly and skilled scientists Wesley Hochachka at Lab of Ornithology, Cornell University, New York, US, Ruud Foppen at Sovon, The Netherlands, Rob Robertson and David Noble at BTO, UK and finally Aleksi Lehikoinen, Finnish Lab of Ornithology, University of Helsinki. Also thanks to all my co-authors, every one of you improved the quality of the papers in this thesis. I am also grateful for permission to include those papers for which I am not the first author in the thesis. I enjoyed the process of working with you all and learned so much from doing so.

I sincerely thank the Innovation Fund Denmark, 15. Juni Fonden and Aage V Jensen Naturfond for providing the economic foundation to allow the project to happen.

Last but not least, thanks to my wife Charlotte and our children Alberte, Eskild and Elise for your endless support and patience all through the project.

Resume

Termen ’citizen science’ anvendes selv på dansk til at beskrive projekter, hvor almindelige borgere bidrager med at indsamle data til videnskabelige projekter. Af og til omtales det også som borgervidenskab. Citizen science udgør et uomgængeligt element i fugleovervågning i Danmark ligesom i de fleste andre lande. Den store frivillige indsats skaber betingelserne for at ’tage temperaturen på fuglebestandene’, så samfundet som helhed får viden om status og udvikling for fuglenes udbredelse og antal. Nogle af de danske projekter har genereret sammenlignelige data i over 40 år.

Denne PhD fokuserer på at anvende de indsamlede data bedst muligt. Det forsøges at svare på spørgsmål om, hvorvidt vi kan bruge de allerede indsamlede data bedre, om vi kan dække flere arter bedre og mere effektivt, og om hvorvidt vi skal igangsætte nye projekter, der kan øge vores kendskab til de arter, som vi tilstræber at overvåge og beskytte. Analysen viser os, at disse data skaber en væsentlig viden om arter, naturtyper og fuglområder. Endnu vigtigere er det dog, at disse data også skaber et vidensgrundlag for at forklare udviklingen i de enkelte arters bestandsudvikling, hvilket er afgørende for at kunne understøtte forvaltningstiltag og skabe betingelser for beskyttelse af arter og deres leveområder.

Målet med artiklerne i denne afhandling er at demonstrere, hvordan disse citizen science-data kan bidrage til at skabe viden om fuglebestandene. Der inkluderes en vurdering af, hvordan vi kan inddrage andre analyseformer og endvidere, hvordan vi kan supplere med andre former for data og med moderne tekniske løsninger, så vi opnår en større forståelse for, hvad der forklarer ændringerne i fuglebestandene.

Med udgangspunkt i fugleovervågningen i Danmark før og nu foreslås i den første artikel initiativer, der vil kunne forbedre fugleovervågningen fremover. Der argumenteres for specialiseret overvågning af arter og naturtyper og for opstart af projekter, der kan skabe viden om fuglebestandenes demografi, altså deres størrelse, sammensætning og udvikling, samt om de forhold og egenskaber, der har indflydelse herpå. Der opfordres til øget samarbejde og debat mellem de relevante forskere, naturforvaltere, grønne organisationer samt fugle- og naturinteresserede for at udvikle strategier for en bedre fremtidig fugleovervågning.

Resten af artiklerne udgør ’brikker’ i det store puslespil, der udgør den samlede forståelse af, hvilke faktorer, der forklarer udviklingen i de danske fuglebestande. Punkttællingsdata anvendes i analyser, der viser, at landbrugslandet er den naturtype med størst generel bestandsnedgang og endvidere, at der til trods for forskelle i landbrugsdriften i forskelle egne af landet kun er ganske få forskelle på de regionale bestandstendenser.

I andre artikler fokuseres der på stæren, der er en af arterne med meget stor bestandsnedgang gennem de undersøgte 40 år. Stærens adfærd og krav til leveområdet undersøges og beskrives, og variationerne i stærens regionale bestandsudvikling relateres til variationer i regionale ændringer af landbrugspraksis for at kunne forstå, hvad der har forårsaget den dramatiske bestandsnedgang i stærebestanden.

Tilsvarende overvågningsprojekter i flere lande har skabt tidsserier på mere end 30 år, der kan anvendes til at sammenligne bestandsudviklingen for de almindelige fugle mellem de forskellige lande og endvidere med ændringer i klima og ændringer i landskabsudnyttelse. Artiklerne viser, hvilke ændringer vi kan se i

fuglenes udbredelse og bestandsstørrelser og hvilke konsekvenser, ændringerne i miljø og klima har på fuglesamfundet.

De seneste 15 års store og stigende, usystematiske indsamling af data i DOFbasen anvendes til beregning af bestandstendenser, der sammenlignes med de systematisk indsamlede data fra punkttællinger og beskriver styrkerne og begrænsningerne ved anvendelse af DOFbasens data.

Som eksempel på DOFbasens muligheder og med inddragelse af andre typer data præsenteres til sidst et studie af status og bestandsudvikling for invasive fuglearter i Danmark, der viser, hvordan usystematiske data kan bidrage til nationale og europæiske biodiversitetsprogrammer inden for naturbeskyttelse og naturforvaltning.

Samlet set demonstrerer afhandlingen, hvordan information om fugleforekomster, baseret på forskellige kilder til citizen science-data, kan være ekstremt brugbar til at opfylde de lovpligtige krav i forbindelse med national og international (fx EU-) lovgivning og dermed bidrage til naturbeskyttelse og naturforvaltning.

Summary

Citizen science makes a major contribution to contemporary bird monitoring in Denmark, just as it does throughout many other parts of the world. Involving thousands of participants on a voluntary basis to generate avian distributional and abundance data has become the standard for 'measuring the temperature' of common bird populations. Some Danish monitoring projects have now lasted more than 40 years and there is no current reason to believe that the citizen scientist contribution will decrease in the future.

This PhD focuses on making the best use of the data from existing citizen science monitoring programmes in Denmark. It also poses the questions: can we use the data in better ways, can we cover more species more effectively and can we initiate projects that will increase our knowledge of the species we strive to and need to monitor? What we learn from this analysis is that while such data are extremely useful for generating new knowledge about species, habitats and sites. However, the results from such analyses play an even more vital role in providing the knowledge base for supporting the effective management interventions and enlighten the development of conservation policies for species and their habitats by understanding more about the drivers for changes in population abundance.

The papers included in this thesis aim to demonstrate how citizen science based monitoring data contribute to our knowledge of bird populations. They include an assessment of how we can improve the use of the existing data through novel applications and how we might combine avian monitoring data with other data sources and modern techniques to obtain a better understanding of the drivers of observed changes in bird populations.

Based on an analysis of existing and present bird monitoring in Denmark, the first paper suggests future monitoring initiatives and argues for inclusion of more specialised monitoring on species and habitats and for initiating studies on demography. The paper urges more collaboration, debate and discussion among researchers, managers, NGO's and the birdwatching community to begin to develop avian monitoring strategies for the future.

The rest of the papers contribute pieces to the jigsaw puzzle that represents our understanding of the drivers behind contemporary population changes among Danish bird populations. The thesis presents analysis of point count data used to monitor common breeding birds in Denmark to show declines are most severe amongst specialist farmland birds and that despite differences in farming practice in different regions of the country, there were few differences in regional birds trends to gain insight into causes of change. Other sections focus upon the causes of individual species trends, using the Starling as a study species. This is a species showing long-term declines over the last 40 years, which is investigated to understand differences in regions trends, habitats needs and behaviour, as well as its response to changes in the farmland landscape which could contribute to explaining its recent dramatic decline.

Now that citizen science monitoring in different countries have generated time series of 30 or more years, abundance data can be used to compare with changes in climate and land use, and also comparable to similar data from other countries. Thesis papers show how wintering birds have responded, in terms of abundance and distribution, to changes in climate over time and how we can compare the relative effects of land use and climate change on changes in the bird community.

A comparison between data gathered from Common Bird Monitoring breeding bird data and DOFbasen entries showed the strengths as well as the limitations of using systematic versus unstructured data, especially to track declines amongst common bird species in Denmark.

Finally, with the increase in gathering of opportunistic bird observations, a case study is presented using data from the Danish bird portal DOFbasen to support monitoring of invasive alien species in Denmark to show unsystematically gathered data can contribute to national and European biodiversity conservation and management programmes.

Overall, the thesis demonstrates how avian abundance information derived from different citizen science data sources can be extremely useful in directly supporting biodiversity conservation and management, providing vital support to meeting statutory obligations under national and international (e.g. EU) legislation.

Introduction

How can we improve citizen science based bird population monitoring in Denmark?

Citizen science relies on the active contribution of non-professionals to collect, record and report data to professionals who collate, analyse and transform such material into usable products for third parties, thereby creating opportunities for research and monitoring that would otherwise not be feasible.

DOF-BirdLife Denmark's (DOF) own suite of citizen science activities have created programmes that successfully deliver the highest quality of data, analysis and reporting but has the potential to be used to an even greater extent to support ecological research, conservation management actions and policy development. The use of these and similar data demonstrate how citizen science data can deliver high quality science and show how to maximise the potential of citizen science projects, both now and in the future.

The aim of this PhD-project, as outlined in the original PhD application, was to undertake extensive studies of declining bird species and their habitat use based on data contributed by DOF volunteers to various different projects and databases. This process should attempt to include different sources of data and exploit different analytical techniques that can improve upon our current understanding of population changes and the factors that may be responsible for these observed patterns. By including cross-cutting analyses of all Danish breeding birds derived from data collected over the last 40 years and including new modern techniques, we have searched for adequate explanations for the declines within and between species. Because so much of the Danish habitat is cultivated land, particular emphasis has been placed on the status and trends in farmland bird populations, assessing the absolute and relative effects of agricultural change on avian communities and species. We have sought to find evidence to support hypotheses relating to the key drivers of changes in distribution and abundance of the declining species. Focus on the Starling *Sturnus vulgaris* enabled some testing of hypotheses relating to the factors affecting the regional difference rates of decline emerging from analyses of citizen science monitoring data. In this way, it was possible to compare trends in the largely mixed agriculture of western Jutland (where grazing animals remain reasonably common to provide what has been traditionally thought of as suitable Starling habitat) with those in the east, where arable agriculture has increasingly become the norm. Such results enabled the refining of hypotheses relating to regional Starling status and trends that could be tested by applying state-of-the-art telemetry at a farm where Starlings have been the subject of an in-depth citizen science study for 45 years (see below).

Dedicated studies provide information on the drivers of changing populations as well as the basis for management and conservation

One aim of analysing different types of citizen science data at different geographical scales was to produce a variety of studies that may inspire other similar investigations. Data from citizen science programmes most often comprise simple observations of abundance at a known site, known time and often known habitat. Many observers contribute to standardised surveys, which demand systematic counts gathered under strict guidelines that permit more robust statistical analyses, such as the point counts that are used to generate breeding bird indices under DOFs Common Bird Monitoring programmes. However, observers are increasingly submitting all their observations as a record of their experiences in the field (most of which constitute unsystematically gathered data). Clearly, there is a greater value in data derived from systematically collated information, but the increasing existence of large numbers of unsystematically derived observations makes it possible to at least assess the value of such data and its potential contribution to specific types of avian monitoring. The generation of population trends for breeding and wintering bird populations over many years has been the traditional end-point of much bird monitoring in Europe and North America. However, there has been relatively less attention paid to assessing the variation between habitats and at different spatial scales and the relative roles that environmental variation play in determining how bird population abundance changes over time. In addition to using data from citizen science programmes, parts of the PhD aimed to build upon the knowledge from these time series by adding additional relevant information. These including exploiting data from other sources or using modern techniques to obtain knowledge on individual birds' precise positions to understand the species' preferred habitat. The type of data used for each investigation and the major findings arising from them are here presented for each of the nine papers in the thesis.

First (Paper 1) the role of the citizen scientist is described and how we can promote debate and discussion to improve the existing citizen science contribution to bird monitoring in Denmark. Papers 2 and 3 then examine the trends emerging for all common Danish breeding birds, and investigate patterns among the declining species. Hereafter (Papers 4 and 5), the focus is upon only one case study species, the Starling, which is one of the species showing the fastest declines, integrating other sources of relevant information to better understand the regional differences in abundance and breeding trends among breeding Starling in relation to changing agriculture within Denmark. Because changes in climate and land use are hypothesised to have major impacts on bird community composition, data on all species (both wintering and breeding birds) included in the Common Bird Monitoring were analysed to find support for the relative consequences of these two major sources of environmental change on avian populations (Papers 6 and 7). Finally (in Papers 8 and 9), specific questions are posed about the utility of unsystematically derived data which is entered into DOFbasen, the Danish bird portal. Comparisons between breeding bird point counts and DOFbasen data showed that unsystematic data were less effective at detecting population declines than data from carefully designed monitoring programmes, whereas DOFbasen provided a valuable tool to describe the status, abundance and distribution of seven critical invasive alien species in Denmark, which were otherwise difficult to monitor in Denmark by other methods.

Paper 1 is a commentary that describes the past, present and potential future contribution of avian citizen science programmes in Denmark. The latter focuses on the potential of such studies based on the ongoing activities, analysis of the gaps in the existing effort, links to similar activities in neighbouring countries and reflections on the interest for participation expressed by volunteers in some of the ongoing activities. The analyses include a gap-analysis of all 227 Danish breeding bird species to show which breeding bird species are currently not covered effectively to provide information on status and trends and how the Danish monitoring "community" could better cover a larger number of these bird species. As a review of avian citizen science programmes in Denmark, this chapter takes on the role of a more traditional Introduction section, with the result that this section is perhaps rather shorter than traditional.

Paper 2 used trends from 102 Danish breeding birds based on the Common Bird Monitoring programme, initiated in 1976. Restricting the data to those from 1987-2014 to be able to include the same time series for all species, enabled the analysis and comparison of mean trends for all species within the same habitat. The 2020 EU biodiversity strategy aims to halt the loss of biodiversity and ecosystem services and here we draw attention to the continuing decline of farmland birds, demonstrating that of the 16 specialised farmland species, those breeding on the ground are those in most rapidly decline.

Paper 3 focused on the 16 farmland specialist birds and tested whether we could use regional Common Bird Monitoring data from different parts of Denmark to see if there were differences in population trends for these specialised species. Despite the marked differences between the mixed farming of western regions of Denmark and the predominantly arable cultivation in the eastern region, there was very little difference between bird trends in the different regions. We only found contrasting trends between regions in one species, the Corn Bunting *Emberiza calandra* and conclude therefore that the general decline among the farmland species is most likely caused by the overall intensification in agriculture.

Paper 4 also used breeding bird data from the Common Bird Monitoring programme, contrasting regional trends for the Common Starling that have shown a 60% national decline during the last four decades. The aim of this study was, at a regional scale, to compare the Starling breeding bird trends with the trends in number of dairy cattle and area of grassland. The study confirmed that not only does the extent of grassland available to breeding Starlings affect their relative abundance, but that the intensity of grazing of these grasslands was also of importance. These results were important in providing evidence that developments in the dairy sector have had major consequences for the breeding Starling in Denmark.

Paper 5 follows from the previous paper by testing the hypotheses that individual breeding adult Common Starlings forage selectively upon grazed grasslands. This was the first ever GPS logger study on Starlings to test predictions about general habitat selectivity in the agricultural landscape and increasing feeding selectivity with distance from nest location. Seventeen Starlings provisioning their young in nest boxes were fitted with GPS loggers at a dairy farm in Southwest Jutland with the aim of understanding their habitat choice at increasing distances from the nest and their general patterns of crop/habitat preference. The results showed that the Starlings foraged within a few hundred meters from the nest and selected for grazed grassland. They avoided altogether winter crops and other forms of high, dense vegetation and were increasingly selective with distance from the nest box. These results highlight the importance of grazed foraging habitats close to the nest site of breeding Starlings. The ecological capacity of intensively managed farmland for insectivorous birds such as the Starling is declining because of the conversion of the most strongly selected land cover type (grazed grassland) to those habitats that were far less selected in this study.

Paper 6 used winter bird count data from 50 species in 1980/1981–2013/2014 generated by the Common Bird Monitoring from four countries, The Netherlands, Denmark, Sweden and Finland. We analysed country-specific population growth rates in relation to species' climatic summer and winter niches, habitat preference and migratory behaviour. The main conclusions were that the generally decreasing winter population trends of cold-dwelling breeding species probably reflect the general decline in population sizes of these species. In contrast, increasing winter population trends for populations in the colder parts of the winter distribution indicate a redistribution of wintering individuals towards the north-east. Both these patterns are likely caused by climate change.

Paper 7 exploited the Common Bird Monitoring breeding bird annual indices to compare the relative importance of climate change and agricultural land-use change for changes in abundance within the avian community between 1983 and 2013. Because different environmental drivers affect population abundance simultaneously, it can be difficult to disentangle their effects. The results from modelling clearly showed that the environmental-data approach suggested that agricultural land-use change has decreased the average abundances of species in the community, affecting total community size while the species-attribute based approach suggested that climate change has caused more variation in individual species abundance, affecting community composition.

Paper 8 aimed to assess the correlation between trends estimated from structured monitoring data and the increasing availability of citizen science information stored in online public databases of unstructured data. In Denmark we have both types of data, the structured data represented by Common Bird Monitoring breeding bird data and the unstructured represented by records from DOFbasen. We included 103 species during 1986-2013 to compare trends from the two datasets, showing that population trends estimated from structured and unstructured data were generally positively correlated. However, there was substantial variation among species, and the declines of many common species were not detected with unstructured citizen science data. We therefore conclude that, as expected, structured monitoring programmes are more powerful to detect population trends than unstructured citizen science data.

Paper 9 describes how unsystematically derived observational data, such as those derived from DOFbasen, can still potentially complement existing avian monitoring mechanisms. A novel data requirement to fulfil information needs under the new European Union Regulation on Invasive Alien Species (IAS) implemented in January 2015 highlighted the lack of monitoring of such alien species in Denmark. We used a range of different projects to contribute data from 2005-2014 on the current geographical and numerical distribution of the few serious IAS present in Denmark. We reviewed the status, abundance and distribution of seven critical IAS that have occurred in Denmark in the last 10 years and conclude that none of these pose a major threat as things stand at the present. We show how these monitoring programmes, not least DOFbasen, can be indispensable in supporting the direct management of alien species problems in this country. This confirms the need for continued surveillance of all avian IAS through data collection that is essential if we are to continue to monitor effectively the future extent and nature of the problems posed by such species.

Citizen science based bird population studies in Denmark now and in the future

Seen from the point of view of governmental statutory agencies, ornithological NGOs, the specialist birdwatching community and the general public, the most important function of avian population monitoring has to be as an early warning system to detect major changes in bird distribution and abundance to trigger safeguard mechanisms before these trends become critical. The work presented here has attempted to use such sources of data and link these to other sources of data (such as climate and habitat change) with the aim of better understanding the factors that contribute to the observed patterns of change. This has been achieved in the different analyses by using different methods to use different sources of data to best effect. In doing so, it became obvious that there are data inadequacies associated with some species compared to others and for this reason it became obvious that some review of the extent and efficacy of existing citizen science data to provide avian monitoring data was a necessary element of this thesis. For this reason, Paper 1 provides such an independent review for a wider audience rather than presenting it in this introductory section, even though it contributes to the overall aim of the PhD project.

The current degree of citizen science avian monitoring in Denmark is therefore presented and discussed in Paper 1 of this thesis in order to stimulate some creative thoughts and discussion on how we can improve the situation in the immediate future. We still have a long way to go before we have an ideal system in place, but hopefully this paper will provide some of the context and basic information to promote debate among the very many stakeholders and responsible authorities in Denmark that will help shape this extraordinary source of monitoring data in years to come.

Monitoring is conceived as a means of 'taking the temperature of bird populations' i.e. to test how healthy the state of current bird populations may be. There are many potential means of monitoring changes in bird populations and since one design may not always suit all species, we may need to implement several methods in order to monitor all species effectively due to the differences in their abundance, distribution and behaviour. Monitoring forms the basis for providing a basic understanding of the status and trends of each species to enable decisions on their effective management. This is vital for government agencies and appropriate NGOs who need such data in order to fulfil requirements under national and international legislation, as well focus priorities for work plans. However, the gaps in our ability to both monitor trends and effectively interpret the factors responsible for changes in distribution and abundance also highlight the areas where we need to add dedicated research and obtain more detailed information upon which to provide the science base for implementing the necessary management and conservation initiatives. Despite the fact that birds are relatively easy to monitor compared to other groups of organisms such as insects or mammals, monitoring birds is often not as easy as we would like. There is a major need to develop the way in which we monitor bird populations, how we can include more species and how we can extract as much information as possible to get sufficient information to actually enable us to focus the effective management of declining species.

At present, there are major differences in how monitoring is performed between different European countries but since they 'know no borders' and birds are highly mobile, we increasingly need to combine the results from different countries and to improve the quality of our activities through collaboration. Fortunately, there is considerable interest in and enthusiasm for collaboration among avian biologists and this is evident from the number of diverse researchers from different organisations in different countries that have contributed to the body of work presented in this thesis. This has enabled the use of state-of-the-art modelling techniques to address comparative questions about the relative contributions of different environmental parameters to avian community composition that have not been addressed before as well as application of state-of-the-art technology to tracking Starlings on a southern Jutland dairy farm to generate novel and insightful data on habitat use. Such collaboration takes time to build trust and working relationships, but also creates networks of cooperation that endure, supporting future continuation of such team work and innovation. There also remains much to be done, not least in being more strategic about how citizen science networks can be stimulated, supported and grown most effectively. Although this thesis represents a major step forward, there remains much to be done in terms of effectively setting out an aspirational programme about where to take avian citizen science in the immediate future.

List of manuscripts

Paper 1:
Heldbjerg, H., Fox, A.D. & Vikstrøm, T. Submitted. How can we improve future citizen science based bird monitoring in Denmark? Submitted, as a commentary for Dansk Orn. Foren. Tidsskr.

Paper 2:
Heldbjerg, H., Sunde, P. & Fox, A.D. 2017. Continuous population declines for specialist farmland birds 1987-2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. Bird Conservation International. https://doi.org/10.1017/S0959270916000654

Paper 3:
Heldbjerg, H. & Fox A.D. 2016. Regional trends amongst Danish specialist farmland breeding birds. Dansk Orn. Foren. Tidsskr. 110: 214-222.

Paper 4:
Heldbjerg, H., Fox, A.D., Levin, G., Nyegaard, T. 2016. The decline of the Starling *Sturnus vulgaris* in Denmark is related to changes in grassland extent and intensity of cattle grazing. Agriculture, Ecosystems & Environment 230: 24 – 31.

Paper 5:
Heldbjerg H., Fox A.D., Thellesen P.V., Dalby L. & Sunde P. 2017. Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. PLoS ONE 12(8): e0182504. https://doi.org/10.1371/journal.pone.0182504

Paper 6:
Lehikoinen, A., Foppen, R.P.B., Heldbjerg, H., Lindström, Å., van Manen, W., Piirainen, S., van Turnhout, C.A.M. & Butchart, S.H.M. 2016. Large-scale climatic drivers of regional winter bird population trends. Diversity and Distributions 22: 1163–1173.

Paper 7:
Bowler, D.E., Heldbjerg, H., Fox, A.D, O'Hara, R., Böhning-Gaese, K. Submitted. Disentangling the effects of multiple environmental drivers on population changes within communities. Submitted Journal of Animal Ecology.

Paper 8:
Kamp, J., Oppel, S., Heldbjerg, H. Nyegaard, T. & Donald, P. F. 2016. Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark. Diversity and Distributions 22: 1024-1035.

Paper 9:
Fox, A.D., Heldbjerg, H. & Nyegaard, T. 2015. Invasive alien birds in Denmark. Dansk Orn. Foren. Tidsskr. 109: 193-205.

Henning Heldbjerg's own contribution to papers in the PhD thesis *Citizen Science Based Bird Population Studies*.

Paper	**Status**	**Research phase**			**Writing phase**		
		Major	**Proportional**	**Minor**	**Major**	**Proportional**	**Minor**
Paper 1	Submitted	x			x		
Paper 2	Published	x			x		
Paper 3	Published	x			x		
Paper 4	Published	x			x		
Paper 5	Published	x			x		
Paper 6	Published		x				x
Paper 7	Submitted		x				x
Paper 8	Published		x				x
Paper 9	Published		x			x	

Additional papers co-authored during the Ph.D. period:

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Stephens, P.A., Mason, L.R., Green, R E., Gregory, R.D., Sauer, J.R., Alison,J., Aunins,A., Brotons,L., Butchart, S.H.M., Campedelli,T., Chodkiewicz,T., Chylarecki,P., Crowe,O., Elts,J., Escandell,V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P., Willis, S.G. 2016. Consistent response of bird populations to climate change on two continents. – Science 352:84–87.

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PAPER 1

HOW CAN WE IMPROVE FUTURE CITIZEN SCIENCE BASED BIRD MONITORING IN DENMARK?

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Manuscript

Photo: Henning Heldbjerg

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Abstract

Citizen science has become an indispensable means of obtaining the information necessary for maintaining bird monitoring programmes. The aim of this paper is to inspire creative thought and discussion among the ornithological community, scientists and decision makers in Denmark to improve the quality and extent of breeding bird monitoring in Denmark. We review the past and present status of monitoring programmes in Denmark and use this information as a basis for discussing how we could best improve citizen science based bird population programmes in Denmark in the future. We undertake a gap analysis to establish some immediate priority areas for attention. In particular, we argue for initiating programmes that deliver information on demography parameters such as survival, reproduction, immigration and emigration to better interpret overall trends in abundance. We suggest combining data from different monitoring programmes to develop the possibilities for the integrated analyses of population counts and demographic data within population models. This will enable a better understanding of the demographic processes driving population changes and contribute to more effective management and conservation of key species in the future.

Introduction

There is a long tradition of monitoring bird abundance and distribution in Denmark and neighbouring countries. This monitoring has become highly dependent on the commitment, interest and willingness of volunteers to participate and contribute. This commentary aims to describe the existing extent of citizen science based bird population monitoring and to build on what has been done in the past and in recent years to stimulate debate about how this can be better maintained and improved to secure a major contribution to avian research and conservation within Denmark in the future. It also concludes by undertaking a gap analysis to establish some immediate priority areas for attention in the future.

One major objective of this exercise was to establish an exhaustive annotated list of all breeding species recorded in Denmark to quantify the degree to which each of these species is covered by the various existing monitoring programmes to elucidate which species currently suffer inadequate coverage and recommend where we need to set additional focus in the years to come.

The aim is not to come with a definitive list of what to do next, but rather to inspire creative thought and discussion among the ornithological community, scientists and decision makers in Denmark to improve the quality and extent of breeding bird monitoring in Denmark for the benefit of future generations.

Definitions

Citizen science has been defined as ‘projects, where volunteers partner with scientists to answer real-world questions’ (www.birds.cornell.edu) and such public participation is now heavily involved in environmental research and monitoring across the world. Monitoring focuses on changes in state. It usually compares measurements at different places and times with re-measurements as a key part of a monitoring programme. In population monitoring, the intent is usually to detect a population trend and the rate at which change is occurring (i.e. whether a population is stable, decreasing or increasing, and whether that change is slowing or accelerating). The target may be a population of a single species, populations of numbers of species, or composition of selected ecosystems (Greene 2012). Such work is most successful where there is a strong partnership between the amateurs and the professionals, based on their complementary roles (Greenwood 2007).

Why do we need citizen science?

In the nature conservation world, citizen science has become an indispensable means of obtaining extensive information on very broad scales; in the absence of professional networks to supply environmental data, it forms the basis for governmental decision-making processes and policy development. It is also important for supporting the development of policy, prioritisation and work programmes within the NGO sector. For example, it has become vital in many practical ways in supporting the conservation of avian species, management of sites and regulation of hunting. Citizen science has become the accepted means of generating crucial data on bird population sizes and rate of change to fulfil the requirements of national and international legislations and agreements, such as the European Union Birds and Habitats Directives and establishing population sizes for site designation under the Ramsar Convention based on their support of 1% of flyway populations. By virtue of the existing extensive networks of volunteers coordinated by relatively few professionals, citizen science has become absolutely indispensable to perform surveys undertaken at a variety of spatial scales (from the site level to covering whole continents) driven by highly competent and motivated but ultimately volunteer participants.

The participation of such large numbers of volunteers generates information that would otherwise be impossible to derive (Greenwood 2007). This relates to a) the logistics of carrying out surveys at very large numbers of sites over short time periods, b) maintenance of long time series based on similar effort every year and c) the financial cost because employing professionals to gather comparable data (even if logistically possible) would inflate total budgets to levels rendering them impossible to perform.

However, we must never forget that major contributions from citizen science also arise as a result of projects coordinated by individuals or groups of dedicated birdwatchers that over time become specialists in their target species or habitats. Such studies may either result directly in scientific publications with or without the coordination or help of professionals (e.g. Thellesen 2017; Østergaard 2017) or create a substantial foundation of knowledge and expertise upon which to facilitate further studies (e.g. Heldbjerg et al. 2017).

Citizen science in Denmark in the past

Before the formal creation of research establishments and centres of learning, all human curiosity relating to our environment could have been considered to constitute a form of “citizen science”! “Ordinary” people, receiving no financial or commercial gain from their endeavours, driven by pure curiosity and their fascination for birds in their immediate surroundings contributed to the very first citizen science activities relating to birds in Denmark. When Hans Christian Cornelius Mortensen started ringing Starlings *Sturnus vulgaris* to find whether the same birds returned to his nest boxes each year and understand where they travelled in winter, he was amongst the earliest and most famous to make contributions to Danish citizen science (Preuss 1997). The first truly national Danish monitoring project covering the entire country was a site-based survey of the most important bird areas, initiated in 1960 by DOF-Birdlife Denmark (Dansk Ornitologisk Forening (DOF)), the results of which were published in 1971 (Ferdinand 1971). This and similar repeat surveys were undertaken in 1960-71, 1978-81, 1993-96 and 2003-13 (Flensted & Vikstrøm 2006; Vikstrøm et al. 2015). From the mid-1960s to mid-1970s, various DOF volunteer groups undertook surveys of different bird groups (e.g. rare species, raptors and waders; see Møller 2006). During the same period, the first national mid-winter monitoring of migratory waterbirds was undertaken in a joint project coordinating professionals (undertaking aerial survey from aircraft) with large numbers of volunteers undertaking land-based counts (Joensen 1974). This was repeated again in 1987-1992 and 2000 (Petersen et al. 2006) and as part of the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments (NOVANA) in 2004, 2008 and 2013 (Holm et al. 2016), with monitoring at reduced coverage in many of the intervening years. Monitoring of wintering geese and swans was included annually since 1981 and 1992, respectively (Holm et al. 2016).

The first initiative to map the distribution of all Danish breeding birds was the first DOF atlas undertaken in 1971-1974, involving 745 volunteers (Dybbro 1976). The second DOF Atlas was undertaken in 1993-1996, by then involving 750 participants, which included an attempt at estimating relative breeding bird densities of the common species (Grell 1998). A subsequent specialist survey attempted to determine breeding birds of small rural biotopes in Denmark (Meltofte et al. 2009). In May 2002, the Danish national bird reporting portal DOFbasen went online (Nyegaard et al. 2012), that built upon some prior initiatives taken by some of the local branches of DOF. The aim of this data portal website www.dofbasen.dk was to facilitate online reporting of all bird observations from any part of the country throughout the year.

The regular annual monitoring of the relative abundance of common birds in Denmark ("Common Birds Monitoring"), is based on observers sampling local avian abundance by undertaking mapped and timed point counts in the field. Initiated in the winter of 1975-1976 for wintering birds and in 1976 for breeding birds (Møller 2006), these are now among the oldest bird monitoring programmes in Europe (Heldbjerg et al. 2015). This annual survey has now provided population indices for all common birds for more than 40 years and as well as being a vital measure of the health of Danish birds that has contributed to numerous significant research projects (e.g. Fox 2004, Heldbjerg et al 2016, Lehikoinen et al. 2016).

Additional intensive site-based monitoring (performed by professional ornithologists) at field stations was established by different governmental departments between the 1930s and 1980s at some of the most important breeding and staging areas for waterbirds in Denmark, namely at Vejlerne, Tipperne, Vorsø and Langli, with monitoring of migrant passerines undertaken on Christiansø (Lyngs 2006). These programmes were all closed down (or activities significantly reduced) in the 1990s. These stations undoubtedly provided valuable annually reported results that cannot be replaced at present, but the major costs of supporting these potentially very significant programmes failed to guarantee their continuity. The lesson to be learned here might be that very ambitious (and thus costly) programmes may suffer a higher risk of failing to last for longer periods, which seems to contrast the apparent robustness of the rather simpler but nevertheless successful and so far persistent citizen science surveys.

Present citizen science in Denmark

The Danish Ministry of Environment and Food has obligations under international conventions and international (e.g. EU) law to report on the status of key species and habitats, including birds. To meet these reporting responsibilities, existing monitoring programmes are designed to fulfil commitments, for example, to the European Commission under the Birds and Habitats Directives, based around NOVANA (Miljøstyrelsen et al. 2017).

In addition, there is also considerable interest among the general public, as well as among the various relevant NGO's, to know more about the status and trends of Danish breeding birds that are not necessarily the focus of international requirements.

Currently, most Danish bird monitoring projects are organised and run by DOF-Birdlife Denmark (DOF) and/or the Department of Bioscience, Kalø, Aarhus University. Some, such as NOVANA and the CBM, are run as partnerships, financed to varying degrees by The Ministry of Environment and Food. Other projects are financed by private charity foundations, such as the Atlas programme (which was supported by the Aage V Jensen Foundation). In recent years, many monitoring

Table 1. Overview of the most significant citizen science national monitoring projects for birds undertaken in Denmark during 1960-2017.
Oversigt over de mest betydningsfulde, frivilligt baserede, nationale fugleovervågningsprojekter i Danmark i perioden 1960-2017.

Project ***Projekt***	**First year** ***Første år***	**Last year** ***Sidste år***	**Publication** ***Publikation***
(No English title); *Større danske fuglelokaliteter*	1960	1971	Ferdinand 1971
(No English title); *Fuglene i landskabet*	1960	1977	Ferdinand 1980
Mid-winter monitoring of staging waterfowl; *Midvintertællinger*	1965	1973	Joensen 1974
Atlas I: (No English title); *De danske ynglefugles udbredelse*	1971	1974	Dybbro 1976
Common Bird Monitoring, winter; *Punkttællinger, vinter*	1975/1976	Ongoing	Moshøj et al. 2017
Common Bird Monitoring, breeding; *Punkttællinger, ynglefugle*	1976	Ongoing	Moshøj et al. 2017
Rare and threatened breeding birds in Denmark	1976	1991	Sørensen 1995
(No English title); *Status for danske fuglelokaliteter*	1978	1981	Dybbro 1985
Mid-winter waterbirds in Denmark; *Midvintertællinger*	1987	1992	Petersen et al. 2006
Atlas II: (No English title); *Fuglenes Danmark*	1993	1996	Grell 1998
(No English title); *Fuglenes Danmark: Fuglelokaliteterne i Nordjyllands (etc.) Amt*	1993	1996	Various authors 1997-1999
DATSY - Rare and threatened breeding birds in Denmark; *DATSY - Truede og sjældne ynglefugle*	1998	2012	Grell et al. 2004; Nyegaard et al. 2014
Mid-winter waterbirds in Denmark; *Midvintertællinger*	2000	2000	Petersen et al. 2006
DOFbasen (www.dofbasen.dk); *www.dofbasen.dk*	2002	Ongoing	Nyegaard et al. 2012
IBA Caretaker project; *Status og udviklingstendenser for Danmarks internationalt vigtige fugleområder*	2003	2013	Vikstrøm et al. 2015
Mid-winter counts; *Midvintertællinger*	2004	Ongoing	Holm et al. 2016
Birds in Danish gardens in winter; *Den Store Vinterfugle-tælling*	2007	2011	Meltofte & Larsen 2015
Atlas III; *Atlas III*	2014	2017	Levinsky 2016

programmes remain ongoing (DOFbasen, CBM, Mid-winter counts) or are being periodically repeated (Atlas III; 2014-2017; Table 1).

Monitoring species

There is an undoubtedly pressing and continuing need for monitoring of species and habitats if we are ever to maintain and improve upon current levels of biodiversity in Denmark. This requires knowledge of the state of species and habitats and the effects of implemented local (i.e. site based) and national initiatives and action plans (Miljøstyrelsen et al. 2017). Species monitoring aims to track changes in distribution as well as abundance, from the local up to the national and international levels, since national schemes also need to feed into an international perspective, in order to differentiate local changes in distribution and abundance from patterns at the population flyway level as well as generating flyway population estimates.

Denmark has initiated systematic monitoring of habitats and species included in the Habitats and Birds Directives through the launch of the NOVANA (Holm et al. 2016). The main objective of this was to monitor population size and distribution of breeding birds and regularly occurring migratory bird species following Article 4.2 of the Birds Directive. Since 2004, the Mid-winter counts are also (after a period when we lacked such monitoring) part of this monitoring framework (Holm et al. 2016).

Annually monitoring of abundance

Knowledge about the year-to-year relative abundance of avian species is obtained by different monitoring programmes depending on the species, for example, how numerous it is, how secretive it is and when it is active during the day. So, for instance, Common Birds Monitoring data are gathered in winter and during the breeding period by 300 volunteers to generate samples of relative abundance and contribute to the estimation of annual indices for 80-110 species, which are reported annually (Moshøj et al. 2017).

At the other end of the abundance scale, more focussed and intense monitoring is required to generate national trends for rare and scarce breeding birds. For many years, DOF maintained a programme for Threatened and Rare Breeding Birds, known as DATSY, to generate annual population estimates for such species (Grell et al. 2004; Nyegaard et al. 2014; Table 1). The programme connected birdwatchers with interest in one or more of these rare breeding birds and their joint efforts have provided improved estimates of abundance and a mechanism for assessing changes in the size of national populations. Initially this programme was funded by the Aage V Jensen Foundation (Flensted & Vikstrøm 2006) and later as part of the 'agreement between DOF and MoE' (Nyegaard 2016). From 2013 onwards, this group of birds has only been covered for some of those listed on Annex 1 of the Birds Directive and from 2018 only on sites designated for those species (Miljøstyrelsen et al. 2017). As a result of these changes, we will no longer be able to produce reliable annual population estimates and trends for any of these species excepting White-tailed Eagle *Haliaeetus albicilla*, Montagu's Harrier *Circus pygargus*, Golden Eagle *Aquila chrysaetos* and Osprey *Pandion haliaetus* for which there exist specific citizen science monitoring programmes organised within DOF.

Regular but less than annually NOVANA monitoring

With the exception of Cormorant *Phalacrocorax carbo*, which is monitored in detail by annual nest counts (Bregnballe & Nitschke 2017), the monitoring of coastal and colonial breeding birds is restricted to those species listed on Annex 1 in the Birds Directive and only at the sites designated for a given species. The aim of these programmes is to monitor and document the status and trend of the distribution and abundance of the listed species (Miljøstyrelsen et al. 2017). However, this monitoring is maintained through a rolling plan on a 6 years cycle, alternating between species from year to year, monitoring a given species every two or three years and for some species including national coverage (including areas outside sites designated for the Annex 1 species) once in every 6 years period. This is relevant for 36 of the breeding birds listed on Annex 1 that are part of the so-called 'Intensive 1 monitoring of breeding birds' (Appendix 1; Miljøstyrelsen et al. 2017). The monitoring is largely undertaken by staff at the Environmental Protection Agency and consultants paid for the purpose.

The rest of the breeding birds listed on Annex 1 (11 species) comprise part of the 'Intensive 2 monitoring of breeding birds': Black Stork *Ciconia nigra*, White Stork *Ciconia ciconia*, White-tailed Eagle, Montagu's Harrier, Golden Eagle, Osprey, Peregrine *Falco peregrinus*, Mediterranean Gull *Larus melanocephalus*, Short-eared Owl, *Asio flammeus*, Boreal Owl *Aegolius funereus*, Tawny Pipit *Anthus campestris*, (Appendix 1). These species are monitored based on quality assured data derived from DOF/DOFbasen, i.e. entirely based on citizen science records (Holm & Søgaard 2017).

Distribution

Avian distribution has traditionally been described via the Danish atlas surveys performed to date every c. 20 years. The 3rd breeding bird atlas (based on fieldwork in 2014-17) is ongoing, generating comparable data using the same methods to the two previous atlases which mapped the distribution of all Danish breeding birds. The current project includes a new initiative to estimate both relative and absolute bird densities in both winter and during the breeding season, based on line transects with distance bands. This is expected to provide improved and reliable national population estimates for c. 30 (winter) and 45 (breeding) species (Levinsky 2016).

DOFbasen has become an important tool for hosting vast numbers of casual (i.e. unsystematically compiled) avian records. The numbers of sites, observers and records have increased every year until 2016 when contributions seem to have stabilized at c. 1.5 million records contributed by c. 2400 observers from c. 14000 sites annually. The unsystematic nature of the data restricts the use and interpretation of such data, although complete lists of timed visits are encouraged and are potentially far more valuable that casual incomplete records (Kamp et al. 2016). Nevertheless, the vast number of records accumulated provides another valuable source of information on avian abundance and distribution all year round.

Monitoring sites

International legislation also obliges Denmark (as other nations) to monitor the most important sites for biodiversity, which are statutorily protected for their birds under the cohesive network of NATURA 2000 protected areas throughout the EU. Two typical types of NATURA 2000 sites are scheduled for birds, breeding areas for scarce breeding species that are listed on Annex 1 of the Birds Directive and those sites of international importance for their wintering, staging and breeding species. The Danish Environmental Protection Agency is responsible for reporting the status and trends at the NATURA 2000 sites to EU. Municipalities, large land owners and NGO's such as the Bird Protection Fund (which works closely with DOF) also share an interest in tracking changes in biodiversity at the sites by monitoring different organism groups.

Government requires site quality monitoring and bird numbers are an attribute of this. Site-based knowledge is also relevant for understanding whether the decline of a given species reflects a flyway decline rather than degradation in local site quality. This underlines the need to describe changes in distribution and abundance at flyway level and the importance of differentiating contributions from local changes to site quality with changes in regional and global distribution and abundance at larger spatial scales. If declines are the result of reductions in site quality, such local site monitoring can also be used to test whether sympathetic site management also has a beneficial effect on restoring numbers. Thus, a cohesive integrated site-based monitoring forms the basis for contributing to management and conservation at both the site and flyway levels.

DOFs Important Bird Area (IBA) "Caretaker" project was almost exclusively based upon citizen science monitoring to provide detailed knowledge on avian abundance at the most important bird sites in Denmark. The focus was primarily on those species for which any given site was designated under the Birds Directive. This work was funded by the Aage V Jensen Foundation during 2003-2013 (Vikstrøm et al. 2015) but has presently no funding or dedicated platform. Currently 130 IBAs regularly support more than 1% of the flyway population of a species or are judged by other criteria to be of international importance to one or more species of breeding, staging or migrating birds under this programme (Vikstrøm et al. 2015).

DOF "Caretakers" are often involved in actively managing the sites to benefit the birds and nature conservation interest and enhance the visitor experience for the public visiting such sites. They also help in communicating the value of the sites by leading field trips into areas, maintaining websites etc. Finally, they support governmental bodies, the wider community and landowners to protect sites and the organisms they support by raising awareness of the environmental pressures acting upon and damaging the sites.

As part of the NOVANA monitoring programme, the important bird areas, Wadden Sea, Tøndermarsken, Fjords in West Jutland and Vejlerne are also monitored (Holm et al. 2016). This work includes coverage of the breeding birds in these areas and is mainly done by consultants with little or no citizen science involvement.

Parameters relevant for distribution and abundance

Population parameters

The basic objectives for monitoring any species are to establish their distribution (where is a given species?), phenology (when is a species at a given site?) and abundance (how many are there?). While information on distributions is mainly obtained by the Atlas surveys and abundance by the Common Bird Monitoring and Mid-winter counts, DOFbasen provides information on the phenology at any one site, all year round from very many sites. The disadvantage of the latter is that data are not systematically collected and observers typically only provide presence data but not absence data, which makes it much more difficult, if not impossible, to estimate the changes over time and the variation between areas (Kamp et al. 2016). However, it is possible and encouraged within DOFbasen to indicate if you have entered data on all registered species and thus use so-called 'timed full lists' to overcome this problem.

Understanding factors affecting distribution and abundance

For a number of species we are witnessing considerable changes in distribution and/or abundance over time. The reasons for these changes can relate to factors such as climate and land use changes and other human effects (e.g. hunting or disturbances) as well as a consequence of changes in other species' populations. The changes in distribution and abundance are obviously important for statutory agencies and NGOs charged with protecting and maintaining distributions and abundances of species under international legislation and interests of their members. However, to target appropriate management strategies, we require more than just information on numbers and distribution, and we need to see if changes relate to reduced reproductive success or survival, because causal factors may be manifest at different times in the annual cycle and therefore in different geographical areas. It is therefore equally important to understand the mechanisms behind the observed changes in order to implement effective management to restore declining populations. In the end, there may be good value for money gained from converting knowledge (i.e. about species increasing or decreasing) into targeted management actions. Obviously if you do not know where or when the key factors causing population decline occur, you will be unable to focus your actions, a very powerful reason for tracking demographic measures simultaneously with population trajectories.

Demographical parameters

For any population, changes in abundance and/or distribution arise from changes in demography, i.e. survival, reproductive success, emigration or immigration, as well as changes in sex ratio. A proportion of all birds will die every year, with some annual variation in this rate. Survival rate is often lower for the birds in year(s) before maturity and such changes may be largely confined to only one age class. If the survival rate increases or decreases in any of the age classes, it will inevitably have consequences for the population size. Since many small-bodied birds are relatively short-lived, annual changes in population size are highly dependent on the relative production of a large number of fledglings. Such populations need to produce sufficient young to replace annual numbers dying or the population declines. In contrast, many long-lived birds are more susceptible to change in adult survival. This is especially the case among huntable species, where shooting mortality may be additive (rather than compensatory, where hunters remove a harvestable surplus of individuals which would have died of other causes anyway) to natural mortality making them sensitive to immediate reductions in population size as a result of an increase in harvest.

For all species, however, even greater insights into the process limiting reproductive success may be derived from understanding the steps faced by birds along the route to successfully produce sufficient young to independence (Newton 2014). These include: age of first breeding and breeding propensity throughout adult life, the number of eggs laid, the proportion of the eggs that hatch, the number of hatchlings that fledge and the number of clutches laid per season. Such parameters can be derived for the commoner species through nest recording schemes and such data can be derived from citizen science networks given proper encouragement and training to observers to ensure minimum levels of disturbance associated with such data gathering activities.

With detailed and focused studies, like CES (Constant Effort Site ringing) it is possible to estimate the annual production of a given species and over time, generate estimates of survival. For other species, similar information can be obtained from studying plumage characters on wings from hunted species (see below).

For a few species, it is only possible to estimate the annual production of young outside the breeding season. Some goose species like the Dark-Bellied Brent Goose *Branta bernicla bernicla* can be aged during the winter where they spend the winter in family groups at the staging sites. This gives the opportunity to estimate the annual ratio between young and adult birds several thousand kilometres away from the breeding grounds and to identify the often complex and interacting drivers of change in reproductive success linked to Arctic lemming and predator populations (Nolet et al. 2013).

There can be many explanations for changes in the demographical parameters of avian populations over time, such as climate change, changes in land use (crops, agricultural treatment), other human (hunting, disturbance) and biological effects (competition, predation, parasite level etc.). Population models can help reveal to what degree different parameters affect avian abundance (e.g. Bowler et al. submitted) and how demographic factors contribute to annual rates of change in population size, including immigration/emigration rates at the site level (Weegman et al. 2016). Such insights can help us understand where and when to look for limiting and regulating factors in the environment. Such knowledge is a powerful tool for guiding policy and management actions.

Other methods to describe the demographic parameters

There are other measures for providing insight to the demographical parameters.

Ringing

Bird ringing recoveries not only enlighten us about their migration (e.g. Lyngs 2003, Bønløkke et al. 2006, Hammer et al. 2014) but also play a vital role in identifying changes in demographical parameters.

Ringing can provide crucial information on annual production, survival and dispersal. Changes in any of these parameters will inevitably contribute to changes in demography. Modern ringing schemes emphasise systematic and structured capture and recapture of birds to maximise the return on investment. Such an approach enables estimation of the annual productivity based on age determination ratios among individuals in the catch, following sets of pre-agreed plumage characteristics followed by citizen science contributors and survival from relative contributions of young to adults in the catch sample and from the probabilities of recapture respectively. Constant Effort Site ringing (CES) generates annual estimates of productivity and survival. This was started in Denmark in 2004 and by 2015 consisted of five contributing ringing sites (Knudsen 2015, Ettrup 2016, Ettrup & Madsen in press). A similar Retrapping Adults for Survival project (RAS), launched by the BTO in the UK was designed to estimate annual adult survival rates (as in the case of hirundines, Robinson et al. 2008) and has yet to be introduced in Denmark. Although the capture and marking of birds is restricted to ringers, for many species (e.g. gulls and geese) the reading of conspicuous markers on birds in the field are reliant on networks of amateur enthusiasts. Traditional rings fitted to birds are made of steel or aluminium and bear a return address and a unique code which is usually only possible to read if the bird is caught or found dead. Colour rings and other more conspicuous individual marks gives the opportunity to determine the identity of an individual at a distance with certainty without the need to catch it, making such schemes important for their contribution to survival and other studies.

Recent high-technology developments have produced GPS-loggers that can be deployed on birds, which have enabled extremely detailed information on geographical positions, altitude, speed and behaviour, often with additional data, to be downloadable directly to the computer. Such devices provide new possibilities to study wildlife but size of device still limits the species that can be studied due to the size/weight of the loggers relative to bird size, as well as equipment costs. So far, these are so costly and require such special technical skills, so they remain in the realm of citizen science/professional partnerships (Heldbjerg et al. 2017).

Hunting

Hunters are also in a unique position to contribute valuable monitoring data, which are otherwise difficult or impossible to derive. The willingness of hunters to participate as citizen scientists can contribute valuable information, especially new knowledge on demographic parameters of quarry species. The most fundamental and important contribution is the simple reporting of annual numbers of individuals brought down per species (ultimately to generate local, regional and national annual hunting harvest data). However, the determination of annual sex and age class contributions to the overall population by the submission of wings from hunter shot birds and the reporting of shot birds bearing unique markings.

In Denmark, hunting is restricted to species for which there is good scientific evidence that population can withstand current levels of hunting pressure without diminishing population size, often described as 'sustainable hunting'. Such species are subject to legislative scientific review every four years. In order to be able to provide such confirmation for a given species, fundamental knowledge about the species' demography is essential. In Denmark, there has been a very long history, extending back to 1941, of requiring hunters to report hunting bags for all quarry species (Christensen et al. 2013). All Danish hunters are obliged to report the sizes and species composition of their annual harvest, which generates annual data on the size of the kill for all huntable species. Although changes in these parameters may potentially provide proxies for changes in population sizes, such relationships are complicated by changes in hunting season length, hunter effort and self-regulation applied by hunters themselves in the face of increasingly rare prey (Kahlert et al. 2015). The Danish Wing Survey, that is an important part of the Danish hunting bag statistics, was started in 1970 with a study on Woodcocks *Scolopax rusticola* (Clausager 1973). In the 1980s, the survey was extended to also include ducks and wading birds, and later still, geese and gulls were also included (Bioscience 2017a). The wing survey is based on voluntary contributions from hunters, resulting in more than 13,000 wings annually providing information on the annual variation in sex ratio and age ratio (e.g. Christensen & Fox 2014).

Considerations for the future citizen science on birds in Denmark

When discussing how to improve existing avian monitoring in Denmark we must be aware that bird populations may be limited at any time of the year and that migratory species only occur in Denmark at certain times of the year. For this reason, it makes sense to treat periods in the annual cycle separately, based on the seasons, i.e. breeding, winter and migration.

Millions of migrating birds pass through Denmark every spring and autumn. Systematic monitoring of this fascinating phenomenon can provide information on relative abundance and annual productivity at flyway levels. Migrants include many species that are only in Denmark for a short period and with a high turnover. The important sites for staging migrants are not necessarily the same as for breeding birds or wintering birds and the monitoring therefore must be coordinated with respect to other parts of the EU Birds Directive (article 4 stk. 2; Miljøstyrelsen et al. 2017). Although Denmark is clearly globally significant for the large numbers of passing and staging bird numbers, for the scope of this analysis, the discussion about the future activities in this paper is limited to considering citizen science based bird monitoring of Denmark's breeding and wintering birds.

Large numbers of individuals of many bird species occur in Denmark during winter. Monitoring results provides information on the variation in abundance and distribution and contributes to understanding what impact the variation in weather (temperature, precipitation, snow cower) or the fruit mast production has on the movements and winter quarter choice for the different species (Fox et al. 2009, Lindén et al. 2011). Our knowledge about the variation in winter bird distributions could be further improved by initiating a dedicated winter bird atlas, comparable to those in other countries (e.g. UK (Balmer et al. 2013) and Catalonia (Herrando et al. 2011)). Monitoring during winter could potentially also involve thousands of citizen science observers in projects like "Feeder watch", where people not necessarily very interested in birds report bird abundance on their garden feeders. Such schemes provide detailed information on the variations in abundance and distribution of winter birds and involve citizen scientists not normally involved with environmental monitoring. As such, such schemes can provide an important recruitment function to broaden the interest of observers in the natural world and potentially to make further contributions to bird or biodiversity monitoring. Such schemes now exist in many countries but not in Denmark at present. Although it may appear to be on the periphery of standard monitoring, such schemes still have the potential to offer supplementary information to more mainstream monitoring mechanisms. For instance, "Feeder watch" turned out to be the key monitoring mechanism to follow the spread of the infectious disease Trichomonosis due to the protozoan parasite *Trichomonas gallinae* (Robinson et al. 2010).

Furthermore, for many of the northernmost of breeding birds, such as many species of ducks and geese, accurate assessment of total population size is only possible when aggregated on their relatively restricted wintering areas, compared to their very low breeding densities over vast areas in summer. This period is also critical in their annual life cycle for survival between breeding periods and site based data also provides vital insight upon which to base the construction of site safeguard networks to protect vital habitat outside of the breeding season.

One dilemma we face in considering potential improvements to the monitoring of breeding birds and wintering birds in Denmark, is that there are two obvious ways to go. One could pursue a quantitative approach, where we seek to include as many species as possible, or a qualitative approach where we try to include collection of demographical parameters for a limited number of selected species. Either way, we must be aware that no matter how many species we monitor we can only understand the key drivers behind population changes if we include demography parameters, so preferably, we should attempt to embrace both approaches.

The following section will focus on monitoring of breeding birds and on the quantitative approach, because the detailed knowledge that exists for many species that are breeding in Denmark and their population size makes it possible to undertake a gap analysis to describe which species are not covered by existing monitoring programmes. Wintering birds and the qualitative approach are only described in broad terms below.

A gap analysis of the monitoring of breeding birds in Denmark

In order to provide a framework for effective avian monitoring of breeding birds in Denmark in the future, we need to analyse how well we monitor changes in avian population abundance and distribution now. Such an attempt was performed by DOF's Scientific Committee in 2000 (Thorup et al. 2000) but the challenge to review and update our needs remains just as relevant today.

Do we obtain adequate monitoring data on changes in annual population size for all bird species in Denmark?

The breeding period results in rapid population level changes in a relatively short period from its annual lowest to its highest level, representing the only part of the annual cycle when population numbers increase. Poor reproduction constrains the population to remain at a low level until the next reproductive period. For this reason, attention is focussed upon this vital part of the annual cycle during a period when the breeding birds are confined to the breeding range.

To identify those breeding species that are insufficiently monitored to provide reliable annual population estimates and trends at present, we undertook a gap analysis, covering all species that have ever bred regularly in Denmark (227 species; Appendix 1). In order to focus only on those which are 'Regular' breeding species at present, all 'Regionally extinct' species (9 species) and 'Occasional' breeding birds (24) were excluded. In addition, we chose to exclude all introduced/invasive alien breeding alien species (Canada Goose *Branta canadensis*, Egyptian Goose *Alopochen aegyptiaca*, Pheasant *Phasianus colchicus* and Rock Dove *Columba livia*).

Species that have bred in ten consecutive years over any given time period in Denmark are considered 'Regular' breeding birds, including those assigned to the Danish Red List (Bioscience 2017b). Since the last version from 2009, four species, Whooper Swan *Cygnus cygnus*, Mediterranean Gull, Golden Eagle and Boreal Owl were added as recent regular breeding birds (Knud Flensted, pers comm). The status for each species has been updated until 2017, including records of last confirmed breeding, based on information from Dybbro (1978), Grell (1998), Nyegaard et al. (2014), Olsen (1992) and unpublished information from DOFbasen and Atlas (Appendix 1).

After excluding these species, we are left with 190 regular breeding species, for which we have estimates for size of the Danish bird populations, as provided for the European Red List (Birdlife International 2015) but these have been adapted where additional information was found. Of these, 110 are sufficiently abundant and detectable to produce a breeding population index with an acceptable degree of confidence, as part of the CBM scheme. The CBM scheme generates annual changes in population size as an index, i.e. as relative annual changes with no direct relationship with absolute population sizes. In general, the more common a species is, the more precise the population index; however, for the purpose of this analysis, all species with a CBM index are included, independent of the degree of precision. At the other extreme of avian abundance, we also know with a high degree of accuracy the situation for a few of the very rare breeding birds, i.e. those that have received special attention through different projects (at present only four species) for which we are more or less able to determine the entire population. The intermediate group of 76 regular breeding species (Appendix 2) are far more difficult to monitor, since they are too numerous to count individually and too scarce (or difficult) to monitor by traditional means. In fact, we are currently unable to effectively monitor the majority of the species in the 1-10000 pairs categories adequately (Fig 1).

To improve the monitoring of some of these species, we will need to search for patterns among them. First, we can assign the species as (i) 'Predictable' (20 species that effectively breed at the same sites year after year), and (ii) 'Unpredictable', (56 species which may shift their breeding sites between a large number of places of which we are not always aware). The 'unpredictable' group comprise 11 nocturnal species and 45 diurnal, while the 'predictable' group comprises only diurnal species.

In the 'Predictable' group, the majority are coastal breeders (11; 55%) or inland wetland breeding birds (25%) (Table 2). A similar pattern is found in the 'Unpredictable' group (39% in wetland and 16% at the coast), but here is also an additional significant habitat group in forest (30%).

The majority of the species in the 'unpredictable' group (66%) are day-active and solitary nesting, indicating that monitoring will only adequately cover this group if it is carried out within a sampling framework and performed at large spatial scales. Twenty-one of the day-active solitarily nesting species (46%) occur on inland wetlands, which would therefore seem to represent a good starting point for adequately monitoring a broad suite of these species.

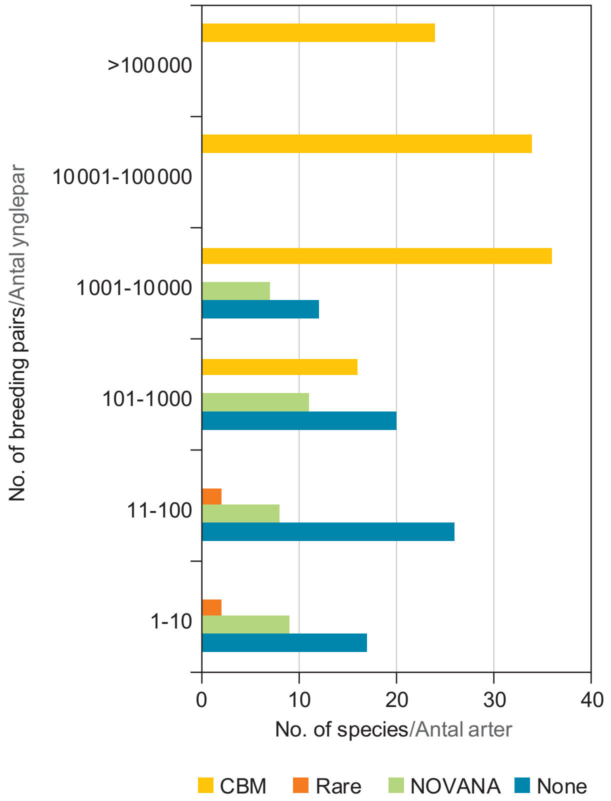

Figure 1. Histogram showing the degree of monitoring cover for 190 regular breeding bird species in Denmark. Well-covered rare species (Rare; 4 species) are indicated in orange, Common Bird Monitoring species (CBM; 110) in yellow and those species not currently monitored (None; 76) in blue. In addition, of the not monitored species, those covered by the NOVANA programme every 2nd or 3rd year at sites where they are designated for is shown in light green (NOVANA; 35).

Graden af årlig overvågning af de 190 regelmæssige ynglefugle i Danmark. Sjældne arter (4) er vist med orange, punkttællingsarter (110) med gul og arter uden årlig national dækning (76) med blå farve. De af de ikke dækkede arter, der er delvist dækket af NOVANA (35) med tællinger hvert 2. eller 3. år på de områder, der er udpeget for arten er vist med lys grøn farve.

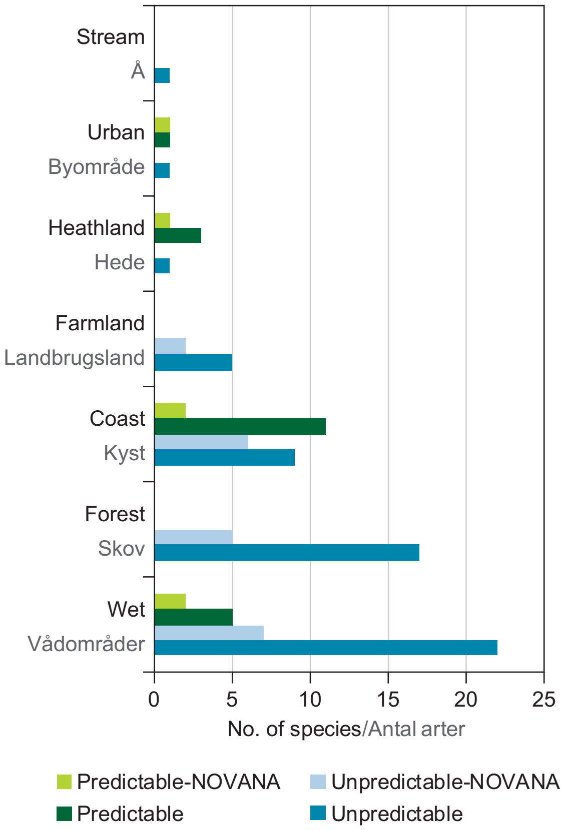

Figure 2. Breeding habitat of 76 regular Danish birds with no annual monitoring coverage at present that occur at 'Predictable' (dark green) as well as 'Unpredictable' (dark blue) breeding sites. Additional NOVANA monitoring (less then annual coverage; only Annex 1 species and only at sites designated for these) is included for comparison ('Predictable' (light green); 'Unpredictable' (light blue)).

Ynglehabitat for 76 danske ynglefugle uden årlig overvågning, der forekommer på 'forudsigelige' (mørkt grøn) eller 'uforudsigelige' (mørkt blå) ynglelokaliteter. NOVANA-overvågede arter er tillige vist opdelt på forudsigelige (lyst grøn) og uforudsigelige arter (lyst blå).

Table 2. Number of regular breeding bird species in Denmark not annually monitored, divided into different groups based on habitat categories, whether the breeding sites are predictable, the optimal monitoring period during the day and nesting habits.

Fordeling af de regelmæssigt ynglende fuglearter i Danmark uden årlig fugleovervågning, opdelt på naturtype, forudsigelighed af yngleplads, tidsrum for primære aktivitet og kolonialitet.

Sites	**Time**	**Nesting**	**Wet**	**Forest**	**Coast**	**Farmland**	**Heathland**	**Urban**	**Stream**	**SUM**
Lokalitet	***Tid***	***Vådområde***	***Vådområde***	***Skov***	***Kyst***	***Agerland/Eng***	***Hede***	***By***	***Å***	
Predictable	Night *Nat*	0	0	0	0	0	0	0	0	
Forudsigelig	Day *Dag*	Colonial *Koloni*	2	0	8	0	0	0	0	10
	–	Solitary *Enkeltvis*	3	0	3	0	3	1	0	10
SUM			**5**	**0**	**11**	**0**	**3**	**1**	**0**	**20**
Unpredictable	Night *Nat*		2	5	0	4	0	0	0	11
Uforudsigelig	Day *Dag*	Colonial *Koloni*	2	0	6	1	0	0	0	9
	–	Solitary *Enkeltvis*	18	12	3	0	1	1	1	36
SUM			**22**	**17**	**9**	**5**	**1**	**1**	**1**	**56**
SUM all/*I alt*			**27**	**17**	**20**	**5**	**4**	**2**	**1**	**76**

Nineteen of the day-active species (34%) are colonial breeders, roughly half each in the 'Predictable' and 'Unpredictable' groups. Monitoring of such species obviously necessitates counting methods designed for and dedicated to that specific purpose. In several countries monitoring of colonial breeding birds such as Grey Heron are well established (e.g. Marchant et al. 2004).

Nocturnal species (14%) constitute a discrete set of species needing specially designed monitoring programmes such as the one established by the Swedish Bird Survey at Lund University (Green et al. 2017).

The results from the gap analysis (Table 2) offer a useful basis for discussing the kind of monitoring that could and should be initiated to cover the greatest number of species in the most cost-efficient way. In this context, it will also be important to consider how well the NOVANA monitoring has been able to provide trends for the species included in this list. This depends very much on what proportion of a population lives in a given study area, i.e. those sites designated for the given species. Figure 2 shows the number of species included in the NOVANA monitoring compared with the required coverage in each habitat. It reveals that 29–40% of the species in the three habitats with most species lacking annual national monitoring are partly covered by the NOVANA monitoring.

Can we get more out of the existing data?

We should also consider whether the extent of existing monitoring provides sufficient information to support their effective conservation. There are two ways to achieve a better understanding of the factors acting to constrain a species in time and space. Firstly, we could start by better using the existing information in the CBM on habitat and geographical distribution of count locations in Denmark to study variation in space and habitat. Examples of this are analyses undertaken for Corn Bunting (Fox & Heldbjerg 2008) and specialized farmland birds (Heldbjerg & Fox 2016). The CBM offers largely untapped potential to support such analyses on e.g. declining species. Secondly, the use of the habitat information is partly limited by the coarse habitat classifications used in this programme to date. Each of the common species' use of the nine defined habitats (Coniferous woodland, Deciduous woodland, Arable, Grassland, Heath, Dunes/ Shore, Bog/Marsh, Lake and Urban) have been analysed (Larsen et al. 2011) for the purpose of defining and using habitat indicators (Eskildsen et al. 2013). These analyses can show whether a given species has a preference for instance for arable farming land, but does not show if and how population size and density may vary between different crops. As a result, we learn little about how specific changes in agricultural production in the farmland landscape impact upon the abundance of the common farmland birds, because we cannot see, for instance, when spring cereal is converted to winter cereal or fodder beats to winter oil seed rape and what effect this may have on a given species. Inclusion of such information could be an obvious next step to improve the quality of on-site monitoring, as well as generating additional research questions and a means of answering these.

Could we answer more specific habitat specific questions?

If we are not able to capture the relevant detailed information within the existing monitoring programmes, another way of tackling this could be to establish short and focused projects with more narrow aims than the traditional monitoring programmes. If we could involve a large number of citizen scientists in short and well defined projects across the country, we could obtain more detailed new information on a large scale within limited habitats. For example, we could highlight the effects of changes in the composition in mosaics of human land use in Denmark. These include the dramatic increases in the farmed area under oil seed rape or maize or the differences in bird community composition and abundance in forest patches consisting of 100-year-old trees compared to patches with the age of 50 or 25 years. Such analyses would generate results that are of immediate use in relation to sympathetic habitat management.

Can we include demography for better understanding of the observed trends?

We now move from the HOW-step (how-are-the-trends?) to the WHY-step (why-is-the-trend-as-it-is?), where new projects will have to be initiated to provide demographical information. Nest record schemes provide vital knowledge on clutch and brood size and are useful for understanding the variation over time and eventual differences between regions and habitats in such metrics. This in turn provides insight into patterns of reproductive success (see above) which can potentially be built into models to predict species' trends. Combining such methods with marking of adult birds for information on age of first breeding, breeding propensity and survival, such schemes can dramatically contribute knowledge about the demography of common species. The UK (Crick et al. 2003) and the Netherlands (Sovon 2017) have instigated coordinated programmes (such as the Nest Record Scheme and focused ringing schemes) to measure productivity and survival to support the construction of population models to better understand where annual bottle-necks occur in the annual cycle. The potential for involving large numbers of citizen scientists in nest record studies is substantial. However, developing such a scheme will probably require some years to establish the worth, the degree of interest and the required infrastructure and effort to get such a scheme up and running.

Integrated population model

In order to understand why a species is declining we need to effectively combine information from several sources. In Denmark, we have a good understanding about whether species are increasing, decreasing or remaining stable, based on indices and trends. Unfortunately, we can only rarely explain the drivers that are operating on a population to cause the observed patterns in the trends. We will need to establish programmes that focus on these elements. If we can derive such information for a broad number of species, we will have information available for a given species once the trends suggest that it is in trouble.

By combining information from several sources of monitoring data to develop integrated analyses of population counts and demographic data in population models, we will be able to better understand the demographic processes driving population changes (Baillie 1990; Fig. 3). Robinson et al. (2014) combined abundance data from CBM with chick production and nesting success from Nest Record Scheme and with survival estimates for different age classes from mark-recapture data from the Ringing Scheme. Using an integrated approach (combining datasets on different demographic parameters) allowed important demographic parameters to be identified for a number of species. Such an approach has also been used to give a better understanding of the causes of declines in Wadden Sea birds (van der Jeugd et al. 2014).

Citizen science – potential, motivation and limits

Before embarking upon a discussion about whether we could start new, or improve existing, monitoring programmes, we need to be convinced that there are citizen scientists willing to participate in such programmes. To understand this, we need to better understand the motivation of Citizen Scientists to contribute to such projects. For a large proportion of people contributing to citizen science projects, the overriding motivation is simple, namely that they find the work enjoyable (Greenwood 2007). This was confirmed by a recent questionnaire (Mathiasen in prep.) from Denmark among the 3rd bird atlas project and CBM programme participants (N = 434 respondents). The three most important motivating factors for participation in similar potential projects was an interest in birds (95% of the answers), an interest in nature (86%), and a desire to contribute knowledge (77%). Asked for suggestions for future projects, participants generated great variance in their preferences, but most expressed interest in participating in more bird monitoring projects with a scientific purpose and of relevance for conservation.

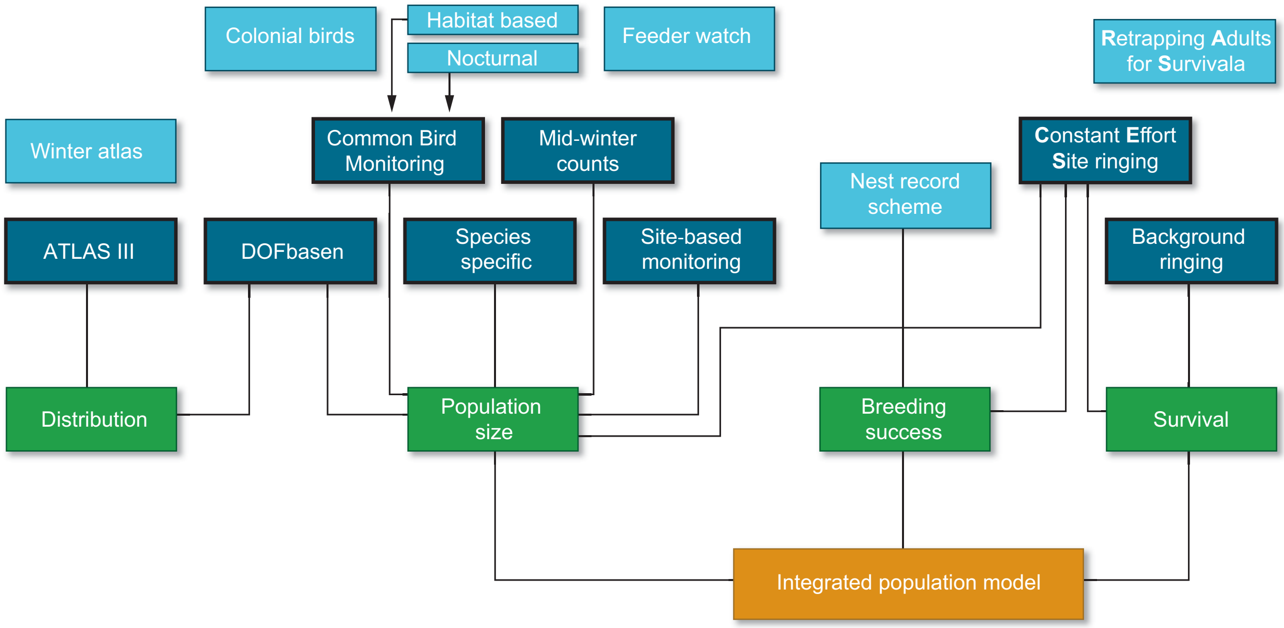

Figure 3. Diagram showing existing (dark blue) and suggested (light blue) Danish schemes and how they can contribute to the knowledge on the most important parameters needed for an Integrated Population Model.

Diagram, der viser eksisterende (mørkt blå) og foreslåede (lyst blå) fugleovervågningsprojekter i Danmark, og hvordan de kan bidrage til de væsentligste parametre, der er relevante for en Integreret Populationsmodel.

To sustain, maintain and grow such a dedicated group of volunteers, it is important to maintain their interest and willingness to participate in the citizen science projects. In the light of the circa 1,450 observers which participated in the Atlas III project so far, it seems that we still have a large and highly motivated group of participants willing to support such programmes. Most people simply like to help and are interested to contribute as long as they see appropriate use of their data and as long as they feel comfortable carrying out the methods that they are asked to undertake. The nature of the feedback to each of the participants is also extremely important and the professional project managers must make sure that they demonstrate their gratitude, appreciation and understanding, that the continuing contributions are greatly valued and that they contribute to some clearly defined greater goal. Such feedback can range from a simple thank you for the annual contribution to a statement in a report or a scientific paper that this was only possible due to the participation of hundreds of participants. Participants want and need to know what was discovered as a result of their efforts, and therefore have similar needs to those coordinating the work (see also Greenwood 2007). Feedback in all forms must convince most of the volunteers that by their own relatively modest effort, they have contributed to a much more massive compilation of knowledge at the local, regional and/or European scale. It should also enable participants to understand how their work supports the bigger picture and contributes overall to the findings of the project.

There are several ways to broaden the citizen science involvement in bird monitoring projects, but there are of course also limitations to this. We have seen that the Danish citizen scientists in general are happy to be involved but the limits to this involvement should be explored before initiating new citizen science projects. We forget at our peril that these brilliant folk do the work for nothing apart from their own enjoyment and we should be very careful about over exploiting such incredible goodwill. There are of course limits to the complexity of the tasks for which they are being asked to contribute with their free time and labour. This could relate to the field activities or to the way the data are reported and uploaded.

Many people prefer to work with methods with which they are comfortable, but for professional project coordinators, it is important to try to educate and challenge the citizen science community to use other methods. As an added project to the 3rd Danish bird atlas, avian density data are gathered using line transect and distance bands (Levinsky 2016). This is the first time such methods have been proposed and initially they were met with widespread scepticism among participants. As a result, organisers were encouraged to engage in more thorough communication and discussion both internally and with the citizen scientist community. This exchange of views led to improvements in the clarity of the goals of the project, clearer instructions and improved understanding amongst survey participants, but also, necessarily, to some weakening of the original data demands for the surveys. As a result, the observers were convinced that it was worth giving the techniques a try and the technical changes resulted in changes in attitudes on all sides. The result has been a success, with highly satisfactory results in terms of involvement and quality of data (although the data have yet to be analysed). This process surely will inspire coming projects, including those still to be initiated in the future. However, there remains the risk that potential participants will refuse to take part if the demands to participate are too complex, to demanding or too ambitious, underlining the clear need to consult effectively to better understand the feelings of the citizen science community ahead of novel surveys. Data inputting is now mostly done by the observers themselves via apps in the field or via a portal after the fieldwork, imposing yet more demands on participants. However, we should be eternally grateful that it is much easier now compared to the transfer of data from note book to forms that needed to be submitted by post to be centrally analysed, which was still the "gold" standard up until a few years ago. This is a crucial part since even the most skilled and dedicated participants may decide to stop their involvement if they find it too complicated to enter and upload data. For this reasonthe third British Atlas project (2007-11) retained the possibility for the participants to submit data on paper as well as online (Balmer et al. 2013).

Another issue concerns the quality of the observations themselves. It is important to bear in mind that there is a risk that involving far more people in a certain project may result in the increasing participation of less skilled observers, which may affect data quality, depending on the nature of the survey. Surveying only the commoner bird species allows participation of far more people than surveying all bird species. To fulfil the ultimate scientific objective, it is an important pre-requisite to ensure that data are collected to a given standard after which the professional organisers will have to make sure that the contributions meet the threshold for quality assurance. It is often advisable to combine the monitoring project with an outreach and education programme, to improve skills among volunteers and to educate to create a more skilled and interested community of potential citizen scientists. Dynamic, attractive and informative feedback may also retain volunteers and improve their skills over time. In this way, recruits may first become engaged by participating in a less demanding project such as the Feeder Watch project and over time become involved in more demanding programmes such as the CBM (Greenwood 2007). In addition, good communication from professional organisers will also reach a large part of people who will never be adequately skilled to participate but are still interested in the monitoring and its results and may even appeal to young people, who are often (considered to be) most notable by their absence in contributing to such programmes.

Conclusions and recommendations

The aim of this paper has not been to develop a simple recipe for the future monitoring of breeding birds in Denmark, but rather to create a foundation for a discussion within the bird monitoring community about future directions, outlining what we can, should and will do in the future. In the longer term, we need to be thinking about developing more detailed strategies to enable us to reach our specific goals.

In Denmark, there are currently relatively few organisations involved in bird monitoring. In order to maintain and improve the monitoring it is essential for this relatively small community to regularly to discuss goals and objectives. This is vital to establish what is needed to adequately generate the necessary data on the distribution and abundance of all species, improve species, habitat and geographical coverage, involve new generations of observers, as well retaining the current network of stalwarts and to effectively integrate demographic parameters in the monitoring.

We should aim to 'pick the low hanging fruits' by considering adaptations of existing monitoring schemes and collation of existing data to achieve greater aims without compromising quality or quantity. We should also consider initiating new monitoring schemes to cover missing elements in our current monitoring portfolio, e.g. species, habitats, demography parameters, other taxa than birds, detailed and focused studies etc.. We should also ensure that we generate the data we need to answer specific research questions and to enable the effective conservation and management of Danish birds in the future (Table 3).

We argue for the need to focus in future on monitoring the less numerous avian species of wetland, coastal and forest habitats and that nocturnal species also need particular attention. We also urge the initiation of projects that provide information on demographical parameters, in order to support ultimately the establishment of Integrated Population Monitoring modelling which would vastly benefit from the integration of information from the different sources.

Monitoring biologists across Europe are also working increasingly closely together in networks like BirdLife International, the European Bird Census Council and Wetlands International, which makes it easier to collaborate and to learn from each other's experiences. New Danish initiatives may find help and guidance from similar suitable programmes in neighbouring countries and thereby make it easier to start and run well-designed programmes, as well as generating comparable results from different countries. Our scientific understanding

Table 3. Overview of suggested areas to improve the monitoring of the breeding birds and winter birds in the future years with the indication of the main observer type relevant to involve for each.

Oversigt over foreslåede områder, hvorpå den danske fugleovervågning kan forbedres, og med angivelse af, hvilken type observatør, der ønskes involveret på hvert område.

Observer type ***Observatørtype***	**Abundance/distribution** ***Forekomst/udbredelse***	**Detailed studies** ***Detaljerede studier***	**Demography** ***Demografi***
Interested in birds *Fugleinteresseret*	Feeder watch *Foderbrætsundersøgelse*		Nest Record Scheme *Redeundersøgelser*
Skilled birder *Fuglekyndig*	Habitat studies *Naturtype-studier*		
	Nocturnal species *Nat-aktive fugle*	Species-specific *Artsspecifikke studier*	
	Colonial birds *Kolonirugere*	Communities *Fuglesamfundsstudier*	
	Winter atlas *Vinteratlas*		
Ringer *Ringmærker*			CES/*CES* RAS/*RAS*
Citizen scientist-Professional interface *Citizen scientist-professionel grænseflade*		Expert facilitated collaboration *Ekspertbaseret samarbejde*	

only increases by enlarging our scope from the single point count to the relatively little area of Denmark to looking at patterns at far larger scales, such as Scandinavia or Europe.

Acknowledgements

We gratefully acknowledge the thousands of citizen scientists taking part in different DOF projects in the past 50 years. Thanks also to the bio-team in DOF for discussions to support the gap analysis and help with the overall species list. HH acknowledges the support of an industrial PhD stipend awarded by Innovationsfonden, which, together with Aage V. Jensen Naturfond and 15. Juni Fonden also supported this work.

Resumé

Hvordan kan vi forbedre fugleovervågningen i Danmark fremover?

I overvågningen af danske fugle og dansk natur har kyndige frivillige ulønnede deltagere altid spillet en væsentlig rolle. Dette samarbejde mellem borgere og uddannet fagpersonale omtales, selv på dansk, som ’citizen science’ med ’’borgervidenskab’ som et alternativt navn. Det er blevet den accepterede standard, at overvågning løses ved inddragelse af citizen scientist, hvilket gør det muligt at gennemføre et stort antal tællinger på kort tid, at fortsætte undersøgelser over mange år og at holde omkostningerne tilstrækkeligt lave til at sikre gennemførelse.

Danmark har brug for overvågning for at kunne opfylde forpligtigelserne i henhold til europæisk og international lovgivning og for at kunne tage de nødvendige beslutninger vedrørende forvaltning og beskyttelse af den danske natur. Desuden har organisationer som DOF og BirdLife International en stærk interesse i at kende status og udvikling for de danske fugle.

Formålet med artiklen er at tage afsæt i den tidligere og nuværende fugleovervågning for at undersøge, hvor vi kan gøre det bedre i Danmark i fremtiden. Dette præsenteres i håb om, at folk med behov for eller interesse i at kende de danske fugles status og tendenser, vil blive inspireret til at skabe et grundlag for bedre fugleundersøgelser og fuglebeskyttelse i Danmark fremover.

I løbet af 1960'erne opstod de første store landsdækkende overvågningsprogrammer med optællinger på de bedste fuglelokaliteter og midvintertællinger. I 1970'erne fulgte atlasundersøgelse og punkttællinger. Flere programmer er gennemført eller gentaget siden da, og fra 2002 fulgte DOFbasen på www.dofbasen.dk (tabel 1).

Den nationale årlige overvågning af de danske fugle består nu af dels punkttællinger, der anses for tilstrækkeligt pålidelige til at give et bestandsindeks (men ikke et bestandsestimat) for 110 arter af ynglefugle og 80 arter af vinterfugle, dels en særlig arts-fokuseret indsats for fire sjældne arter, , nemlig Havørn, Hedehøg, Kongeørn og Fiskeørn, for hvilke det er muligt at registrere hvert enkelt par. Desuden gennemføres der i regi af NOVANA en overvågning, der dækker de områder, for hvilke de arter, der er på liste 1 på Fugledirektivet, indgår i udpegningsgrundlaget. Disse arter er desuden nationalt dækkende hvert sjette år (se appendiks 1).

Danmark har stor betydning for trækkende og overvintrende fugle, men overvejelser om en forbedret overvågning af trækfugle indgår ikke i denne artikel. Hvis vi skal lave en bedre overvågning af de danske fugle om vinteren og i ynglesæsonen fremover, kan vi enten forsøge at inkludere flere arter eller forsøge at lave en bedre overvågning af udvalgte arter.

Blandt de 190 regelmæssige ynglefugle i Danmark er der 76 arter, der ikke indgår i den eksisterende årlige overvågning. En analyse viser, at disse arter har bestande skønnet til 1-10.000 par og således kan betegnes som sjældne og fåtallige arter (Fig. 1); nogle af disse arter er dog dækket af NOVANA-overvågningen (Fig. 2). Endvidere ses det, at de mangelfuldt dækkede arter primært findes i de tre naturtyper skov, vådområder og kyst. I sidstnævnte naturtype er 70 % ydermere kolonirugende arter. Endelig er 11 af arterne nataktive (tabel 2). Alle disse forhold er afgørende at kende til, når man skal prioritere, hvilken målrettet indsats, der skal supplere den eksisterende fremover.

Hvis målet er at få et dybere kendskab til baggrunden for de bestandstendenser, vi ser (bestandsfremgang, -nedgang, stabilitet, fluktuation), bliver vi nødt til at inkludere demografiske parametre. Hvis en bestand ændrer sig, skyldes det ændringer i en eller flere af parametrene overlevelse, ungeproduktion samt ind- og udvandring. Inkluderes studier af disse parametre, kan vi få mere viden om, hvorfor en bestand ændrer sig, i modsætning til nu, hvor vi må nøjes med at konstatere, hvor meget den ændrer sig. For at opnå viden om disse parametre, kræves særlige indsatser som fx etablering af et rederegistreringsprojekt, men det er også muligt at bruge data fra ringmærkningsprojekter som 'Constant Effort Site' – ringmærkning (med konstant fangstindsats af ynglefugle) og anvendelse af mærknings-/aflæsningsprojekter (Fig. 3). Desuden kan vingeundersøgelser af nedlagte, jagtbare arter give viden om køns- og aldersfordelingen hos disse arter og således give øget viden om variationen af den årlige ungeproduktion. Vinterindsatsen kan med fordel udvides med et vinteratlas for at få bedre kendskab til arternes udbredelse og variationen i forekomsten mellem årene samt med en velovervejet have-/foderbrætsundersøgelse, der kan give detaljeret viden om arternes vinterforekomst og involvere en masse nye fugleinteresserede.

Den danske fugleovervågning udføres i samarbejde med europæiske og internationale samarbejdspartnere som BirdLife International, European Bird Census Council og Wetlands International. Eventuelle nye tiltag kan med fordel drage nytte af de erfaringer, der er opnået i andre lande. Desuden kan nogle indsatser med fordel gennemføres sammen med andre lande, så vi i fællesskab kan dække større geografiske områder og sammenligne udviklingen i de forskellige delområder.

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Appendix

Appendix 1: List of all breeding birds in Denmark, showing their breeding status, population estimate (c. 2011) and coverage under existing monitoring projects. *Oversigt over alle danske ynglefugle med angivelse af status, bestandsestimat (ca. 2011) og nuværende overvågningsprojekt.*

Appendix 2: List of regular breeding birds in Denmark which currently lack monitoring schemes, with an indication of whether the breeding sites are predictable or not, the optimal monitoring period during the day, nesting habits and habitat type. *Oversigt over regelmæssige danske ynglefugle uden årlig overvågning. Endvidere er vist forudsigelighed af yngleplads, tidsrum for primære aktivitet, kolonialitet og naturtype.*

Appendix 1

Species no.	English (Latin)	Danish	Status	Breeding population 2011	Last confirmed breeding	Last breeding reference	Project	NOVANA	Invasive
00070	Little Grebe (Tachybaptus ruficollis)	Lille Lappedykker	Regular	1700	2017		CBM		
00090	Great Crested Grebe (Podiceps cristatus)	Toppet Lappedykker	Regular	3500	2017		CBM		
00100	Red-necked Grebe (Podiceps grisegena)	Gråstrubet Lappedykker	Regular	1400	2017		CBM		
00110	Horned Grebe (Podiceps auritus)	Nordisk Lappedykker	Regionally extinct	0	2006	Confirmed 2006 (DATSY) Probable 2014 (Atlas)			
00120	Black-necked Grebe (Podiceps nigricollis)	Sorthalset Lappedykker	Regular	250	2017				
00220	Northern Fulmar (Fulmarus glacialis)	Mallemuk	Occasional	0	2000	Confirmed 2000 (DATSY)			
00720	Great Cormorant (Phalacrocorax carbo)	Skarv	Regular	25542	2017		CBM	1	
00950	Eurasian Bittern (Botaurus stellaris)	Rørdrum	Regular	300	2017			1	
01210	Great Egret (Ardea alba)	Sølvhejre	Occasional	0	2016	Confirmed 2016 (Atlas)			
01220	Grey Heron (Ardea cinerea)	Fiskehejre	Regular	4200	2017		CBM		
01310	Black Stork (Ciconia nigra)	Sort Stork	Regionally extinct	0	1983-86	Confirmed 1983-86 (DATSY)		2	
01340	White Stork (Ciconia ciconia)	Hvid Stork	Regular	1	2017			1	
01440	Eurasian Spoonbill (Platalea leucorodia)	Skestork	Regular	101	2017			1	
01520	Mute Swan (Cygnus olor)	Knopsvane	Regular	3600	2017		CBM		
01540	Whooper Swan (Cygnus cygnus)	Sangsvane	Regular	3	2017				
01610	Greylag Goose (Anser anser)	Grågås	Regular	11000	2017		CBM		
01630	Snow Goose (Chen caerulescens)	Snegås	Occasional	0	2016	Confirmed 2016 (Atlas)			1
01660	Canada Goose (Branta canadensis)	Canadagås	Regular	x	2017				1
01670	Barnacle Goose (Branta leucopsis)	Bramgås	Regular	2000	2017			1	
01700	Egyptian Goose (Alopochen aegyptiaca)	Nilgås	Regular	x	2017				1
01710	Ruddy Shelduck (Tadorna ferruginea)	Rustand	Occasional	?	1994	Confirmed 1994 (Grell)			1
01730	Common Shelduck (Tadorna tadorna)	Gravand	Regular	1500	2017		CBM		
01780	Mandarin Duck (Aix galericulata)	Mandarinand	Occasional	x	2006	Confirmed 2006 (DOFbasen)			1
01790	Eurasian Wigeon (Anas penelope)	Pibeand	Regular	0	2017	Confirmed 2017 (Atlas)			
01820	Gadwall (Anas strepera)	Knarand	Regular	500	2017				
01840	Eurasian Teal (Anas crecca)	Krikand	Regular	50	2017				
01860	Mallard (Anas platyrhynchos)	Gråand	Regular	20000	2017		CBM		
01890	Northern Pintail (Anas acuta)	Spidsand	Regular	25	2017				
01910	Garganey (Anas querquedula)	Atlingand	Regular	150	2017				
01920	Blue-winged Teal (Anas discors)	Blåvinget And	Occasional	0	1986	Confirmed 1986 (DOFbasen; Olsen)			
01940	Northern Shoveler (Anas clypeata)	Skeand	Regular	800	2017				
01960	Red-crested Pochard (Netta rufina)	Rødhovedet And	Regular	9	2017				
01980	Common Pochard (Aythya ferina)	Taffeland	Regular	280	2017		CBM		
02030	Tufted Duck (Aythya fuligula)	Troldand	Regular	900	2017		CBM		
02040	Greater Scaup (Aythya marila)	Bjergand	Occasional	0	2006	Confirmed 2006 (DOFbasen)			
02060	Common Eider (Somateria mollissima)	Ederfugl	Regular	23000	2017		CBM	1	
02180	Common Goldeneye (Bucephala clangula)	Hvinand	Regular	100	2017				
02210	Red-breasted Merganser (Mergus serrator)	Toppet Skallesluger	Regular	3100	2017		CBM		
02230	Common Merganser (Mergus merganser)	Stor Skallesluger	Regular	75	2017				
02250	Ruddy Duck (Oxyura jamaicensis)	Amerikansk Skarveand	Occasional	0	2006	Confirmed 2006 (DOFbasen)			1
02310	European Honey Buzzard (Pernis apivorus)	Hvepsevåge	Regular	650	2017			1	
02390	Red Kite (Milvus milvus)	Rød Glente	Regular	120	2017		CBM	1	
02430	White-tailed Eagle (Haliaeetus albicilla)	Havørn	Regular	54	2017		Special	2	
02560	Short-toed Snake Eagle (Circaetus gallicus)	Slangeørn	Regionally extinct	0	1877/1882	Confirmed 1877/1882 (Olsen)			
02600	Western Marsh Harrier (Circus aeruginosus)	Rørhøg	Regular	650	2017		CBM	1	
02610	Northern Harrier (Circus cyaneus)	Blå Kærhøg	Occasional	0	2002	Confirmed 2002 (DATSY)		1	
02630	Montagu´s Harrier (Circus pygargus)	Hedehøg	Regular	23	2017		Special	2	

Species no.	English (Latin)	Danish	Status	Breeding population 2011	Last confirmed breeding	Last breeding reference	Project	NOVANA	Invasive
02670	Northern Goshawk (Accipiter gentilis)	Duehøg	Regular	270	2017		CBM		
02690	Eurasian Sparrowhawk (Accipiter nisus)	Spurvehøg	Regular	2100	2017		CBM		
02870	Common Buzzard (Buteo buteo)	Musvåge	Regular	5000	2017		CBM		
02960	Golden Eagle (Aquila chrysaetos)	Kongeørn	Regular	3	2017		Special	2	
03010	Osprey (Pandion haliaetus)	Fiskeørn	Regular	3	2017		Special	2	
03040	Common Kestrel (Falco tinnunculus)	Tårnfalk	Regular	1500	2017		CBM		
03100	Eurasian Hobby (Falco subbuteo)	Lærkefalk	Regular	17	2017				
03200	Peregrine Falcon (Falco peregrinus)	Vandrefalk	Regular	15	2017			2	
03320	Black Grouse (Lyrurus tetrix)	Urfugl	Regionally extinct	0	1988	Confirmed 1988 (DATSY) and 1991 (dofbasen.dk/ART)			
03670	Grey Partridge (Perdix perdix)	Agerhøne	Regular	6000	2017		CBM		
03700	Common Quail (Coturnix coturnix)	Vagtel	Regular	1830	2017				
03940	Common Pheasant (Phasianus colchicus)	Fasan	Regular	x	2017				1
04070	Water Rail (Rallus aquaticus)	Vandrikse	Regular	1100	2017		CBM		
04080	Spotted Crake (Porzana porzana)	Plettet Rørvagtel	Regular	46	2017			1	
04210	Corn Crake (Crex crex)	Engsnarre	Regular	160	2017			1	
04240	Common Moorhen (Gallinula chloropus)	Grønbenet Rørhøne	Regular	3600	2017		CBM		
04290	Eurasian Coot (Fulica atra)	Blishøne	Regular	6800	2017		CBM		
04330	Common Crane (Grus grus)	Trane	Regular	142	2017			1	
04500	Eurasian Oystercatcher (Haematopus ostralegus)	Strandskade	Regular	7000	2017		CBM		
04550	Black-winged Stilt (Himantopus himantopus)	Stylteløber	Occasional	3	2014	Confirmed 2014 (Atlas)			
04560	Pied Avocet (Recurvirostra avosetta)	Klyde	Regular	2400	2017			1	
04690	Little Ringed Plover (Charadrius dubius)	Lille Præstekrave	Regular	300	2017				
04700	Common Ringed Plover (Charadrius hiaticula)	Stor Præstekrave	Regular	1500	2017		CBM		
04770	Kentish Plover (Charadrius alexandrinus)	Hvidbrystet Præstekrave	Regular	43	2017			1	
04850	European Golden Plover (Pluvialis apricaria)	Hjejle	Regular	1	2017			1	
04930	Northern Lapwing (Vanellus vanellus)	Vibe	Regular	20000	2017		CBM		
05120	Dunlin (Calidris alpina)	Almindelig Ryle	Regular	135	2017			1	
05170	Ruff (Calidris pugnax)	Brushane	Regular	66	2017			1	
05190	Common Snipe (Gallinago gallinago)	Dobbeltbekkasin	Regular	1300	2017		CBM		
05200	Great Snipe (Gallinago media)	Tredækker	Regionally extinct	0	1902	Confirmed 1902 (Olsen); Probable 2017 (Atlas)			
05290	Eurasian Woodcock (Scolopax rusticola)	Skovsneppe	Regular	2000	2017				
05320	Black-tailed Godwit (Limosa limosa)	Stor Kobbersneppe	Regular	532	2017				
05410	Black-tailed Godwit (Numenius arquata)	Storspove	Regular	451	2017		CBM		
05460	Common Redshank (Tringa totanus)	Rødben	Regular	9000	2017		CBM		
05530	Green Sandpiper (Tringa ochropus)	Svaleklire	Regular	30	2017				
05540	Wood Sandpiper (Tringa glareola)	Tinksmed	Regular	94	2017			1	
05560	Common Sandpiper (Actitis hypoleucos)	Mudderklire	Occasional	0	2015	Confirmed 2015 (Atlas); Probable 2017 (DOFbasen)			
05610	Ruddy Turnstone (Arenaria interpres)	Stenvender	Regular	36	2017				
05750	Mediterranean Gull (Larus melanocephalus)	Sorthovedet Måge	Regular	22	2017			2	
05780	Little Gull (Hydrocoloeus minutus)	Dværgmåge	Regular	1	2017			1	
05820	Common Black-headed Gull (Chroicocephalus ridibundus)	Hættemåge	Regular	80000	2017		CBM		
05900	Mew Gull (Larus canus)	Stormmåge	Regular	33000	2017		CBM		
05910	Lesser Black-backed Gull (Larus fuscus)	Sildemåge	Regular	5000	2017		CBM		
05920	Herring Gull (Larus argentatus)	Sølvmåge	Regular	65000	2017		CBM		
06000	Great Black-backed Gull (Larus marinus)	Svartbag	Regular	1800	2017		CBM		
06020	Black-legged Kittiwake (Rissa tridactyla)	Ride	Regular	340	2017				
06050	Gull-billed Tern (Gelochelidon nilotica)	Sandterne	Regular	1	2017			1	
06060	Caspian Tern (Hydroprogne caspia)	Rovterne	Regular	8	2017			1	

Species no.	English (Latin)	Danish	Status	Breeding population 2011	Last confirmed breeding	Last breeding reference	Project	NOVANA	Invasive
06110	Sandwich Tern (Sterna sandvicensis)	Splitterne	Regular	3868	2017			1	
06150	Common Tern (Sterna hirundo)	Fjordterne	Regular	425	2017		CBM		
06160	Arctic Tern (Sterna paradisaea)	Havterne	Regular	4500	2017			1	
06240	Little Tern (Sternula albifrons)	Dværgterne	Regular	410	2017			1	
06270	Black Tern (Chlidonias niger)	Sortterne	Regular	53	2017			1	
06280	White-winged Tern (Chlidonias leucopterus)	Hvidvinget Terne	Occasional	0	2016	Confirmed 2016 (Atlas)			
06340	Common Murre (Uria aalge)	Lomvie	Regular	2900	2017			1	
06360	Razorbill (Alca torda)	Alk	Regular	1300	2017			1	
06380	Black Guillemot (Cepphus grylle)	Tejst	Regular	1530	2017			1	
06630	Pallas´s Sandgrouse (Syrrhaptes paradoxus)	Steppehøne	Occasional	0	1888	Confirmed 1888 (Olsen)			
06650	Rock Dove (Columba livia)	Klippedue (Tamdue)	Regular	x	2017				1
06680	Stock Dove (Columba oenas)	Huldue	Regular	950	2017		CBM		
06700	Common Wood Pigeon (Columba palumbus)	Ringdue	Regular	290000	2017		CBM		
06840	Eurasian Collared Dove (Streptopelia decaocto)	Tyrkerdue	Regular	26000	2017		CBM		
06870	European Turtle Dove (Streptopelia turtur)	Turteldue	Regular	100	2017				
07085	Monk Parakeet (Myiopsitta monachus)	Munkeparakit	Occasional	0	c. 1990	Confirmed c. 1990 (DOFbasen)			1
07240	Common Cuckoo (Cuculus canorus)	Gøg	Regular	17000	2017		CBM		
07350	Barn Owl (Tyto alba)	Slørugle	Regular	65	2017				
07440	Eurasian Eagle-Owl (Bubo bubo)	Stor Hornugle	Regular	70	2017			1	
07570	Little Owl (Athene noctua)	Kirkeugle	Regular	30	2017				
07610	Tawny Owl (Strix aluco)	Natugle	Regular	3100	2017		CBM		
07670	Long-eared Owl (Asio otus)	Skovhornugle	Regular	2000	2017				
07680	Short-eared Owl (Asio flammeus)	Mosehornugle	Regular	5	2017			2	
07700	Boreal Owl (Aegolius funereus)	Perleugle	Regular	7	2017			2	
07780	European Nightjar (Caprimulgus europaeus)	Natravn	Regular	510	2017			1	
07950	Common Swift (Apus apus)	Mursejler	Regular	15000	2017		CBM		
08310	Common Kingfisher (Alcedo atthis)	Isfugl	Regular	300	2017			1	
08400	European Bee-eater (Merops apiaster)	Biæder	Occasional	3	2017				
08410	European Roller (Coracias garrulus)	Ellekrage	Regionally extinct	0	1868	Confirmed 1868 (Olsen)			
08460	Eurasian Hoopoe (Upupa epops)	Hærfugl	Regionally extinct	0	1977	Confirmed 1977 (DOFbasen; Olsen); Probable 2014 (Atlas)			
08480	Eurasian Wryneck (Jynx torquilla)	Vendehals	Regular	48	2017				
08560	European Green Woodpecker (Picus viridis)	Grønspætte	Regular	320	2017		CBM		
08630	Black Woodpecker (Dryocopus martius)	Sortspætte	Regular	225	2017		CBM	1	
08760	Great Spotted Woodpecker (Dendrocopos major)	Stor Flagspætte	Regular	38500	2017		CBM		
08830	Middle Spotted Woodpecker (Dendrocopos medius)	Mellemflagspætte	Regionally extinct	0	1959	Confirmed 1959 (Olsen); Probable 2016 (Atlas)			
08870	Lesser Spotted Woodpecker (Dendrocopos minor)	Lille Flagspætte	Regular	50	2017				
09680	Short-toed Lark (Calandrella brachydactyla)	Korttået lærke	Occasional	0	2011	Confirmed 2011 (DOFbasen); Probable 2014 (Atlas)			
09720	Crested Lark (Galerida cristata)	Toplærke	Regular	2	2017			2	
09740	Woodlark (Lullula arborea)	Hedelærke	Regular	400	2017			1	
09760	Eurasian Skylark (Alauda arvensis)	Sanglærke	Regular	700000	2017		CBM		
09810	Sand Martin (Riparia riparia)	Digesvale	Regular	11000	2017		CBM		
09920	Barn Swallow (Hirundo rustica)	Landsvale	Regular	230000	2017		CBM		
10010	Common House Martin (Delichon urbicum)	Bysvale	Regular	38000	2017		CBM		
10050	Tawny Pipit (Anthus campestris)	Markpiber	Regular	2	2017			2	
10090	Tree Pipit (Anthus trivialis)	Skovpiber	Regular	10000	2017		CBM		
10110	Meadow Pipit (Anthus pratensis)	Engpiber	Regular	21000	2017		CBM		
10135	Eurasian Rock Pipit (Anthus petrosus)	Skærpiber	Regular	100	2017				
10170	Western Yellow Wagtail (Motacilla flava)	Gul Vipstjert	Regular	6200	2017		CBM		
10190	Grey Wagtail (Motacilla cinerea)	Bjergvipstjert	Regular	400	2017		CBM		
10200	White Wagtail (Motacilla alba)	Hvid Vipstjert	Regular	130000	2017		CBM		
10500	White-throated Dipper (Cinclus cinclus)	Vandstær	Regular	1	2011	Confirmed 2011 (DATSY) and 2016 (Atlas); Probable 2017 (DOFbasen)			
10660	Winter Wren (Troglodytes troglodytes)	Gærdesmutte	Regular	130000	2017		CBM		

Species no.	English (Latin)	Danish	Status	Breeding population 2011	Last confirmed breeding	Last breeding reference	Project	NOVANA	Invasive
10840	Dunnock (Prunella modularis)	Jernspurv	Regular	50000	2017		CBM		
10990	European Robin (Erithacus rubecula)	Rødhals	Regular	160000	2017		CBM		
11030	Thrush Nightingale (Luscinia luscinia)	Nattergal	Regular	9000	2017		CBM		
11040	Common Nightingale (Luscinia megarhynchos)	Sydlig Nattergal	Occasional	0	2006	Confirmed 2006 (DOFbasen); Probable 2017 (Atlas)			
11060	Bluethroat (Luscinia svecica)	Blåhals	Regular	314	2017			1	
11210	Black Redstart (Phoenicurus ochruros)	Husrødstjert	Regular	500	2017		CBM		
11220	Common Redstart (Phoenicurus phoenicurus)	Rødstjert	Regular	50000	2017		CBM		
11370	Whinchat (Saxicola rubetra)	Bynkefugl	Regular	2700	2017		CBM		
11390	European Stonechat (Saxicola rubicola)	Sortstrubet Bynkefugl	Regular	58	2017				
11460	Northern Wheatear (Oenanthe oenanthe)	Stenpikker	Regular	2000	2017		CBM		
11870	Common Blackbird (Turdus merula)	Solsort	Regular	1700000	2017		CBM		
11980	Fieldfare (Turdus pilaris)	Sjagger	Regular	500	2017		CBM		
12000	Song Thrush (Turdus philomelos)	Sangdrossel	Regular	220000	2017		CBM		
12010	Redwing (Turdus iliacus)	Vindrossel	Occasional	0	2003	Confirmed 2003 (DOFbasen); Probable 2014 (Atlas)			
12020	Mistle Thrush (Turdus viscivorus)	Misteldrossel	Regular	15000	2017		CBM		
12360	Common Grasshopper Warbler (Locustella naevia)	Græshoppesanger	Regular	1100	2017		CBM		
12380	Savi´s Warbler (Locustella luscinioides)	Savisanger	Regular	20	2017				
12430	Sedge Warbler (Acrocephalus schoenobaenus)	Sivsanger	Regular	2000	2017		CBM		
12480	Blyth´s Reed Warbler (Acrocephalus dumetorum)	Buskrørsanger	Occasional	0	2012	Confirmed 2012 (DOFbasen); Probable 2014 (Atlas)			
12500	Marsh Warbler (Acrocephalus palustris)	Kærsanger	Regular	28000	2017		CBM		
12510	Eurasian Reed Warbler (Acrocephalus scirpaceus)	Rørsanger	Regular	34000	2017		CBM		
12530	Great Reed Warbler (Acrocephalus arundinaceus)	Drosselrørsanger	Regular	7	2017				
12590	Icterine Warbler (Hippolais icterina)	Gulbug	Regular	7500	2017		CBM		
12730	Barred Warbler (Sylvia nisoria)	Høgesanger	Regionally extinct	0	1998	Confirmed 1998 (DATSY) and 2003 (DOFbasen); Probable 2008 (DATSY/ DOFbasen)			
12740	Lesser Whitethroat (Sylvia curruca)	Gærdesanger	Regular	100000	2017		CBM		
12750	Common Whitethroat (Sylvia communis)	Tornsanger	Regular	320000	2017		CBM		
12760	Garden Warbler (Sylvia borin)	Havesanger	Regular	130000	2017		CBM		
12770	Eurasian Blackcap (Sylvia atricapilla)	Munk	Regular	440000	2017		CBM		
12930	Greenish Warbler (Phylloscopus trochiloides)	Lundsanger	Occasional	0	2014	Confirmed 2014 (Atlas); Probable 2017 (DOFbasen)			
13080	Wood Warbler (Phylloscopus sibilatrix)	Skovsanger	Regular	4200	2017		CBM		
13110	Common Chiffchaff (Phylloscopus collybita)	Gransanger	Regular	300000	2017		CBM		
13120	Willow Warbler (Phylloscopus trochilus)	Løvsanger	Regular	260000	2017		CBM		
13140	Goldcrest (Regulus regulus)	Fuglekonge	Regular	29000	2017		CBM		
13150	Firecrest (Regulus ignicapilla)	Rødtoppet Fuglekonge	Regular	25	2017				
13350	Spotted Flycatcher (Muscicapa striata)	Grå Fluesnapper	Regular	7000	2017		CBM		
13430	Red-breasted Flycatcher (Ficedula parva)	Lille Fluesnapper	Occasional	0	2016	Confirmed 2016 (Atlas); Probable 2017 (DOFbasen)			
13490	European Pied Flycatcher (Ficedula hypoleuca)	Broget Fluesnapper	Regular	8000	2017		CBM		
13640	Bearded Reedling (Panurus biarmicus)	Skægmejse	Regular	2000	2017				
14370	Long-tailed Bushtit (Aegithalos caudatus)	Halemejse	Regular	4700	2017		CBM		
14400	Marsh Tit (Poecile palustris)	Sumpmejse	Regular	13000	2017		CBM		
14420	Willow Tit (Poecile montana)	Fyrremejse	Regular	500	2017				
14540	European Crested Tit (Lophophanes cristatus)	Topmejse	Regular	15000	2017		CBM		
14610	Coal Tit (Periparus ater)	Sortmejse	Regular	90000	2017		CBM		
14620	Blue Tit (Cyanistes caeruleus)	Blåmejse	Regular	235000	2017		CBM		
14640	Great Tit (Parus major)	Musvit	Regular	700000	2017		CBM		
14790	Eurasian Nuthatch (Sitta europaea)	Spætmejse	Regular	26000	2017		CBM		

Species no.	English (Latin)	Danish	Status	Breeding population 2011	Last confirmed breeding	Last breeding reference	Project	NOVANA	Invasive
14860	Eurasian Treecreeper (Certhia familiaris)	Træløber	Regular	13000	2017		CBM		
14870	Short-toed Treecreeper (Certhia brachydactyla)	Korttået Træløber	Regular	1500	2017				
14900	Eurasian Penduline Tit (Remiz pendulinus)	Pungmejse	Regular	6	2017				
15080	Eurasian Golden Oriole (Oriolus oriolus)	Pirol	Regular	9	2017				
15150	Red-backed Shrike (Lanius collurio)	Rødrygget Tornskade	Regular	1500	2017		CBM	1	
15200	Great Grey Shrike (Lanius excubitor)	Stor Tornskade	Regular	5	2017				
15390	Eurasian Jay (Garrulus glandarius)	Skovskade	Regular	32000	2017		CBM		
15490	Eurasian Magpie (Pica pica)	Husskade	Regular	180000	2017		CBM		
15570	Spotted Nutcracker (Nucifraga caryocatactes)	Nøddekrige	Regular	2	2009	Confirmed 2009 (DATSY) and 2016 (Atlas); Probable 2017 (Atlas)			
15600	Western Jackdaw (Corvus monedula)	Allike	Regular	100000	2017		CBM		
15630	Rook (Corvus frugilegus)	Råge	Regular	75000	2017		CBM		
15671	Carrion Crow (Corvus corone)	Sortkrage	Regular	1000	2017		CBM		
15673	Hooded Crow (Corvus cornix)	Gråkrage	Regular	150000	2017		CBM		
15720	Northern Raven (Corvus corax)	Ravn	Regular	1000	2017		CBM		
15820	Common Starling (Sturnus vulgaris)	Stær	Regular	270000	2017		CBM		
15910	House Sparrow (Passer domesticus)	Gråspurv	Regular	490000	2017		CBM		
15980	Eurasian Tree Sparrow (Passer montanus)	Skovspurv	Regular	450000	2017		CBM		
16360	Common Chaffinch (Fringilla coelebs)	Bogfinke	Regular	1300000	2017		CBM		
16380	Brambling (Fringilla montifringilla)	Kvækerfinke	Occasional	0	1974	Confirmed 1974 (Dybbro)			
16400	European Serin (Serinus serinus)	Gulirisk	Regular	20	2017				
16490	European Greenfinch (Chloris chloris)	Grønirisk	Regular	500000	2017		CBM		
16530	European Goldfinch (Carduelis carduelis)	Stillits	Regular	230000	2017		CBM		
16540	Eurasian Siskin (Spinus spinus)	Grønsisken	Regular	200	2017				
16600	Common Linnet (Linaria cannabina)	Tornirisk	Regular	100000	2017		CBM		
16635	Lesser Redpoll (Acanthis cabaret)	Lille Gråsisken	Regular	6000	2017		CBM		
16650	Two-barred Crossbill (Loxia leucoptera)	Hvidvinget Korsnæb	Occasional	5	2015	Confirmed 2015 (DOFbasen; Atlas)			
16660	Common Crossbill (Loxia curvirostra)	Lille Korsnæb	Regular	850	2017		CBM		
16680	Parrot Crossbill (Loxia pytyopsittacus)	Stor Korsnæb	Occasional	0	2017	Confirmed 2017 (Atlas)			
16790	Common Rosefinch (Erythrina erythrina)	Karmindompap	Regular	50	2017				
17100	Eurasian Bullfinch (Pyrrhula pyrrhula)	Dompap	Regular	15000	2017		CBM		
17170	Hawfinch (Coccothraustes coccothraustes)	Kernebider	Regular	9500	2017		CBM		
18570	Yellowhammer (Emberiza citrinella)	Gulspurv	Regular	310000	2017		CBM		
18770	Common Reed Bunting (Emberiza schoeniclus)	Rørspurv	Regular	36000	2017		CBM		
18820	Corn Bunting (Emberiza calandra)	Bomlærke	Regular	28000	2017		CBM		

Appendix 2

Species no.	English (Latin)	Danish	Site	Time	Nesting	Habitat
00120	Black-necked Grebe (Podiceps nigricollis)	Sorthalset Lappedykker	Unpredictable	Day	Colonial	Wet
00950	Eurasian Bittern (Botaurus stellaris)	Rørdrum	Unpredictable	Night	Solitary	Wet
01340	White Stork (Ciconia ciconia)	Hvid Stork	Unpredictable	Day	Colonial	Farmland
01440	Eurasian Spoonbill (Platalea leucorodia)	Skestork	Predictable	Day	Colonial	Coast
01540	Whooper Swan (Cygnus cygnus)	Sangsvane	Unpredictable	Day	Solitary	Wet
01670	Barnacle Goose (Branta leucopsis)	Bramgås	Unpredictable	Day	Colonial	Coast
01790	Eurasian Wigeon (Anas penelope)	Pibeand	Unpredictable	Day	Solitary	Wet
01820	Gadwall (Anas strepera)	Knarand	Unpredictable	Day	Solitary	Wet
01840	Eurasian Teal (Anas crecca)	Krikand	Unpredictable	Day	Solitary	Wet
01890	Northern Pintail (Anas acuta)	Spidsand	Unpredictable	Day	Solitary	Wet
01910	Garganey (Anas querquedula)	Atlingand	Unpredictable	Day	Solitary	Wet
01940	Northern Shoveler (Anas clypeata)	Skeand	Unpredictable	Day	Solitary	Wet
01960	Red-crested Pochard (Netta rufina)	Rødhovedet And	Predictable	Day	Solitary	Wet
02180	Common Goldeneye (Bucephala clangula)	Hvinand	Unpredictable	Day	Solitary	Wet
02230	Common Merganser (Mergus merganser)	Stor Skallesluger	Predictable	Day	Solitary	Wet
02310	European Honey Buzzard (Pernis apivorus)	Hvepsevåge	Unpredictable	Day	Solitary	Forest
03100	Eurasian Hobby (Falco subbuteo)	Lærkefalk	Unpredictable	Day	Solitary	Forest
03200	Peregrine Falcon (Falco peregrinus)	Vandrefalk	Predictable	Day	Solitary	Coast
03700	Common Quail (Coturnix coturnix)	Vagtel	Unpredictable	Night	Solitary	Farmland
04080	Spotted Crake (Porzana porzana)	Plettet Rørvagtel	Unpredictable	Night	Solitary	Wet
04210	Corn Crake (Crex crex)	Engsnarre	Unpredictable	Night	Solitary	Farmland
04330	Common Crane (Grus grus)	Trane	Unpredictable	Day	Solitary	Wet
04560	Pied Avocet (Recurvirostra avosetta)	Klyde	Predictable	Day	Solitary	Wet
04690	Little Ringed Plover (Charadrius dubius)	Lille Præstekrave	Unpredictable	Day	Solitary	Wet
04770	Kentish Plover (Charadrius alexandrinus)	Hvidbrystet Præstekrave	Predictable	Day	Colonial	Coast
04850	European Golden Plover (Pluvialis apricaria)	Hjejle	Predictable	Day	Solitary	Heathland
05120	Dunlin (Calidris alpina)	Almindelig Ryle	Predictable	Day	Solitary	Coast
05170	Ruff (Calidris pugnax)	Brushane	Predictable	Day	Solitary	Coast
05290	Eurasian Woodcock (Scolopax rusticola)	Skovsneppe	Unpredictable	Night	Solitary	Forest
05320	Black-tailed Godwit (Limosa limosa)	Stor Kobbersneppe	Predictable	Day	Colonial	Coast
05530	Green Sandpiper (Tringa ochropus)	Svaleklire	Unpredictable	Day	Solitary	Forest
05540	Wood Sandpiper (Tringa glareola)	Tinksmed	Predictable	Day	Colonial	Wet
05610	Ruddy Turnstone (Arenaria interpres)	Stenvender	Unpredictable	Day	Solitary	Coast
05750	Mediterranean Gull (Larus melanocephalus)	Sorthovedet Måge	Unpredictable	Day	Colonial	Coast
05780	Little Gull (Hydrocoloeus minutus)	Dværgmåge	Predictable	Day	Colonial	Wet
06020	Black-legged Kittiwake (Rissa tridactyla)	Ride	Predictable	Day	Colonial	Coast
06050	Gull-billed Tern (Gelochelidon nilotica)	Sandterne	Unpredictable	Day	Colonial	Coast
06060	Caspian Tern (Hydroprogne caspia)	Rovterne	Predictable	Day	Colonial	Coast
06110	Sandwich Tern (Sterna sandvicensis)	Splitterne	Unpredictable	Day	Colonial	Coast
06160	Arctic Tern (Sterna paradisaea)	Havterne	Unpredictable	Day	Colonial	Coast
06240	Little Tern (Sternula albifrons)	Dværgterne	Unpredictable	Day	Colonial	Coast
06270	Black Tern (Chlidonias niger)	Sortterne	Unpredictable	Day	Colonial	Wet
06340	Common Murre (Uria aalge)	Lomvie	Predictable	Day	Colonial	Coast
06360	Razorbill (Alca torda)	Alk	Predictable	Day	Colonial	Coast
06380	Black Guillemot (Cepphus grylle)	Tejst	Predictable	Day	Colonial	Coast
06870	European Turtle Dove (Streptopelia turtur)	Turteldue	Unpredictable	Day	Solitary	Forest
07350	Barn Owl (Tyto alba)	Slørugle	Unpredictable	Night	Solitary	Farmland
07440	Eurasian Eagle-Owl (Bubo bubo)	Stor Hornugle	Unpredictable	Night	Solitary	Forest
07570	Little Owl (Athene noctua)	Kirkeugle	Unpredictable	Night	Solitary	Farmland
07670	Long-eared Owl (Asio otus)	Skovhornugle	Unpredictable	Night	Solitary	Forest
07680	Short-eared Owl (Asio flammeus)	Mosehornugle	Unpredictable	Day	Solitary	Wet
07700	Boreal Owl (Aegolius funereus)	Perleugle	Unpredictable	Night	Solitary	Forest
07780	European Nightjar (Caprimulgus europaeus)	Natravn	Unpredictable	Night	Solitary	Forest
08310	Common Kingfisher (Alcedo atthis)	Isfugl	Unpredictable	Day	Solitary	Wet
08480	Eurasian Wryneck (Jynx torquilla)	Vendehals	Unpredictable	Day	Solitary	Forest

Species no.	English (Latin)	Danish	Site	Time	Nesting	Habitat
08870	Lesser Spotted Woodpecker (Dendrocopos minor)	Lille Flagspætte	Unpredictable	Day	Solitary	Forest
09720	Crested Lark (Galerida cristata)	Toplærke	Predictable	Day	Solitary	Urban
09740	Woodlark (Lullula arborea)	Hedelærke	Unpredictable	Day	Solitary	Forest
10050	Tawny Pipit (Anthus campestris)	Markpiber	Predictable	Day	Solitary	Heathland
10135	Eurasian Rock Pipit (Anthus petrosus)	Skærpiber	Unpredictable	Day	Solitary	Coast
10500	White-throated Dipper (Cinclus cinclus)	Vandstær	Unpredictable	Day	Solitary	Stream
11060	Bluethroat (Luscinia svecica)	Blåhals	Unpredictable	Day	Solitary	Wet
11390	European Stonechat (Saxicola rubicola)	Sortstrubet Bynkefugl	Unpredictable	Day	Solitary	Heathland
12380	Savi´s Warbler (Locustella luscinioides)	Savisanger	Unpredictable	Day	Solitary	Wet
12530	Great Reed Warbler (Acrocephalus arundinaceus)	Drosselrørsanger	Unpredictable	Day	Solitary	Wet
13150	Firecrest (Regulus ignicapilla)	Rødtoppet Fuglekonge	Unpredictable	Day	Solitary	Forest
13640	Bearded Reedling (Panurus biarmicus)	Skægmejse	Unpredictable	Day	Solitary	Wet
14420	Willow Tit (Poecile montana)	Fyrremejse	Unpredictable	Day	Solitary	Wet
14870	Short-toed Treecreeper (Certhia brachydactyla)	Korttået Træløber	Unpredictable	Day	Solitary	Forest
14900	Eurasian Penduline Tit (Remiz pendulinus)	Pungmejse	Unpredictable	Day	Solitary	Wet
15080	Eurasian Golden Oriole (Oriolus oriolus)	Pirol	Unpredictable	Day	Solitary	Forest
15200	Great Grey Shrike (Lanius excubitor)	Stor Tornskade	Predictable	Day	Solitary	Heathland
15570	Spotted Nutcracker (Nucifraga caryocatactes)	Nøddekrige	Unpredictable	Day	Solitary	Forest
16400	European Serin (Serinus serinus)	Gulirisk	Unpredictable	Day	Solitary	Urban
16540	Eurasian Siskin (Spinus spinus)	Grønsisken	Unpredictable	Day	Solitary	Forest
16790	Common Rosefinch (Erythrina erythrina)	Karmindompap	Unpredictable	Day	Solitary	Coast

Definitions	Description	Reference
Regular breeding	Breeding 10 consecutive years	Bioscience 2017b; updated to 2017
Regionally extinct	Has been a regular breeding bird in Denmark but is extinct here now	Bioscience 2017b; updated to 2017
Occasional	Breeding less frequent than 10 consecutive years	
Breeding population 2011/2012	The estimates for the Danish bird populations provided for this publication, however adapted where additional information	Birdlife International 2015
Last breeding references	"Last breeding year for species with a 2011/2012 population estimate of zero. Only confirmed breeding. In addition, probable breeding if this is more recent"	
	Atlas	Atlasbasen https://dofbasen.dk/atlas/ approached primo October 2017
	DOFbasen	www.dofbasen.dk; approached primo october 2017
	Dybbro	Dybbro, T. 1978: Oversigt over Danmarks fugle. – Dansk Ornitologisk Forening.
	Grell	Grell, M.B. 1998: Fuglenes Danmark. – Gads Forlag & Dansk Ornitologisk Forening.
	DATSY	Nyegaard, T, H. Meltofte, J. Tofft & M.B. Grell. 2014: Rare and threatened breeding birds in Denmark 1998-2012. In Danish with an English summary. – Dansk Orn. Foren. Tidsskr. 108: 1-144.
CBM	Common Bird Monitoring	Moshøj et al. 2017
Special	Special initiatives to count the national population anually	
NOVANA	National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments	Miljøstyrelsen et al. 2017

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PAPER 2

CONTINUOUS POPULATION DECLINES FOR SPECIALIST FARMLAND BIRDS 1987-2014 IN DENMARK INDICATES NO HALT IN BIODIVERSITY LOSS IN AGRICULTURAL HABITATS

HENNING HELDBJERG, PETER SUNDE and ANTHONY DAVID FOX

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Continuous population declines for specialist farmland birds 1987-2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats

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Summary

The 2020 EU biodiversity strategy aims to halt the loss of biodiversity and ecosystem services, but this requires effective monitoring to determine whether these aims are achieved. Common bird monitoring continuously assesses changes in the avian community, providing a powerful tool for monitoring temporal changes in the abundance and distribution of these upper trophic level consumers. Two-thirds of Denmark's land area is intensively farmed, so agricultural habitats make a major contribution to Danish biodiversity. We looked for changes in abundance amongst farmland birds in Denmark during 1987–2014 to test for reductions in declines and to predict whether the 2020-target can be expected to be achieved. Sixteen specialist farmland species were those showing the most rapid declines amongst 102 common breeding species in Denmark. Of these, those species nesting on the ground showed significant long-term declines, which was not the case for those that nest elsewhere, i.e. in hedgerows, trees and buildings. There was no evidence to suggest that these trends were attributable to widespread declines in long-distance migrant species (as reported elsewhere), which may be affected by conditions at other times in the annual cycle. We therefore conclude that continued declines in specialist farmland breeding bird species are due to contemporary agricultural changes within Denmark and urge habitat- and species-specific analysis to identify the core causes of these changes and halt the declines.

Introduction

In 2011, the European Commission adopted a new strategy to halt the loss of biodiversity by 2020 and restore previous losses as far as this is feasible. The situation amongst the farmland birds relates especially to the third of six targets in the strategy that focuses on improving the integration of biodiversity conservation into key policies for agriculture and forestry (European Commission 2011).

Denmark has one of Europe's most intensively farmed landscapes, with approximately 66% of the total area cultivated (Danmarks Statistik 2009) mostly under winter wheat, grass ley, fodder and spring barley (Brink and Jensen 2012). The total area of arable agriculture has been more or less stable at c.27,000 km^2 during 1920–1980, since when there has been a slight decline (Levin and Normander 2008). Danish farmland consists of two major predominant landscape types, arable areas (where tillage predominates) and mixed farming (with more permanent and managed grassland). These two types of farming have become increasingly regionally discrete, with pastoral agriculture primarily practiced in the west of Denmark and a more homogeneous arable landscape predominating in the east of the country, a process that has continued since the 1980s (Reenberg 1988).

The intensity of agricultural activity has been increasing in both the arable and pastoral sectors and in particular, arable practices have changed over time, especially in choice of crops, which has had an adverse effect on associated bird populations in Denmark (Fox 2004) as elsewhere in Europe (Donald *et al.* 2001) and across continents (Reif 2013).

The reformed EU Common Agricultural Policy (CAP) for 2014–2020 aims at reducing biodiversity loss but has been criticised for having 'such diluted environmental prescriptions that they are unlikely to benefit biodiversity' (Pe'er *et al.* 2014). Because such a high proportion of Denmark is subject to intensive cultivation, farmland makes a disproportionate contribution to the maintenance of Danish biological diversity. This is particularly the case amongst bird species, which are a conspicuous and well monitored element of Danish biodiversity and which contribute greatly to that of farmland landscapes. Because of their mobility and situation in the upper trophic levels of such ecosystems, birds are considered to be good habitat indicators, showing sensitivity and rapid responses to anthropogenic change in the environment. Furthermore, monitoring data exist in the form of long term time-series on their abundance and distribution across large parts of Europe (Gregory and van Strien 2010). Here, we use data from the Common Bird Monitoring programme to study whether there has been a reduction in the decline of specialised farmland birds in Denmark, and use this information to provide a basis for raising key questions in the Discussion section about how we can achieve the 2020 goal.

Populations of common birds have been monitored in all Danish habitats and regions since the mid-1970s, providing information on changes in population size and their trends for common breeding bird species in Denmark over nearly 40 years. This programme is a powerful tool for monitoring changes in abundance within the bird community in any given period, as well providing insight to enable judgements as to whether the 2020-target is likely to be achieved. An earlier analysis showed that after major changes in the 1980s, the breeding birds of Danish farmland had shown less radical variation in abundance up until the early 2000s than in UK (Fox 2004). However, that study considered a wide spectrum of generalist avian species occurring in agricultural landscapes in Denmark, of which only limited proportions of their populations depend purely upon farmland as breeding habitat.

Here, we divide our study into two major parts. Firstly, we take the broad perspective and compare the rates of change of specialist farmland birds with those which specialised in using other habitats. Secondly we define a group of breeding bird species that show a high degree of specialism for farmland habitats (i.e. those species largely confined to farmland for breeding habitat; see Methods below for specific definitions) for more detailed studies and use these species to compare changes in their abundance during 2001–2014 with those during 1987–2001.

There have been substantial changes in the Danish agricultural landscape in the study period (see Discussion) and we seek to find support for the hypotheses that changes in abundance of different farmland specialist bird species are related to their responses to differences in (i) farming type (species exploiting grasslands versus arable land), (ii) nest-site (those species which nest on the ground, usually within fields, versus those that build their nests elsewhere) to separate those species that nest in the fields and are thus fully dependent on the field environment from those species that are only partly dependent on field habitats and (iii) migratory strategy (long-distance, short-distance versus resident species). We use a model selection framework to explain the trends for each species incorporating these features as explanatory variables, contrasting those in the periods 1987–2001 and 2001–2014.

Materials and methods

Data collection and time series

The Danish Common Bird Monitoring (CBM) programme estimates indices and trends for common birds. It is based upon a point count census of breeding birds undertaken since 1976. This programme has involved sampling bird species abundance at more than 70 routes (>300 routes since 1987; mean ± 95% CI, 1987–2014 = 341 ± 11, median 346.5) throughout the country. Most routes consist of 20 (but always > 10) 'points' which are identical in subsequent years at which all birds seen and heard regardless of distance from observer were registered and recorded in a 5-min observation period (Heldbjerg 2005). Observers simultaneously counting birds also ascribe the habitat in quarters surrounding each count point to one or more of nine predefined basic habitat types: 1) Coniferous woodland, 2) Deciduous woodland, 3) Arable, 4) Grassland, 5) Heath, 6) Dunes/Shore, 7) Bog/Marsh, 8) Lake and 9) Urban. The best covered habitat types were combined into four broader habitat types: Urban (habitat type 9; Annual mean of 10% of totally monitored habitats; Eskildsen *et al.* 2013), Farmland (3,4; 39%), Freshwater (7,8; 10%), Forest (1,2; 38%) whereas the habitats with least coverage are omitted (5,6; 3%). Although only *c*.13.2% of the count points came from purely arable landscapes and c.1.5% from permanent meadows/grassland plots, the majority of the surveyed count points were from 'mixed' habitats, which included extensive areas of farmland. In total an annual mean of 27.8% and 11.1% of all habitat descriptions were from arable habitat and grasslands respectively. Each route was monitored by the same observer each year, at the same time of year (± 7 days), same time of day (± 30 min) and under comparable weather conditions. Although the CBM started in 1976 (Heldbjerg *et al.* 2014), because of rapid increases in the number of participants in the early years we restricted the time series to 1987–2014 to ensure robust and comparable data with more even coverage in all years for the more detailed analysis.

Selection of common bird species

Initially, we included all species from the Danish CBM (Heldbjerg *et al.* 2014). Mallard *Anas platyrhynchos* and Pheasant *Phasianus colchicus* were omitted from the analysis because their Danish populations are heavily influenced by rearing and releases (Noer *et al.* 2009). For the remaining 102 species, we compared the trends for the specialist farmland species with all specialist species from other major habitats in order to compare the trends of farmland specialists to trends of specialists in other habitats.

Defining species relative habitat use

Not all avian species are habitat specialists, in the sense that they are almost exclusively found in only one of the above nine habitat types, so it is important to establish the degree to which species are confined to specific habitats or to what extent they are habitat generalists. Each species' habitat association in the breeding season was defined in terms of their Relative Habitat Use (RHU), calculated as the abundance of a given species in a particular habitat relative to the mean abundance of that species in all other habitats. The number of observed individuals at each point was weighted with the proportion of the given habitat at the point. The sum of the weighted number of individuals of each species in a particular habitat could then be used to calculate a RHU value from the following equation:

$$Relative\ Habitat\ Use = \frac{n_i / p_i}{(N - n_i)/(P - p_i)}$$

where n_i is the number of individuals in the i^{th} habitat, p_i is the total number of i-habitat points, adjusted according to proportional habitat share at each point, N is the total number of individuals and P is the total number of points. For full details and examples, see Larsen *et al.* 2011 (Figure 1) and Eskildsen *et al.* (2013).

A RHU > 2 indicates an abundance in the specified habitat at least twice the mean abundance in all other habitats, representing a High use habitat specialist (HiU). Where 2 > RHU > 1, this indicates an abundance in the given habitat above the mean elsewhere (but less than double) defined here as Intermediate use habitat specialist (IU). Where RHU < 1, the species is considered a generalist, which uses the given habitat less than other habitats, and these are omitted from this study.

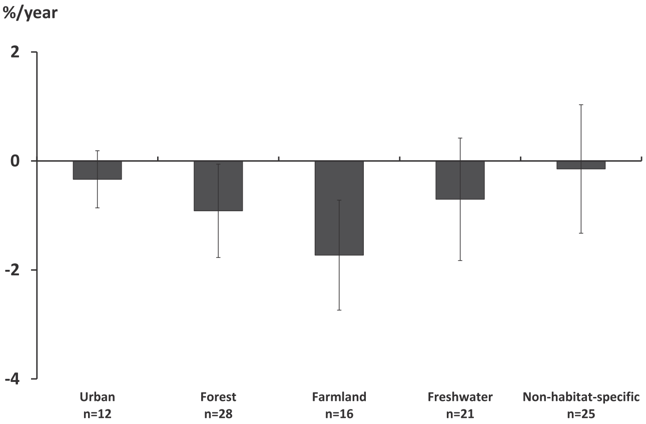

Figure 1. Histograms showing the mean percentage change per year in index values generated by log-linear modelling of Danish breeding bird point count data (± 95% CI) showing long term (1987–2014) trends for 102 common Danish breeding bird species divided into their Relative Habitat Use specialist groups (RHU > 2; HiU).

Defining farmland

The habitat here defined as Farmland (F) is a combination of the two habitat categories in the CBM programme, Arable (A) and Grassland (G) habitats. A consists of arable areas such as fields and fallow land, as well as associated lesser elements within the arable landscape like hedgerows, farms and orchards. G consists of meadows, salt marshes, pastures, dry grassland and other grass-dominated areas with or without scattered trees and/or shrubs.

Defining farmland birds

We defined Farmland birds (FB) as all species which had a RHU value for F (consisting of A and G) that was larger than 1. However, the G constitutes a relatively small area but is broad in its definition (e.g. including salt marshes). G therefore included breeding species that were not typically confined to farmland habitats, which we subsequently removed (e.g. Greater Black-backed Gull *Larus marinus*). We also removed those species with a Danish breeding population of less than 1,000 pairs (e.g. Curlew *Numenius arquata*) and species for which less than 50 individuals were registered per year (e.g. Sparrowhawk *Accipiter nisus*, Common Wheatear *Oenanthe oenanthe* and Grasshopper Warbler *Locustella naevia*). The final list of FB therefore included 41 species (Appendix S1 in the online Supplementary Material).

Levels of analysis

In this study, we undertook two levels of analysis. First, we compared the trends for High Use Farmland Birds (HiUFB) with HiU species of other habitats and then we focused only on farmland birds. For the latter group we first compared HiUFB with Intermediate Use Farmland Birds (2 > RHU > 1; IUFB) and then we combined these two categories to generate a broader category of avian species associated with farmland (RHU > 1; FB).

Defining and comparing specialists in different habitat categories

We followed the indicator species selection from Eskildsen *et al.* (2013) where the HiU indicators for the broad habitats Urban, Farmland, Freshwater and Forest was found to cover 75% of all species included in the CBM and categorized the rest as Non-habitat specific.

We analysed changes in abundance with regard to these major habitats and compared trends (mean percentage change per year), using the additive slope provided by TRIM for 1987–2014 between groups by presenting an assessment of the variance within each group to show differences. In order to describe recent trends in farmland birds we also introduced a change point in 2001 (the last year included in Fox 2004) also used as base year (index 100) and compared the changes before and after this year.

Population indices and trends

Population indices and trends for all 102 species were calculated by fitting a log linear regression model to point count data with Poisson error terms using the software TRends and Indices for Monitoring data (TRIM; Pannekoek and van Strien 2004), where the count at a given site in a given year is assumed to be the result of a site and a year effect. The programme also estimates the dispersion factor, correcting for over-dispersion where this occurs, and takes account of serial correlation between counts at the same site in different years. Standard errors for the indices are generated based on the assumption that the variance is proportional to the mean, and a pattern of serial correlation, which declines exponentially with time between counts (Pannekoek and van Strien 2004). The assessment of the annual rate of change was used in this study to generate species trends, taking the standard errors into account. The population changes were described by indices and we are only interested in the relative changes (not the absolute number) for each species during the study period. Subsequently, individual species indices were combined into a single indicator value in each year for all species belonging to the same farmland birds specialisation category. The multi-species indicators were calculated as the geometric mean of the individual species indices for each year. The index mean is considered a measure of biodiversity change, a stable indicator trend reflects a balance between positive and negative indices whereas a reduction in index mean will occur if more species are declining than increasing and vice versa (Buckland *et al.* 2005; Gregory *et al.* 2005). Two indicators were produced for those bird species which specialised in each habitat: one for HiUFB and one for IUFB. Low-use species with an RHU < 1 were omitted from the analyses on the assumption that such species were habitat generalists.

Since there was a high degree of consistency between the population trends calculated using habitat-specific point counts and using all point counts irrespective of habitat (Eskildsen *et al.* 2013; based on percentage population changes on the same data across 24 years (1986–2009) from 12 habitat categories, $r^2 = 0.82$), in this study we used data from all point counts relating to a given species, not only those from points in their primary habitat.

Model for the trends for all 41 farmland birds

Among the 41 FB we included a number of parameters in a model analysed separately for the earlier (1987–2001) and most recent (2001–2014) 14-year periods by using generalised linear models (GLIMMIX procedure in SAS 9.4) on the basis of maximum likelihood optimisation ('method=mspl' statement).

1. Influence of farmland type

We compared the trends for species in grassland habitat to species in arable habitat. For this purpose we used the RHU in each of the habitat types Grassland (RHUG) and Arable (RHUA) as well as the combined Farmland habitat (RHUF).

2. Influence of nesting site

We compared ground-nesting species to species nesting outside of the fields (defined using Ferguson-Lees *et al.* 2011) to test whether those species habitually exploiting fields for nest sites were more likely to be declining than those more associated with field margins and other elements of the agricultural landscape.

3. Influence of migratory patterns

Declining farmland bird species that winter elsewhere could potentially be subject to factors acting at other points in the annual life cycle other than on Danish farmland. Given the general decline among Trans-Saharan migrants in Denmark (Heldbjerg and Fox 2008) and Europe in general (Vickery *et al.* 2014), we also grouped species by their migratory strategy, i.e. long distance migrants (Trans-Saharan migrants), short distance migrants (Europe and North Africa) and resident species based on ringing-recovery data on Danish breeding birds (Bønløkke *et al.* 2006).

Statistical analysis

The most parsimonious models to describe the trend patterns were identified by comparing AICc weight of 16 candidate models representing all main effect combinations of nesting behaviour (ground nester or not ground nester), migration strategy (resident, short distance migrator, long distance migrator) and specialisation to F, A or G (using log-transformed RHU-variables in order to achieve normal distributed data).

To investigate whether population trends differed between the two periods, we compared AICc weights of models explaining the 14-year population trends in the combined dataset (41 species × 2 periods = 82 trend values). For this analysis, we evaluated models with and without time period, nesting behaviour and specialization to arable land as main effects and interaction terms between time period and nesting behaviour, migration strategy and specialisation to arable land, respectively. Nesting behaviour and specialization to arable land were selected as the top-ranked variables in the initial analysis.

In addition to the candidate models with different predictor combinations of central tendency described above, we also evaluated models with heteroscedasticity (unequal variance) between groups (nesting behaviour, migration strategy and time period).

Results

Farmland specialists compared to specialists in other habitats

Of all the major Danish habitat types, the strongest declines in habitat specialists (RHU > 2, Eskildsen *et al.* 2013) among the 102 common breeding birds in the period 1987–2014 were found in the farmland habitat (Figure 1). The majority of farmland bird populations showed decreasing or stable trends (Table 1) and overall tended to show more negative trends compared to species exploiting other habitats. This fact is the background for more detailed studies on all 41 Farmland birds (FB).

Differences in trends related to the specialization of the farmland birds

Long term (1987–2014) declines amongst the 41 FB species mainly occurred among HiUFB, of which 63% declined and 19% increased. On average, there was an annual -1.55% long term decline (95% CI: -1.76% to -1.33%) in HiUFB species over the period 1987–2014 ($n = 28$, $r^2 = 0.893$, $P < 0.0001$, Fig. 2). In comparison, species categorised as IUFB decreased on average with

Table 1. Numbers of common Danish bird species showing differing long and short term trends, broken down by High use (HiUFB) and Intermediate use (IUFB) of farmland habitats (see text for details).

	1987–2014		1987–2001		2001–2014	
Farmland	HiUFB	IUFB	HiUFB	IUFB	HiUFB	IUFB
Increase	3	9	3	10	3	6
Stable	3	7	4	6	4	4
Decline	10	9	9	9	9	15
SUM	16	25	16	25	16	25

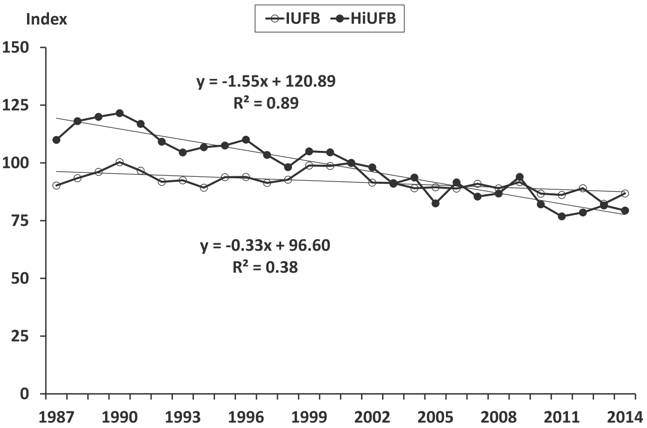

Figure 2. Geometric mean annual indices of 41 farmland species divided into High use farmland species (HiUFB; r^2 = 0.89, $P < 0.0001$, n = 16) and Intermediate use farmland species (IUFB; r^2 = 0.38, $P < 0.001$, n = 25) in 1987–2014. Trend indices are generated from log linear regressions models using the results of Danish Common Bird Monitoring data (Index 100 = 2001).

-0.33% (95% CI: 0.49% to -0.16%, n = 28, r^2 = 0.379, P = 0.0005; Figure 2) per annum over the same period.

During 1987 to 2001 the multispecies indicator of all the 41 FB declined at -0.39% (95% CI: -1.42 to 0.064), a trend that was not statistically significant (P = 0.45). From 2001 to 2014, the average population index of the same 41 FB species declined at -1.22% per annum (95% CI: -1.93 to -0.52%, P = 0.0007). The multispecies indicator for the HiUFB declined significantly in both periods: -1.26% per annum in 1987-2001 (95% CI: -1.94% to -0.58%; P = 0.0017) to -1.48% per annum in 2001-2014 (95% CI: -2.11% to -0.84%; P = 0.0003) while the multispecies index for the IUFB was only significantly declining in 2001–2014: (0.15% per annum in 1987–2001 (95% CI: -0.35% to 0.65%; P = 0.538) to -0.71% per annum in 2001–2014 (95% CI: -1.10% to -0.31%; P = 0.0022).

In 1987–2001, a larger proportion of the IUFB were increasing compared to the HiUFB but the ratio of increasing to declining species in these two groups was the same in 2001-2014, indicating that the IUFB are also now declining (Table 1 and Appendix S1).

Effects of nest sites 1987–2001

Regarding the 41 FB, all models that differentiated between ground-nesters and non-ground nesters had substantially higher AICc-weights than the basic model without any covariates indicating that this is a key factor. None of the models lacking nesting behaviour performed better than the basic model (Table 2). According to the top-ranked model, the mean population trend did not differ from 0 for species not nesting on the ground, whereas ground-nesters declined statistical significantly at greater than 3% per year (Table 2 and Figure 3).

Effects of nest sites 2001-2014

The model discriminating between ground-nesters and non-ground nesters (Nest) and the model that included specialisation to farmland (RHUF) had modestly more support than the basic model without covariates (Table 2), suggesting that ground-nesting FB showed more negative population trends during this period (Figure 3).

Table 2. Parsimony statistics of candidate models to explain variation in population trends of 41 common breeding bird species in Denmark 2001-14 (a) and 1987-2001 (b). wi = Akaike's weight, ER(.) = evidence ratio in Akaike's weights relative to the basic model only estimating the intercept. Abbreviations for predictor variables: Nest = Ground nester or non-ground nester, Mig = Migration strategy (resident, short-distance migrant, long-distance migrant), RHUA = specialization to arable habitats, RHUG = specialization to grassland habitats, RHUF = specialization to farmland habitats.

a)	2001–2014			b)	1987–2001		
Model	ΔAICc	wi	ER(.)	Model	ΔAICc	wi	ER(.)
Nest	0.00	0.229	3.4	RHUA + Nest	0.00	0.276	27.4
RHUF	0.02	0.226	3.4	Nest	0.97	0.170	16.9
RHUF + Nest	1.53	0.107	1.6	RHUF + Nest	1.27	0.146	14.5
RHUG + Nest	2.07	0.081	1.2	RHUG + Nest	1.83	0.110	11.0
.	2.45	0.067	.	RHUA + Nest + Mig	2.18	0.093	9.2
RHUA + Nest	2.45	0.067	1.0	Nest + Mig	2.63	0.074	7.4
Nest + Mig	2.88	0.054	0.8	RHUF + Nest + Mig	2.86	0.066	6.6
RHUA	3.66	0.037	0.5	RHUG + Nest + Mig	4.38	0.031	3.1
RHUF + Mig	3.84	0.034	0.5	.	6.62	0.010	.
RHUG	4.17	0.028	0.4	RHUG	7.03	0.008	0.8
RHUF + Nest + Mig	5.10	0.018	0.3	RHUF	8.14	0.005	0.5
RHUA + Nest + Mig	5.46	0.015	0.2	RHUA	8.89	0.003	0.3
RHUG + Nest + Mig	5.63	0.014	0.2	Mig	9.26	0.003	0.3
Mig	5.83	0.012	0.2	RHUG + Mig	9.36	0.003	0.3
RHUA + Mig	6.66	0.008	0.1	RHUF + Mig	10.81	0.001	0.1
RHUG + Mig	8.04	0.004	0.1	RHUA + Mig	11.82	0.001	0.1

Comparison between Arable and Grassland specialists

Three times as many farmland bird species were significantly declining during 2001–2014 as were significantly increasing amongst the HiUFB and IUFB (Table 1; see Appendix S1 in supporting information). The RHU for each farmland species is included for Arable habitat, Grassland habitat and for the combined Farmland habitat to categorize each species as an Arable species or a Grassland specialist.

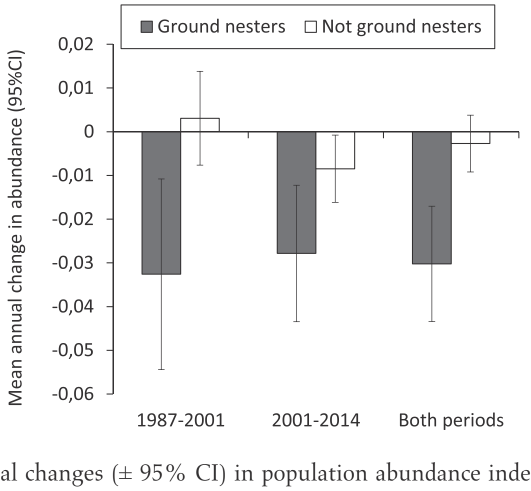

Figure 3. Mean annual changes (± 95% CI) in population abundance index of common Danish farmland bird species divided on period and nesting behaviour (n = 8 ground nesting species, 33 non-ground nesting species).

Of the seven Arable HiU species, five, Kestrel *Falco tinnunculus*, Grey Partridge *Perdix perdix*, Lapwing *Vanellus vanellus*, Skylark *Alauda arvensis* and Yellow Wagtail *Motacilla flava*, have all been declining in this period. Ten out of 17 Grassland HiU species have significantly declined over this period. Greylag Goose *Anser anser*, Marsh Harrier *Circus aeruginosus* and Herring Gull *Larus argentatus* are the only exceptions that were significantly increasing.

Comparison of 1987–2001 vs. 2001–2014 and the two periods combined

The top-ranked model for the combined dataset (trends 1987–2001 and 2001–2014) predicted more negative population trends for ground nesters than non-ground nesters with higher residual variance in the first than in the second period (Table 3). Models including effects of habitat specialisation (RHUF) or migratory behaviour all performed worse than model alternatives without these terms (Table 3). Models with main effects of period or interaction effects of period with nesting behaviour performed marginally worse than model alternatives without these effects (Table 3), suggesting little support for substantial differences in population trend patterns in the two periods. Predictions from models with interactive effects of period and nesting behaviour, suggested that ground nesters declined at an average rate of about 3% per year in both periods, whereas non-ground nesters appeared to be stable in the first period, but declined with an average rate of 1% per year in the second period. The top-ranked model included nesting behaviour without any effect of period. This model generated an average annual decline of c.3% for ground nesters, but found no significant decline for non-ground nesters throughout the entire period, 1987–2014 (Figure 3). Only three out of 16 HiUFB showed significant increases during 1987–2014, namely Marsh Harrier increasing at 3.3% per year, Common Gull *Larus canus* at 2.2 % per year and Common Whitethroat *Sylvia communis* at 0.5% per year. The two former are both breeding in other habitat types and only partly foraging in the farmland habitat, which shows the potential importance of farmland as foraging habitat for birds nesting in other habitats. In contrast, 10 species declined significantly, of which Whinchat *Saxicola rubetra* showed an average decline of > 5% per year, corresponding to a halving of the population within 14 years. Another seven species were declining at > 2% per year, halving their population size within 35 years: Grey Partridge, Oystercatcher *Haematopus ostralegus*, Lapwing, Skylark, Meadow Pipit *Anthus pratensis*, Yellow Wagtail, and Starling *Sturnus vulgaris*.

Table 3. Parsimony statistics of candidate models to explain variation in population trends of common breeding bird species in Denmark 1987-2001 and 2001-14 (n = 82 time series from 41 species, (see Appendix S1). wi = Akaike's weight, ER(.) = evidence ratio in Akaike's weights to 'base' model only estimating the intercept. Abbreviations for predictor variables: Nest = Ground nester or non-ground nester, P = period (1987-2001 vs 2001-2014), Mig = Migration strategy (resident, short-distance migrant, long-distance migrant), RHUA = specialization to arable habitats.

Fixed effects	Heteroscedasticity	ΔAICc	wi	ER(.)
Nest	P	0.00	0.233	518
Nest + P	P	0.29	0.201	448
RHUA + Nest	P	1.35	0.118	264
Nest*P	P	1.41	0.115	256
RHUA + Nest + P	P	1.66	0.101	226
Nest	.	2.29	0.074	165
RHUA + Nest*P	P	2.82	0.057	126
RHUA*P + Nest*P	P	2.82	0.057	126
RHUA*P + Nest	P	3.67	0.037	83
.	P	9.07	0.002	5.6
P	P	9.58	0.002	4.3
.	Nest	11.53	0.001	1.6
.	.	12.50	0.000	.
.	Mig	12.81	0.000	0.9
.	Nest*P	12.73	0.000	0.9

Discussion

This analysis established that Danish specialist farmland birds have shown greater long term declines in abundance than specialists in other habitats. The analysis also showed that amongst these farmland birds, ground nesting species showed greater declines in the period 1987–2001 and whereas in 2001–14 this trend continued, in the latter period there are also significant declines amongst species not nesting on the ground as well.

Long-term declines in farmland bird populations

After apparent stability in 1987–2001, the farmland specialist species in Denmark are now showing long term declines in contrast to species in other habitats. Although less dramatic than in the late 1970s and early 1980s (Eskildsen *et al.* 2013), this is important within Denmark because such a large area of the land surface is under cultivation.

Fox (2004) analysed Danish farmland bird populations in 1983–2001 in relation to changes in 26 agricultural variables, comparing these with the situation in UK and found marked differences between national patterns of agriculture and more favourable population trends in Denmark compared to the UK. The present study included additional data from 13 more years (2002–2014), calculated trends using TRIM software (rather than the chain-index method) and selected species based on their habitat preferences in the Danish landscape. Eskildsen *et al.* (2013) found that while generalist species using farmland showed stable trends, the specialist species have shown consistent declines since the 1990s (see their Figure 3).

The situation in Denmark is now very similar to that found throughout Europe in general. The Farmland Bird Indicator (FBI) combines the aggregate population trends of 39 species classified as farmland birds on a European scale, of which 24 are decreasing and only six are increasing, with a further six showing stable and three uncertain trends. Overall, the indicator shows a decline of 54% during 1980–2012 (EBCC 2014).

Because the farming landscape represents two-thirds of the total land area in Denmark, agri-biodiversity makes an important contribution to overall biological diversity, so it is important to establish hypotheses relating to potential factors responsible for species declines in order to develop adaptive management options and mitigating actions to reduce and reverse species declines where possible.

Arable versus grassland species

The Farmland birds generally showed adverse population trends across both grassland and arable agriculture, however, model selection for the period 1987–2001 suggested that ground-nesting species associated with arable habitat were suffering more acute problems associated with this type of farming.

With the notable exception of Grey Partridge, all of the declining HiU species are associated with grazed grassland habitats at some stage in their breeding cycle, which suggest changes in such habitats may be implicated in their change of status. The consequences of the decline in grazing pressure is known to have an adverse effect on the Starling (Heldbjerg *et al.* 2016). Given the dramatic expansion in rotational grassland throughout Denmark and the removal of grazing animals from grassland outdoors into buildings for most or all of the year, there is an urgent need for more detailed investigation of how these major changes in agriculture affects the changes in population sizes of the species associated with different types of managed grassland (which include Snipe *Gallinago gallinago*, Oystercatcher, Lapwing, Skylark, Meadow Pipit and Yellow Wagtail).

The number of species significantly declining among the IUFB was less than the HiUFB in 1987–2001 but at the same level in 2001-2014, suggesting that the most specialised farmland species experienced the greatest difficulties in the first period but both groups have problems in the contemporary Danish agricultural landscape.

Effects of nest site

Ground-nesting species showed significant decreases, whilst those species not nesting on the ground only shows declines since 2001, even though both sets of species tend to forage within the same habitat. This could suggest some causal link with tillage and conditions within the field where we assume that most nests are placed, but these are factors that need to be further investigated with regards to the species concerned. It has been shown in several studies that the effects of agricultural intensification affects farmland specialists (Donald *et al.* 2001) and habitat generalists if they feed in farmland and especially if they are specialist seed eaters, e.g. Linnet *Carduelis cannabina* (Hewson and Noble 2009, Reif *et al.* 2011). The only arable HiUFB species that was not declining in the long term period and/or the most recent short term period was the Barn Swallow *Hirundo rustica,* which does not nest in fields. The remainder of the ground-nesting species with less affiliation to arable habitat were declining and all eight ground-nesting species of the 41 FB also showed significant declines in the long term and/or the most recent period which underlines the need for further research to uncover the reasons for these patterns. Van Turnhout *et al.* (2010) also found ground-nesting species to be declining in the Netherlands, although Reif *et al.* (2010) found no general relationship between species' nest sites and their population trends in the Czech Republic.

Effects of migratory behaviour

Although we investigated the alternative hypothesis that it could be factors outside the Danish farmland landscape that could be affecting the status of populations, and despite the fact that the three species with the largest decline are African migrants, there was little evidence that long or short distance migrants were suffering more adverse population trends than sedentary birds (confirmed by Vickery *et al.* 2014). This suggests the declines are somehow mainly connected to factors operating within the Danish agricultural landscape. This seems to be the case for the Whinchat, based on levels of unoccupied suitable wintering habitat in Africa, see Hulme and Cresswell (2012), but which is associated with low intensity grazing of marginal grasslands in Denmark, which are increasingly being abandoned or intensified.

Agricultural changes in Denmark

Farmland practices have changed drastically before and up to the start of our study period. The first and most important change that occurred in the Danish farming landscape between the early 1980s and the mid-1990s was the change from spring barley (which declined from 1.4 to 0.6 mill. hectares) to winter wheat (which increased from 0.18 to 0.7 mill. hectares) which undoubtedly affected many farmland specialist bird species at the time (see Figure 1 in Fox 2004). However, since then, the most marked changes in the Danish farming landscape have been: (i) the 50% increase in the area of rotationally managed grassland and clover since 2004, especially after set-aside was removed from the Danish farmland landscape after 2008, (ii) the upsurge in rape cultivation and especially (iii) the 15-fold increase in the area of maize cultivated (Danmarks Statistik 2016; Appendix S2 in the Supplementary Materials). Between 1993 and 2008, 150,000–200,000 ha of land were taken out of production as set-aside. Although some authors suggest very little biodiversity benefit from such land abandonment without set management goals (e.g. Sotherton 1998, Sotherton *et al.* 1994), in Ireland, non-rotational set-aside attracted many birds species, in particular Skylark and Meadow Pipit, at densities much higher than adjacent agricultural fields (Bracken and Bolger 2006). In the UK rotational set-aside was equally effective at attracting higher densities and species diversity of birds in summer compared to adjacent cultivated fields (Henderson *et al.* 2000a, 2000b), including those species showing declines in Danish farmland, Grey Partridge, Skylark, Linnet and Yellowhammer *Emberiza citrinella* (e.g. Buckingham *et al.* 1999). Hence, it seems likely that loss of set-aside in 2008 from the Danish agricultural landscape could have contributed to the declines of some key species since that time. Finally, the most dramatic and ongoing change in the agricultural landscape since the millennium has been the increase in the areas of land cultivated for maize, which have increased from 50,000 ha in 2000 to c.180,000 ha in 2015 (Appendix S2). Maize generally grows too late and develops above ground biomass too densely to support breeding bird species of any kind in Europe (e.g. Engel *et al.* 2012, Sauerbrei *et al.* 2014). Hence, one urgent line of enquiry is to better understand the effects of maize cultivation on breeding birds across Denmark and the consequences for its continued spread in the future.

Although the combination of changes in cropping (cereals, maize and rape) could have contributed to the long-term declines in specialist farmland bird populations, it is not easy to assign specific declines in farmland birds to one single parameter, especially when changes in crop area are spread over many years of gradual change. Reif *et al.* (2008) suggests that we should analyse patterns at a finer scale than the classical broad habitat classes such as "farmland", "forest" etc. to understand the direct reasons behind general declines because habitat association is a continuous rather than categorical variable. There is no doubt we need to understand more about how individual species exploit very specific crops and biotopes and in what ways during the course of the annual avian and agricultural cycle, not least because with a single habitat the same change can adversely affect one species whilst benefitting another.

Achieving the 2020 goal

We now have good knowledge about the trends for each of the common birds in Denmark and we witness a general major decline in avian farmland specialists, which raises two questions. Firstly, do we know what is needed to identify the reasons behind the declines in a way that help to restore the different species to more favourable conservation status? Secondly, does Danish society care enough about these facts to be willing to try to improve the situation for the farmland birds? The key questions here relate to (i) What are the species-specific reasons for declines? (ii) What can we do in practical terms to reverse these trends? (iii) What are the costs of these actions to farmers, society and food security? (iv) Is this a price society is willing to pay? But before we can answer these questions, we will need studies focussed on the key declining species throughout the annual cycle in the Danish farmland landscape as undertaken elsewhere in order to understand their breeding biology and the reasons for the specific declines among farmland species.

Conclusions

This study shows that farmland specialists in Denmark are in decline and most problems are associated with those that nest on the ground which are showing the worst declines. There was also weak support for species associated with arable agriculture are suffering more than those on grazing areas, but species are suffering in both agricultural landscapes. This suggests that species specific studies are needed to understand the changes in abundance of single species in relation to changing patterns of agriculture and especially arable farming in time and space. Such knowledge will be essential if we hope to reverse changes in declining farmland bird populations before 2020 through evidence-based conservation interventions and targeted conservation management actions.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270916000654

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PAPER 3

REGIONAL TRENDS AMONGST DANISH SPECIALIST FARMLAND BREEDING BIRDS

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Photo: Erik Borch

Regional trends amongst Danish specialist farmland breeding birds

HENNING HELDBJERG & ANTHONY D. FOX

(Med et dansk resumé: Regionale bestandstendenser for danske ynglefuglearter specialiseret i landbrugsområder)

Abstract The mean rates of change in annual abundance for 16 farmland specialist breeding bird species based on point counts from three regions of Denmark (West, Central and East) during 1987-2015 inclusive were analysed to see if grassland and arable specialists were showing regional changes that could be related to their respective specializations. Generally, few species showed differences in regional population trends, despite the increasing concentration of mixed (mainly pastoral) agriculture in the West and predominantly arable cultivation in the East. Most grassland and arable specialists were declining in all regions. Only Mew Gull *Larus canus* showed consistent increases in all regions, Western Marsh Harrier *Circus aeruginosus* and Common Whitethroat *Sylvia communis* showed increases in the East and West while Barn Swallow *Hirundo rustica* showed little change in abundance anywhere during the period. Corn Bunting *Emberiza calandra* showed significant declines in the East of Denmark in contrast to stable trends in the Central and Western regions, but was declining everywhere since 2003. The results underline the need to understand how individual farmland species exploit specific crops and micro-biotopes as well as the combination of different crops.

Introduction

The European Commission has undertaken to halt the loss of biodiversity and ecosystem services throughout the European Union (EU) and where possible reinstate previous losses before 2020 (European Commission 2011). The reformed EU Common Agricultural Policy for 2014-2020 also aims to reduce biodiversity loss, although it has been stated that it comprises 'such diluted environmental prescriptions that they are unlikely to benefit biodiversity' (Pe'er *et al.* 2014). More than 60% (c. 27 000 km^2) of Denmark's total surface area is cultivated, making it the most intensively farmed landscape in Europe (Danmarks Statistik 2009, FAOSTAT 2016). Most of the cultivated areas are given over to winter wheat, grass ley and spring barley, although increasing areas produce maize and oilseed rape (Levin & Normander 2008, Brink & Jensen 2012). Given such a high proportion of the land surface is cultivated, farmland contributes disproportionately to maintaining overall biological diversity in Denmark.

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Birds are highly mobile and dispersive, features which make them good indicators of overall habitat quality and disturbance, as they often show rapid and sensitive responses to human-induced changes in their immediate environment. Birds are also well studied and, especially for the commoner species, there exist long term time-series on their distribution and abundance across much of Europe (Gregory & van Strien 2010). As a result, changes in farmland bird populations have come to play an important role in showing the effects of agricultural intensification on wider countryside nature conservation interest, including Denmark where common birds are a conspicuous and well monitored element of Danish biodiversity (e.g. Fox 2004, Eskildsen *et al.* 2013).

A previous analysis of the status and trends of farmland birds in Denmark suggested that, at least some species (e.g. Corn Bunting *Emberiza calandra*) showed more favourable conservation status than was the case in other western European countries, for example Great Britain (Fox 2004). However, more recent analyses based on the BirdLife Denmark's Common Bird Monitoring (CBM) confirm that 16 specialist farmland bird species in Denmark are showing the most rapid declines among 102 common birds associated with a range of other habitats (Heldbjerg *et al.* in print). This new analysis brings into sharp focus the effects that contemporary changes in the Danish agricultural landscape are having on the breeding birds of the country, especially those that are restricted to reproduction in agricultural landscapes. This suggests that current changes in agricultural practice are likely to be affecting bird populations in Denmark. We need to understand what changes in farming that have affected these species and how we can find mechanisms to reduce such adverse effects on their number and distribution.

One way to study this is to adopt a comparative approach to contrast different landscapes to see if specialist farmland bird populations are responding in different ways. Danish farmland can be broadly divided into two major predominant landscape components, an arable type (where tillage predominates, especially autumn sown wheat and rape, as well as spring sown barley) and a mixed farming type (also including permanent, and increasingly, rotational grassland; Brink & Jensen 2012). Since the 1980s, mixed farming has primarily been practiced in the west of Denmark, whilst a more uniform and homogeneous arable practice dominates the landscape in the east (Reenberg 1988). Agricultural intensification has been a feature of both the arable and mixed farming sectors; for instance, arable cropping patterns, the degree of mechanization, use of pesticides and fertilisers have changed over time, often with adverse effects on farmland bird populations in Denmark (Fox 2004) as elsewhere in Europe (Donald *et al.* 2001) and across continents (Reif 2013). Equally, pastoral agriculture has seen increasing numbers of cattle kept indoors throughout the year, a shift from grass and fodder beet to maize and a reduction in permanent pasture, while rotational grassland has increased in extent (Heldbjerg *et al.* 2016, Statistikbanken 2016).

Because we may expect certain specialist farmland birds in Denmark to be either closely associated with features of arable or pastoral agriculture, these patterns offer opportunities to compare regional changes in specialist farmland bird populations to better understand factors affecting their abundance. Hence, we might expect loss of pasture and grazing animals in East to result in a decline for Common Starlings *Sturnus vulgaris*, whereas we would expect a stable trend in West (see Heldbjerg *et al.* 2016). Equally, we may expect a species such as Corn Bunting to be declining in East as a result of intensification of arable agriculture, but show stable trends in West where there remains much spring barley and grassland which are known to be favoured by this species (Fox & Heldbjerg 2008). For this reason, in this analysis, we use data from the BirdLife Denmark's CBM programme (based upon point count census counts undertaken since 1976) to compare trends of specialist farmland species in three Danish regions from west to east to see if we can gain insight from regional patterns in contrasting species.

Materials and methods

Data collection

The CBM programme is based upon a point count census of breeding birds that started in 1976 and is conducted annually within the period 1 May – 15 June. Each route consists of 10-20 marked 'points'. At each point, all birds seen and heard, regardless of distance from the observer, are registered and recorded in a 5-minute observation window (Heldbjerg 2005). All points counted in at least two years by the same observer, at the same time of year (± 7 days), same time of day (± 30 min.) and under comparable weather conditions are included in this analysis. We restricted the time series to 1987-2015 because of the rapid increase in participants in the early years, to ensure robust and comparable data with an equal coverage in all years for the more detailed analysis (Nyegaard *et al.* 2015). Bird species abundance has been sampled annually at > 300 routes since 1987 (mean ± 95% CI 1987-2015 = 340 ± 10, median 346).

Habitats surrounding each count point are ascribed in quarters to one or more of nine predefined habitat categories (coniferous woodland, deciduous woodland, arable, grassland, heath, dunes/shore, bog/marsh, lake and urban; Heldbjerg 2005, Larsen *et al.* 2011, Eskildsen *et al.* 2013). On this basis, 13.2% of points came from purely arable landscapes and 1.5% from permanent meadows/grassland plots; however, the majority of the surveyed plots are from 'mixed' habitats including extensive areas of farmland, such that a total of 27.8% and 11.1% of all habitat registrations are from arable habitat and grasslands, respectively.

Defining species relative habitat use and comparing across habitats

Many species are habitat generalists in the sense that they are not exclusively found in only one of the nine habitat types. We defined species' habitat associations by their Relative Habitat Use (RHU), calculated as the abundance of a given species in a particular habitat relative to the mean abundance of that species in all other habitats. The number of individuals observed at each point was weighted by the proportion of the given habitat at the point. The sum of the weighted number of individuals of each species in a particular habitat could then be used to calculate a RHU value from the following equation:

$$RHU = \frac{n_i/p_i}{(N-n_i)/(P-p_i)}$$

where n_i is the number of individuals in the i^{th} habitat, p_i is the total number of i-habitat points, adjusted according to proportional habitat share at each point, N is the total number of individuals and P is the total number of points. We use the term Farmland as a combination of arable and grassland habitats. For full details and examples, see Fig. 1 in Larsen *et al.* (2011) and Eskildsen *et al.* (2013).

Heldbjerg *et al.* (in print) used values of RHU > 2 ('high use') to indicate an abundance in the specified habitat at least twice the mean abundance in all other habitats, to select farmland habitat specialists (but omitted those with a Danish breeding population of less than 1000 pairs and species for which less than 50 individuals were registered per year (Heldbjerg *et al.* in print). In this way, we restricted the analysis to only covering 16 common farmland specialists for which there existed high-quality data. In this analysis, we also extend this method to define arable and grassland specialists using the same approach. If the ratio of a species' RHU in arable to that in grassland exceeded 1.5, we considered it an arable species and *vice versa.* Species with 0.67 < Ratio < 1.5 were assigned as farmland generalists as they showed no specialization for arable or grassland (see Tab. 1). Since there was a high degree of consistency between the population trends calculated using habitat-specific point counts and using all point counts irrespective of habitat (Eskildsen *et al.* 2013), we used data from all point counts relating to a given species, not only those from points in their primary habitat.

Species, indices and indicators

In this study, we focus only on avian species associated with farmland, arable and grassland habitats. The habitat defined as 'arable' consists of arable areas such as cultivated fields and fallow land, 'grassland' included meadows, salt marshes, pastures, dry grassland and other grass-dominated areas with or without scattered trees and/or shrubs. The common species names and systematic order follows Fjeldså *et al.* (2016).

Indices and trends were calculated by fitting a log linear regression model to point count data with Poisson error terms using the software TRends and Indices for Monitoring data (TRIM; Pannekoek & van Strien 2004), where the observations at a given site in a given year is assumed to be the result of a site and a year effect. The programme also estimates the dispersion factor, correcting for over-dispersion where this occurs, and takes account of serial correlation between counts at the same site in different years. Standard errors for the indices are generated based on the assumption that the variance is proportional to the mean, and a pattern of serial correlation which declines exponentially with time between counts (Pannekoek & van Strien 2004). The TRIM assessment of rate of change was used in this study to generate species trends, taking the standard errors into account. Trends for the 16 species were calculated for three regions of Denmark representing a mixed farming (with grassland) area (West – west coastal counties; based on 437 routes monitored one or more years) and an arable cultivated area (East – Zealand and Bornholm; 605 routes) plus an intermediate area (Central – eastern coastal parts of Jutland and Funen; 358 routes; Fig. 1).

Results

The mean rates of change in annual abundance (± SE) for the selected 16 farmland specialist bird species in the three regions of Denmark from 1987-2015 inclusive are shown in Tab. 1. The majority of the species-regions combinations are declining. The Mew Gull *Larus canus* is the only species significantly increasing in all three regions, where it forages in, but generally does not specifically nest in, farmland habitats. Western Marsh Harrier *Circus aeruginosus* and Common Whitethroat *Sylvia communis* showed increases in East and West, but no significant change in Central, while Marsh Warbler *Acrocephalus palustris* showed a significant increase in West.

Generally, few species showed radical differences in

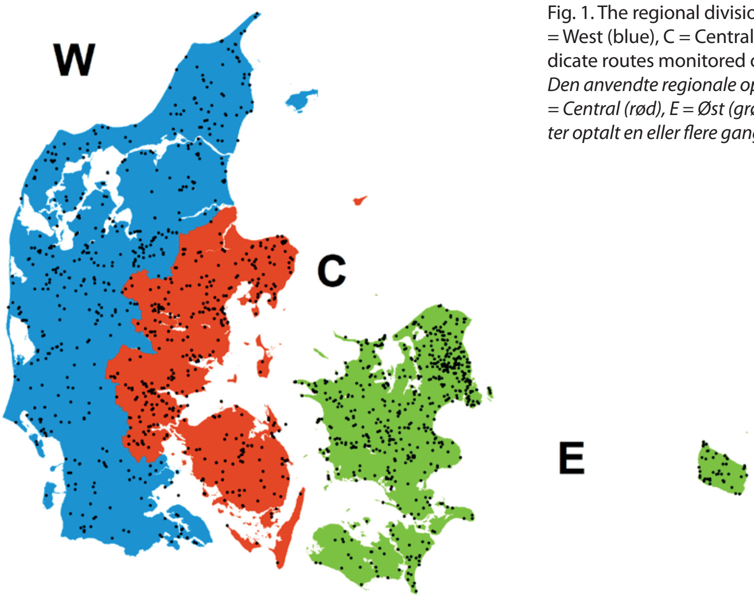

Fig. 1. The regional divisions of Denmark used in this study. W = West (blue), C = Central (red), E = East (green). Black dots indicate routes monitored one or more years during 1987-2015.
Den anvendte regionale opdeling i dette studie. W = Vest (blå), C = Central (rød), E = Øst (grøn). Sorte prikker viser punkttællingsruter optalt en eller flere gange i perioden 1987-2015.

Tab. 1. The 16 Danish farmland specialist species with Relative Habitat Use (RHU) > 2 showing the classification of specialization, the respective RHU values for arable and grassland habitats, the mean number of individuals recorded per year and per region (W = West, C = Central and E = East) of each species (= N) and trends (± 95% CI; **bold** text: p < 0.05, *italics*: p < 0.01)). Species with a ratio of arable RHU to that in grassland which exceeded 1.5 were considered an arable species (identified as A) and *vice versa* (G indicates grassland specialist); species with 0.67 < RHU-ratio < 1.5 we assigned as farmland specialists (F) as they showed no specialization for arable or grassland.
De 16 danske fuglearter specialiserede i det danske landbrugsland med en Relativ Habitatudnyttelse (RHU; se teksten) på > 2, der endvidere viser specialiserings-klassifikation, RHU-værdier i henholdsvis agerland og enge samt det gennemsnitlige antal registrerede fugle per år og region (W = Vest, C = Central and E = Øst) for hver art (= N) og tendens (± 95% CI; ***fed*** *text: p < 0.05, kursiveret: p < 0.01). Arter med en ratio mellem agerlands-RHU og enge-RHU større end 1,5 anses som agerlandsfugle (A), arter med en ratio mindre end 0,67 som engfugle (G) og de resterende som landbrugslandsfugle (0,67 < RHU-ratio < 1.5; F), da de ikke udviser specialisering for hverken agerland eller enge.*

Species ***Art***	**Class.**	**RHU value** ***RHU-værdi***			**N**			**Trend** ***Tendens***		
		F	A	G	W	C	E	W	C	E
Grey Partridge *Agerhøne*	A	5.2	4.2	1.6	25	25	36	***-5.80 ± 1.28***	***-4.12 ± 1.51***	***-2.61 ± 0.89***
Eurasian Oystercatcher *Strandskade*	G	3.1	0.7	8.6	101	111	201	**-1.96 ± 0.86**	***-2.68 ± 0.91***	***-4.28 ± 0.43***
Northern Lapwing *Vibe*	F	5.2	2.6	3.8	491	356	529	***-3.63 ± 0.47***	***-4.22 ± 0.52***	***-1.92 ± 0.35***
Common Redshank *Rødben*	G	2.6	0.5	9.0	104	31	100	**-3.21 ± 1.36**	***-4.71 ± 1.41***	-0.12 ± 0.54
Mew Gull *Stormmåge*	F	2.3	2.0	1.6	375	420	669	***3.41 ± 0.75***	***3.22 ± 0.83***	***2.42 ± 0.52***
Western Marsh Harrier *Rørhøg*	G	2.5	1.7	2.6	16	16	31	***4.80 ± 1.68***	0.79 ± 1.33	***3.85 ± 0.89***
Common Kestrel *Tårnfalk*	F	2.8	2.1	2.1	32	32	41	0.48 ± 0.85	***-2.54 ± 0.85***	**-1.51 ± 0.69**
Eurasian Sky Lark *Sanglærke*	A	5.9	5.6	1.0	1604	1220	1588	***-3.10 ± 0.17***	***-2.78 ± 0.21***	***-2.19 ± 0.16***
Marsh Warbler *Kærsanger*	G	3.2	0.4	4.3	50	96	108	**1.36 ± 0.68**	-0.06 ± 0.49	-0.22 ± 0.39
Barn Swallow *Landsvale*	A	2.8	2.5	1.6	1249	1141	1283	-0.25 ± 0.23	0.16 ± 0.33	0.54 ± 0.28
Common Whitethroat *Tornsanger*	F	2.3	1.9	1.6	634	558	780	**0.40 ± 0.19**	0.43 ± 0.24	***0.78 ± 0.18***
Common Starling *Stær*	F	2.3	1.8	1.9	2012	1405	2160	**-1.39 ± 0.34**	***-4.40 ± 0.42***	***-2.39 ± 0.30***
Whinchat *Bynkefugl*	G	2.8	1.2	4.8	58	14	15	***-6.21 ± 0.71***	-1.12 ± 1.70	***-4.57 ± 1.18***
Meadow Pipit *Engpiber*	G	3.1	0.7	8.3	118	24	49	**-2.79 ± 0.76**	0.85 ± 1.41	**-4.70 ± 0.81**
Yellow Wagtail *Gul Vipstjert*	G	3.7	2.0	3.4	21	NA	20	-2.35 ± 2.15	NA	**-7.30 ± 1.32**
Corn Bunting *Bomlærke*	A	11.3	11.0	0.6	196	65	25	0.56 ± 0.41	1.60 ± 1.67	***-6.88 ± 1.78***

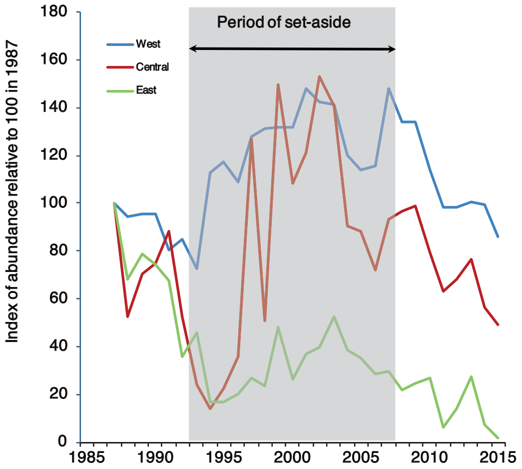

Fig. 2. Indices (Index 100 = 1987) for Corn Bunting *Emberiza calandra* in three regions of Denmark. The set-aside period is indicated by grey shading.
Indeks (Indeks 100 = 1987) for Bomlærke i tre regioner af Danmark. Perioden med brakarealer er vist med grå skygge.

population trends in the different regions of Denmark, despite the increasing concentration of mixed farmland with pastoral agriculture in the west and arable cultivation in the east. The Corn Bunting showed an overall significant decline in the East of Denmark in contrast to a stable trend in the Central and West regions. This species shows quite complex differences in changes in abundance over time and between regions, but basically declined everywhere until the introduction of set-aside in 1993 (Fig. 2). Subsequently, numbers recovered in the West and Central Regions and to a lesser extent in the East, but following the cessation of set-aside in 2007, it has declined in abundance throughout Denmark (Fig. 2); although it seems that it was starting to decline in all regions already from 2003. Barn Swallow *Hirundo rustica* showed no significant trend in any region. The Common Kestrel *Falco tinnunculus* showed declines in the Central and East but was stable in the West. The three wader species, Eurasian Oystercatcher *Haematopus ostralegus*, Northern Lapwing *Vanellus vanellus* and Common Redshank *Tringa totanus* all showed declines across regions (except there was no significant change for Redshank in the East).

Besides the Corn Bunting, the other arable specialists showed similar change across all regions, e.g. Grey Partridge *Perdix perdix* and Eurasian Sky Lark *Alauda arvensis* showing consistent decline. Grassland specialists generally showed declines in all regions, except for Western Marsh Harrier (mentioned above), Marsh Warbler (increasing in West, unchanged in Central and East) and Meadow Pipit *Anthus pratensis*, which was declining in East and West, but showed no change in the Central Region (perhaps due to low sample size in this Region). Common Starling (and Northern Lapwing, mentioned above) showed a consistent decline in all regions.

Discussion

Despite the marked differences between agricultural practices in the West of Denmark compared to the East (more cattle, fodder crops and pasture, and less cereal and other crops in West than in East), we found little convincing evidence for differences between trends in farmland specialist bird populations between regions, suggesting that the general decline of farmland birds is most likely caused by the overall intensification in agriculture. The only major exception was Corn Bunting, which showed unchanged abundance in Central and West, but suffered a significant decline in the East as hypothesized. Although very much an arable specialist, the Corn Bunting requires a mosaic farmland landscape comprising arable fields, but including some grassland (Fox & Heldbjerg, 2008), where it benefits from delayed mowing (Perkins *et al.* 2013). As a result, it especially has benefitted from the increase in the growth of seed grass in Denmark, where single species crops of grass are commercially grown for the production of seed, forming dense grass swards that provide dense cover and are harvested relatively late (late July/early August) compared to hay and silage (A.D. Fox unpubl.). The Corn Bunting has shown major distributional change and numerical decline within Denmark (especially in the East) between the 1970s and 1990s (Grell 1998). These changes continued to the present, presumably due to the continued intensification of arable agriculture in the East region that increasingly removes grassland from the increasingly homogenous farmland landscape. Although the species may have benefitted from the period of set-aside in all regions of Denmark during 1993-2007 inclusive, it shows parallel declines in abundance since 2003, i.e. before the cessation of the set-aside period (Fig. 2), suggesting that also other factors were contributing to the decline.

The Danish population of Mew Gull, the only species significantly increasing in all regions, follows the pattern throughout much of Northern Europe, with increases in the last part of the 20th century followed by more stable trends in more recent times (Birdlife International 2016), indicating that the increase in Denmark probably is related to factors acting on the population at broad spatial scales.

Unfortunately, for most of the farmland specialists featured here, there seems to be continued declines

The Corn Bunting is the only species for which an effect of a higher degree of agricultural intensification in the eastern part of Denmark than in the central and western parts was found. Most other grassland and arable specialists showed similar declines all over the country. Photo: Albert Steen-Hansen.
Bomlærken var den eneste landbrugsart, der gik mere tilbage i Østdanmark end længere vestpå i landet.

amongst species regardless of their association with arable, grassland or general farmland landscapes and that these declines are largely common across regions. This seems to suggest that the adverse changes that are occurring are associated with the increasing intensification of arable as well as pastoral agriculture throughout the country, regardless of whether these are pressures on grassland in predominantly arable areas or tillage practices in predominantly livestock rearing areas.

Because changes in agriculture tend to be gradual, but on a major spatial scale, it is very difficult to understand how they specifically impinge upon breeding bird populations. This is especially the case here, where in spite of major differences in agriculture in different parts of Denmark, there is little sign of contrasting regional trends from which to gain insight about specific impacts of specific change. Farmland practices have changed drastically in Denmark before and during our study period. The first and most important change that occurred in the Danish farming landscape between the early 1980s and the mid-1990s was the change from spring barley (which declined from 1.4 to 0.6 mill. ha) to winter wheat (which increased from 0.18 to 0.7 mill. ha) which undoubtedly affected a number of farmland specialist species at the time (Fox 2004). Subsequently, 150 000-200 000 ha of land were taken out of production as set-aside mostly between 1993 and 2007. Analysis carried out elsewhere suggested very little biodiversity benefit from such land abandonment (e.g. Sotherton 1998). However, effectively managed set-aside with specific management goals has the potential to deliver resource-rich habitat for declining bird species if such management prescriptions form part of its implementation (Sotherton *et al.* 1994). The Corn Bunting population increased from the first year of the set-aside period and has declined since this scheme stopped again. Although field-breeding species such as Corn Bunting and Eurasian Sky Lark may have benefitted locally from the provision of such set-aside, there is generally little evidence that this major change in land use had a major impact on bird populations, although this has never been adequately studied. The last most substantial change in Danish agriculture has occurred after the millennium and is ongoing, namely the increase in the areas of land cultivated for oilseed rape and maize, which have increased from 70 000 and 50 000 ha, respectively, in 2000 to c. 180 000 ha of each in 2015 (Statistikbanken 2016).

In the light of these recent increases in rape and maize, it is interesting to consider the effect of these changes on the bird community. Common Whitethroats prefer rape to other crops in Denmark (Petersen 1996), and it is interesting to speculate whether this species has benefitted from rape becoming increasingly cultivated throughout Denmark, especially in the east and southeast. The Common Whitethroat showed significant increase in East and West while showing a similar tendency (although failing to attain statistical significance) in Central Denmark. This is a species whose abundance crashed across western Europe between the breeding seasons in 1968 and 1969 (Winstanley *et al.* 1974), probably including Denmark (see Berthold 1973), and which has shown relatively little change in abundance since that time (e.g. PECBMS 2014). Results from the Danish CBM suggest a gradual increase in abundance, especially since the mid-1990s. It is important to understand whether such a crop is valuable as breeding habitat, in terms of its ability to support reproductive success comparable or higher than other habitats. Despite the increase in Common Whitethroat abundance at the national level, it is also important to understand, whether rape functions as an ecological trap (by attracting breeding birds from other habitats but failing to support the production of young), as well as the potential threat this poses to the species because of its exposure to agro-chemicals used in relation to this particular crop. Hence, this relationship should be investigated in more detail given that very few other farmland bird specialist species seem to be adapting in a positive way to changes in the contemporary agricultural landscape of Northwest Europe.

Maize generally grows too late and develops above ground biomass too densely to support breeding bird species of any kind in Europe (e.g. Engel *et al.* 2012, Sauerbrei *et al.* 2014), so the 15-fold increase in area of this crop since the 1980s has likely had a dramatic effect on local breeding birds. Unfortunately, we are not aware of any specific Danish studies of the breeding birds of maize fields and this remains an urgent research priority. Hence, one urgent line of enquiry is to better understand the effects of maize and oilseed rape cultivation on breeding birds across Denmark and the consequences for its continued spread in the future.

Although the combination of changes in cropping (cereals, maize and oilseed rape) could have contributed to the long term declines in specialist farmland bird populations, there is no obvious parameter that could account for the overall patterns reported here. Heldbjerg *et al.* (in print) showed that ground nesting farmland specialist species were showing greater rates of decline than those that nested elsewhere, hinting that the changes were in some way linked to nest site as well as foraging areas during the brood rearing period. This supports the assertion of Reif *et al.* (2008) that we should use a finer scale than the classical broad habitat classes as "farmland", "forest" etc. to understand the reasons behind the general decline because habitat is a continuous rather than a categorical variable. In this respect, we need to better understand the effects of the earlier and more vigorous growth of crops (especially early in the season), the increasingly effective weed and insect control, which denies food for birds and the increasing trend to exploit every last piece of productive land that increasingly removes less intensively cultivated biotopes from the increasing homogenous farming landscape. We urgently need to understand far more about how individual farmland species exploit very specific crops and micro-biotopes and the way mosaics of these features are arranged in the landscape during the course of the annual avian and agricultural cycle, not least because within a single habitat the same change can adversely affect one species negatively whilst benefitting another.

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Resumé

Regionale bestandstendenser for danske ynglefuglearter specialiseret i landbrugsområder

Europakommissionen har besluttet at standse tabet af biodiversitet før 2020. Over 60 % af Danmarks areal er landbrugsjord, og dermed er Danmark det mest intensivt dyrkede land i Europa. De arealmæssigt væsentligste afgrøder er vinterhvede, vårbyg, græs og grøntfoder og i de senere år også majs og raps. For at kunne følge udviklingen af biodiversitet i landbrugslandet udgør fuglene en væsentlig gruppe som indikator. En ny undersøgelse af udviklingen for de almindelige danske ynglefugle viser, at det er fuglene i landbrugslandet, der udviser de største bestandsnedgange.

I denne artikel undersøger vi, om udviklingen for de 16 mest specialiserede landbrugslands-arter har været ensartet på tværs af landet. Termen Landbrugsland anvendes som en fælles betegnelse for habitaterne Eng og Agerland. Sammenligningen er baseret på bestandsindeks på baggrund af DOF's punkttællinger, men kun for perioden 1987-2015, da antallet af optalte ruter kun i denne periode vurderes at være tilstrækkeligt stort til at kunne opdele landet i de tre regioner, Vest, Central og Øst (Fig. 1). Den generelle udvikling i landbruget i det seneste halve århundrede har medført, at mælkeproduktionen er flyttet mod vest, så man her har flere køer og mere græs end i den østlige del, hvor der primært er planteproduktion. Udviklingen i begge typer har været markant, og det er vist, at det intensiverede landbrug har haft en betydelig effekt på fuglelivet i Danmark og i Europa generelt.

Vi har endvidere underopdelt de 16 landbrugslands-specialister i specialister i Enge hhv. Agerland eller arter, der anvender begge habitater i Landbrugsland ligeligt (Tab. 1). Til dette formål er anvendt punkttællingernes naturtype-information til beregning af arternes RHU (Relative Habitatudnyttelse), der udtrykker, hvor ofte en art registreres i en naturtype i forhold til i de øvrige.

Resultaterne viser, at langt hovedparten af arterne er i tilbagegang (Tab. 1). Blot tre arter, Rørhøg, Stormmåge og Tornsanger er i generel fremgang på tværs af landet, hvoraf de to førstnævnte arter fouragerer, men ikke yngler i landbrugslandet.

Generelt er der ret lille forskel på arternes bestandsudvikling i de forskellige regioner af landet, og vi kan konkludere, at trods forskellig udvikling i landbrugspraksis i de tre regioner, ses kun få regionale forskelle i arternes bestandsudvikling. Størst forskel ses hos Bomlærke med en markant signifikant tilbagegang i Øst i modsætning til en stabil udvikling i de to øvrige regioner. I alle regioner sås en tilbagegang frem til 1993, hvor brakordningen introduceredes. Dette synes at have haft en positiv effekt på arten, da der sås fremgang i alle regioner herefter. Tilsvarende sås en tilbagegang i alle regioner fra 2003, dvs. nogle år før brakordningen ophørte i 2007 (Fig. 2).

Tornsangeren er generelt i fremgang (landbrugslands-art), mens Landsvalen ikke udviser nogen signifikant tendens i nogen regioner. Tårnfalken er i tilbagegang i Central og Øst og stabil i Vest. De tre vadefuglearter, Strandskade, Vibe og Rødben er i generel tilbagegang i hele landet.

Ud over Bomlærke viser de øvrige agerlandsspecialister en ensartet udvikling på tværs af landet. Fx er både Agerhøne og Sanglærke i tilbagegang i alle regioner. Eng-arterne er generelt i tilbagegang i alle regioner, men fremgang ses dog for Kærsanger i Vest. Landbrugslandsarterne udviser en tilsvarende udvikling på tværs af regionerne med Vibe og Stær i signifikant tilbagegang i alle regioner.

Den generelle bestandsnedgang hos arter specialiseret til landbrugslandet, hvad enten de forekommer mest i eng eller

The Whinchat was among the farmland species showing the most pronounced decreases. Photo: John Larsen.
Bynkefuglen er gået stærkt tilbage i landbrugslandet.

agerland eller ligeligt i begge, indikerer, at den intensive drift af etårige afgrøder såvel som af enge har en negativ effekt på fuglelivet. De væsentligste ændringer i arealet med etårige afgrøder i undersøgelsesperioden er primært ændringerne i arealet fra vårbyg til vinterhvede, brakarealet, der blev taget ud af driften i 1993-2007 og senest den øgede produktion af raps og majs.

De behandlede arter har stort set kun det tilfælles, at de er specialister i landbrugslandet. Hvis vi skal forstå, hvad der forklarer bestandsudviklingen for den enkelte art og hvordan, de hver især bliver påvirket af de ændringer, der sker i afgrødevalg og driftsformer, er vi nødt til at arbejde mere detaljeret med fokus på de enkelte arter og i de forskellige landbrugstyper.

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PAPER 4

THE DECLINE OF THE STARLING *STURNUS VULGARIS* IN DENMARK IS RELATED TO CHANGES IN GRASSLAND EXTENT AND INTENSITY OF CATTLE GRAZING

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The decline of the Starling *Sturnus vulgaris* in Denmark is related to changes in grassland extent and intensity of cattle grazing

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ABSTRACT

The Danish breeding Starling population declined at a mean annual rate of −2.24% ± 0.39 (95% CI) during 1976–2015 (a 60% decline overall). Starling density in the mid-1990s was positively correlated with dairy cattle abundance in 13 local areas. Regional declines in Starling abundance between 2001 and 2014 were positively correlated with loss of high intensity grazing pressure by dairy cattle, as more animal husbandry moved indoors. The long-term decline in national Starling abundance was positively correlated with the long term numbers of dairy cattle grazing outdoors. This study therefore confirms that not only does the extent of available grassland to breeding Starlings affect their relative abundance, but that the intensity of grazing of these grasslands is also of importance.

1. Introduction

Studies of farmland birds have tended to focus on species breeding and/or foraging on arable land (e.g. Robinson and Sutherland, 2002; Robinson et al., 2001). The annual cycle of tillage creates a series of temporary habitat states, with ploughing, for example, exposing invertebrates, seeds and plant storage organs, drilling providing seed, plant growth offering foraging habitat and harvest again providing food from spilled grain (e.g. Robinson and Sutherland, 1999). Not surprisingly, changes in cropping and agricultural practices have had a huge impact on some birds especially seed eating species (e.g. Chamberlain et al., 2000). This has been slightly to the neglect of those common species that are dependent on pastoral systems, a majority of which are more dependent on invertebrates and with seasonal patterns of food provision and availability that do not follow the same “boom and bust” cycle that occurs in arable agriculture (Vickery et al., 2001).

Denmark is predominantly an agricultural landscape (c. 60% of total land area is farmland; Levin and Normander, 2008) which has for centuries supported large numbers of dairy cattle. As the numerically dominant form of reared livestock, dairy cow abundance, nationally and regionally, is closely related to area of managed grassland. Although beef cattle contribute to grazing numbers, dairy cattle are numerically dominant: the ratio of dairy to beef cattle changed from 1:17 in 1982–1:6 in 2013. Dairy cattle require the best managed grassland, so dairy cattle are likely to constitute the key group of livestock that most drives relationships between cattle production, farmland practices, soil invertebrate fauna and their predators.

In this case study, we focus on the effects of regional changes in Danish agriculture on the changes in distribution and abundance of the Starling *Sturnus vulgaris*, a specialist grassland invertebrate feeder and a numerous and widespread species in Denmark as well as throughout Europe. Due to its abundance and association with human habitation it is a familiar and popular bird of societal interest. However, numbers of breeding Starlings in Denmark have declined during the last 40 years (Nyegaard et al., 2015). As a farmland species often associated with grazing cattle we hypothesized that radical changes in pastoral agriculture in the same period could have contributed to the Starling decline.

In this analysis, we first determine the degree to which the Danish Starling population has declined and if there were regional changes that correlate with the changes in the extent of grassland in these areas. Since the Starling depends on short grassland as foraging habitat for provisioning their nestlings

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(Feare, 1984; Devereux et al., 2004), we sought to establish a relationship between the extent of available grassland, the number of cattle and the density of Starlings.

The total area of grassland in Denmark has changed little since 1982, with recent large increases in rotational grassland balancing similar losses in set-aside land, due to the termination of set-aside schemes in 2007/2008 (Danmarks Statistik, 2016). In this context, set-aside land comprises agricultural land, which for a period was taken out of production, typically arable tillage in Denmark, with the aim to reduce agricultural production and which was mostly left as coarse uncultivated grassland. Numbers of dairy cows have declined by >40% from 1 million in 1982–2014 but have stabilized at c. 570,000 since 2004 (Danmarks Statistik, 2016).

Traditionally, dairy farms were small and evenly distributed over the country; milking herds were set out to graze on grassland every day during the warmest half of the year. Nowadays, economies of scale have concentrated dairy herds into larger units where grass is brought to cattle, which are increasingly kept indoors throughout the year (Seges, 2015; Danmarks Statistik, 2016). These changes have brought dramatic changes to the manuring of pastoral land as urine and faecal material is no longer applied "naturally" in a heterogeneous way in time and space by the animals themselves but applied as an intensive carpet of manure spread by the farmer a few times per year.

We investigate to see if regional changes, which comprise pronounced declines in the numbers of dairy farms and cattle in the eastern parts but far lesser declines in western Denmark, have affected the availability of grassland for Starlings, and hence their breeding status in these regions. Given a strong positive relationship between these measures, we reasoned that because dairy cows (and therefore traditionally managed grasslands) have declined most in the central and eastern regions of Denmark, the declines in breeding Starlings would be most severe in those parts of the country; by contrast because numbers of dairy cows and grassland area have changed least in the western part of the country, we would expect lower rates of declines in this area. We also investigated whether there has been a change in the numbers of cattle grazing outdoors to see if the degree to which this occurred could have any detectable effect on the regional Starling trends.

2. Materials and methods

2.1. Data collection

The Danish Common Bird Monitoring (CBM) programme uses point count census data to generate population indices and trends for more than 100 common breeding bird species. The annual sampling now involves circa 370 routes across the country (mean ± CI: 282 ± 32; median 321.5 routes per year during the time series 1976–2015), monitored in the period 1. May–15. June (Nyegaard et al., 2015). Most routes consist of 20 (but always ≥10) marked 'points' at which all birds seen and heard were recorded in a 5-min observation period (Heldbjerg 2005). All routes and points were counted in at least two successive years by the same observer, at the same time of year (±7 days), same time of day (±30 min) and under good weather conditions. Altogether, observations of 225,719 Starlings are included in this study.

The habitats surrounding each point are ascribed in quarters to one or more of nine predefined basic habitat types (Coniferous, Deciduous, Arable, Grassland, Heath, Dunes/Shore, Bog/Marsh, Lake and Urban). In total 29.0% and 8.1% of all habitat registrations were from arable habitat and grassland, respectively (Heldbjerg, 2005; Larsen et al., 2011). The majority of the surveyed plots were from 'mixed' habitats.

2.2. Estimating changes in annual abundance

Indices and trends were calculated by fitting a log linear regression model to point count data with Poisson error terms using the software TRends and Indices for Monitoring data (TRIM; Pannekoek and van Strien, 2004), where the count at a given site in a given year is assumed to be the result of a site and a year effect. The programme also estimates the dispersion factor, correcting for overdispersion where this occurs, and takes account of serial correlation between counts at the same site in different years. Standard errors for the indices are generated based on the assumption that the variance is proportional to the mean, and a pattern of serial correlation, which declines exponentially with time between counts (Pannekoek and van Strien, 2004). The TRIM assessment of rate of change was used in this study to generate species trends, taking the standard errors into account.

The population changes are described by indices (the proportional percentage change in the size of the Starling population in relation to the starting value) and we are therefore only interested in the relative changes (not the absolute number) during the study period, using the additive slope provided by TRIM. Based on the 95% confidence intervals generated about these estimates, we determined which of these datasets showed trends that significantly differed from zero.

In order to compare Starling trends in different regions of the country we analysed the trends for these. The number of counted points per year was reduced when limited to regions, so relatively poor coverage in earlier years constrained us to consider only the period 1990–2015 in the regional analyses.

2.3. Regional starling breeding densities

We used Starling breeding density assessments from the Danish Bird Atlas from 1993 to 1996 (2nd Atlas; Grell 1998). We only included data collected during 10–30 May, the typical nestling period in Denmark, to avoid data from periods including post-breeding flocking behaviour. The density data were derived from Atlas point count censuses consisting of 5-min registrations mostly from 10 points, systematically dispersed within each 5 × 5 km grid square. We included all birds counted in the selected period; 4258 points on 452 routes/squares out of a total of 1602 squares (28.2%).

Since the data on the Starling density were too sparse to use based on the 98 Danish Municipalities as a unit, we amalgamated the density data into the 13 local count areas (which closely corresponded to the former Danish counties) as sampling units. We used the centre coordinate of each atlas square to aggregate all squares within local count areas.

2.4. Regional analysis

For the regional analysis, we divided the country into four regions, three almost equally large parts, West, Central and East, together with the island of Bornholm, which is geographically relatively small and distant from the others (Supplementary material Fig. 3; Table 1). Starling trends were analysed for each of these to compare the rates of decline for support for the hypothesis that the decline was more pronounced in areas with the largest decline in dairy cattle.

2.5. Agricultural statistics

We used area data on the extent of key tillage crops, grassland management types and annual cattle statistics in Denmark obtained from StatBank Denmark, the online repository for Danish agricultural statistics published annually (Danmarks Statistik, 2016). While the data for the whole of the country is provided

Table 1
The regions of Denmark used in the analysis, the total size of the regions, mean annual number of monitored point count routes (1990–2015), the population trend (mean annual percentage change (±95% CI)) of Starlings (1990–2015), the number of observed Starlings, the percentage change in numbers of dairy cows (1989–2010), the density of dairy cows (2010) and the density of high grazing pressure area (2014).

Region	Area (km^2)	N Point counts	Starling trend (%/year)	N Starlings	Cows/km^2	Cow trends (%)	HGP/km^2
West	15,585	114	−1.71 ± 0.61	65,880	21.2	−24.2	0.352
Central	17,555	99	−3.87 ± 0.82	47,338	11.8	−34.0	0.089
East	9193	102	−4.55 ± 0.73	47,472	2.7	−41.1	0.017
Bornholm	588	13	1.49 ± 1.02	10,701	10.0	−13.2	0.352

annually, data from the 98 different municipalities are only registered in selected years. We therefore used the mean of data gathered in the years 1989 and 1999 to describe the cattle and grass statistics per Municipality as close as possible to describe conditions at the time of the 1993–1996 Atlas period and the data from 2010 as reflecting the most recent situation.

We examined agricultural statistics from the 98 Municipalities, to see if there was a change in the regional extent of grassland between 1982 and 2013 and whether the available grassland was comparable with the number of dairy cattle in both periods. If the numbers of dairy cattle were to be a major driver of the production of grass in Denmark, we should expect a relationship between these two parameters in both periods.

Based on the hypothesis that Starling abundance is directly related to the extent of grazed grasslands, we related the densities of Starlings (recorded during the period of Atlas survey work in the mid-1990s) in each of Denmark's 13 local count areas to the number of dairy cows at that time in each of these areas. We also applied generalised linear models taking the standard error (SE) of the indices into account by weighting each index value by the degree of their imprecision. We weighed each point by 1/SE and tested to see if there was a linear relation between Starling breeding indices and the number of outdoor grazing dairy cattle in the periods 1982–2002 (high ratio of grazing cattle) and 2003–2015 (declining ratio of grazing cattle), incorporating the periods as covariates. For comparison we ran the same model with all cattle instead of only the grazing cattle and used ANOVA to compare the models.

2.6. Grazing pressure 2001–2014

The agricultural statistics provide information about the area of grassland but not the type, extent and grazing intensity of different grazed and ungrazed grassland areas. We therefore used agricultural registers from the Ministry of Food, Agriculture and Fisheries for 2001–2014, which provides data on the extent of grazing grassland on each farm to at least attempt to assess regional changes in grazing pressure over time.

For each year and each farm unit the number of dairy cattle units were derived. One unit of dairy cattle is defined as the number of cows, which produce 100 kg nitrogen per year. We applied animal units in order to control for races, ages and changes in animal sizes over time. In 2014, one typical Danish dairy cow corresponded to 0.85 animal units. Dairy cattle were divided into organic and conventional animals due to the large difference in number of grazing days relating to these two groups.

The number of grazing animal units (*GAU*) was calculated as:

$$GAU = AU \times \left(\frac{GDY}{DY}\right)$$

where *AU* is the number of animal units, *GDY* is the number of grazing days per year and *DY* the number of days per year (365). The mean number of days per year a dairy cow grazes on grass on a conventional farm declined from 55 to 18 days between 2002 and 2007 (O. Aaes, pers.comm. Seges 2015). This dramatic decline was primarily the result of dairy cattle being kept indoors, which is increasingly more economically favourable than grazing outdoors. For organic cattle, there is a legal requirement that they are allowed to graze for 150 days of the year (Danish AgriFish Agency 2014), so this value was entered in the calculations for organic cattle.

For each farm unit, the area of rotational grassland was extracted from the agricultural registers. Rotational grassland includes all grassland types (including clover), which are part of an annual rotation cycle, and which can potentially be grazed by dairy cattle. Permanent grassland was not included in the analysis, because most such grassland is no longer of sufficient quality to support dairy cows, which increasingly require highly intensive management to produce swards that are economically viable. Since the registers do not contain information on whether a specific grassland parcel is actually grazed or not, rotational grassland here also includes ungrazed grassland.

For each farm unit, an indicator for grazing pressure (*GP*) was calculated as follows:

$$GP = \frac{GAU}{RG}$$

where *GAU* is the number of grazing animal units and *RG* is the area of rotational grass on the farm unit. We calculated the area with different grazing pressure into four levels, 0–0.5, 0.5–0.75, 0.75–1 and ≥ 1 grazing animal units per hectare and summed these numbers per region and level for each year. The lowest level, 0–0.5 is hereafter referred to as low grazing pressure (considered to be of the very least attraction to foraging Starlings) and the highest level, ≥ 1 is considered as high grazing pressure most likely to maintain a short sward most attractive to breeding Starlings based on the literature (see Discussion). We compared the regional changes in Starling population indices to the change in area of high grazing pressure ($GP > 1$) for 2001–2014.

3. Results

3.1. National and regional starling trends

Data from the Danish point counts show that Starling abundance has continuously declined during 1976–2015, at a mean annual rate of −2.24% ± 0.39 (95% CI, Fig. 1a). This corresponds to a decline in overall abundance of nearly 60% over four decades. The Danish breeding population was estimated at 400,000–600,000 pairs in 2000 (Birdlife International 2004), so assuming that these estimates were accurate, Denmark has lost 313,000–470,000 breeding Starling pairs since the mid-1970s. Excluding Bornholm (which showed a significant positive trend), there were negative trends throughout the country, with largest declines in East and Central Denmark, 2.3–2.7 times more rapid than the decline in West (Table 1).

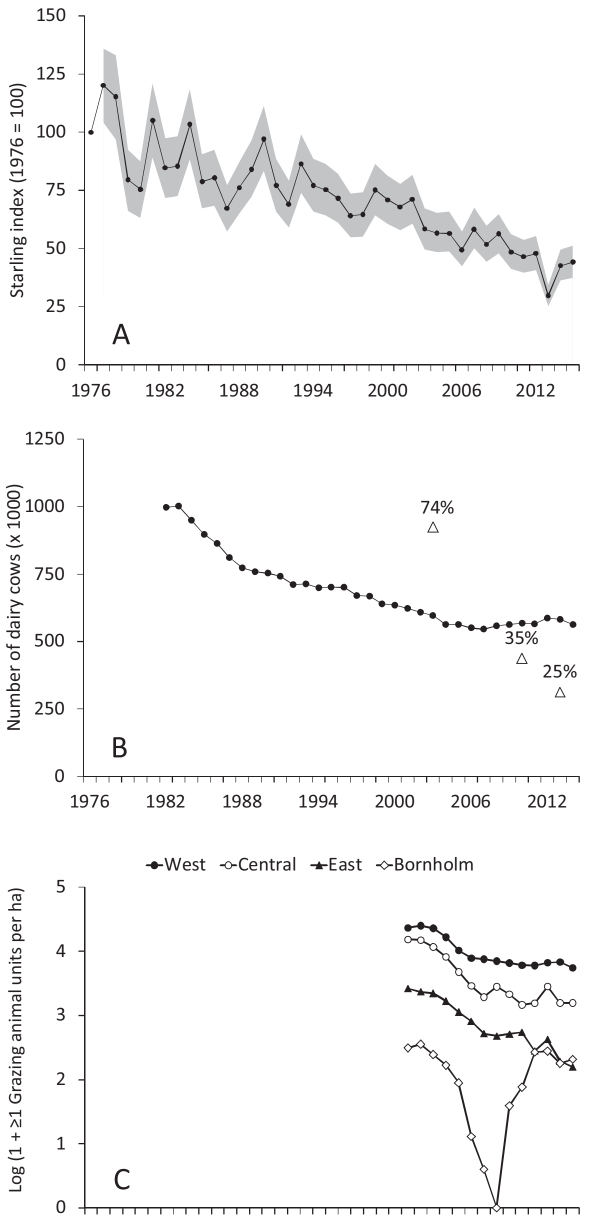

Fig. 1. A) Annual indices ± SE (shading) for the Danish population of Starling *Sturnus vulgaris* during 1976–2015 (1976 = index 100) based on breeding bird point counts. The population has significantly declined at −2.24 ± 0.39% (index ± 95% CI) per annum over the period. The noticeable decline in 2013 was a result of a prolonged winter, which affected the populations in all regions. The indices are based on data from the Danish Common Breeding Bird Monitoring programme run by DOF BirdLife Denmark. B) The annual total number of dairy cows in Denmark during 1982–2014 (circles) and the proportion of these grazing outside on grassland (triangles). C) The total areas (log transformed) of rotational grassland in the four regions of Denmark defined in Supplementary material Fig. 3 indicated by the grazing pressure of ≥1 animal units per hectare rotational grassland. West, shown by black circles declined by 76.4%, Central, open circles by 89.8%, East, grey triangles by 94.0% and Bornholm, open diamonds by 33.4%.

3.2. Cattle and grassland

The relative density of Starlings registered during the nesting period in 1993-96 was significantly positively correlated with the numbers of dairy cows in the 13 local count areas (Linear regression (±SE); $y = 2.37 \times 10^{-6} \times (\pm 7.65 \times 10^{-7}) + 0.90$, $n = 13$, $r^2 = 0.47$, $p = 0.010$; Fig. 2), with highest densities of Starlings and dairy cattle in the west of the country (Jutland; Supplementary material Fig. 3). Since there are very few cows in the Greater Copenhagen area, dominated by urban and suburban areas but also with extensive areas of farmland, and this point is an outlier, we recalculated the regression with the same data minus Greater Copenhagen area and found an improved model fit ($y = 3.08 \times 10^{-6} \times (\pm 5.64 \times 10^{-7}) + 0.71$, $n = 12$, $r^2 = 0.75$, $p \ll 0.001$; Fig. 2).

The number of dairy cattle in Denmark declined by 43.7% in 1982–2014 to c. 560,000, although this has stabilized since 2004, and the proportion of these grazing outside on the grassland declined from 74% in 2003 to 25% in 2013 (Fig. 1b).

The majority of Danish dairy cows are now raised in Jutland, mainly in the western and southern parts (Danmarks Statistik, 2014). Most of the grassland is also restricted to the same municipalities (see Supplementary material Figs. 1 and 2) and there was a very highly significant relationship between the area of grassland and the number of dairy cows in the 98 Danish municipalities, based on the mean of 1989 and 1999 (Linear regression (±SE); $y = 4.59\ (\pm 0.08) + 595$, $n = 98$, $r^2 = 0.973$, $p \ll 0.001$) as well as in 2010 ($y = 1.38\ (\pm 0.04) - 1550$, $n = 98$, $r^2 = 0.93$, $p \ll 0.001$). We therefore consider the number of dairy cattle as a good measure of available grassland throughout Denmark, and conclude that the density of dairy cattle supported by the area of grassland has clearly fallen over this time period.

3.3. Changes in numbers of cows grazing outdoors

Bornholm showed the smallest reduction in the number of dairy cows, with largest reductions in Central and East (Table 1), similar to differences in Starling trends in the four regions.

For 2001–2014 we have an indirect measurement of the number of cattle grazing on a given area of available rotational grassland in each region using the calculation of grazing pressure described in 2.6. This showed that the area of grassland subject to high grazing pressure is declining all across the country (Fig. 1c), although in the West, the relatively larger grassland area has shown a relatively less pronounced decline (Fig. 3). This region still supports a larger area of grassland subject to high grazing pressure than the other regions (4 times more than Central, 20 times more than East), while the absolute area of high grazing pressure has changed little on Bornholm. Albeit that 4 points are too few to contribute to a meaningful regression model, there was a positive correlation between the regional relative change in high grazing pressure and the Starling population trend in the four regions (Fig. 3), implying that the greater the regional reduction in the area with high grazing pressure the greater the decline in Starling abundance.

At the same time, the area of grassland with the lowest level of grazing pressure has increased in all regions. The ratio of the area with a low grazing pressure to the area with a high grazing pressure has changed from a factor of 2.8 to a factor of c. 35 indicating a clear decline in grazing pressure across the country. As could be expected due to the steady decline in both parameters, there was a highly significant correlation at the national scale between the number of dairy cows and the Starling index during 1982–2002 (Linear regression (±SE), $y = 5.1 \times 10^{-5} \times (\pm 1.5 \times 10^{-5}) + 38.8$, $n = 21$, $r2 = 0.36$; $p = 0.01$; see filled symbols, Fig. 4). Based on the only existing results from the three years of surveys undertaken between 2003 and 2014, there was a steep decline in the proportion of the dairy cows that were grazed outside (Fig. 1b). As a result, the area of actively grazed grassland fell and during this period, there was no correlation between the number of dairy cows and Starling index (Linear regression, $y = -1.36 \times 10^{-4} \times (\pm 1.73 \times 10^{-4}) + 127.34$, $n = 12$, $r^2 = 0.06$; $p = 0.45$; see the open symbols in Fig. 4). For the latter period, we also correlated the Starling index to the estimated number of grazing dairy cattle (calculated by multiplying the number of dairy cattle reported in the national

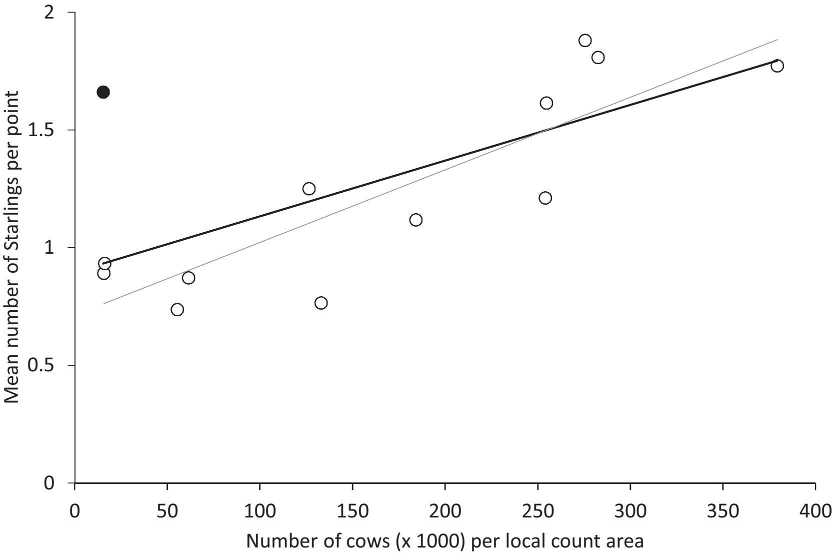

Fig. 2. Regression of the mean number of Starlings recorded per point during fieldwork for the Danish Breeding Bird Atlas in 1993–1996 (n = 4258 points on 452 routes; 13 local count areas) as a function of the mean of 1989 and 1999 numbers of dairy cows registered in the same areas. The regression is shown with (all circles, heavy line $r^2 = 0.47$) and without Copenhagen area (open circles, thin line $r^2 = 0.75$), see text for details.

statistic surveys by the percentage known to be grazing outside; see Fig. 1b). With only three years of data (diamond symbols in Fig. 4), we extended the regression using data from 1982 to 2002 (filled symbols in Fig. 4) and found a significant relationship, with the three points falling within the confidence limits of the regression model (Linear regression ± SE), $y = 6 \times 10^{-5} \times (\pm 8 \times 10^{-6}) + 30.9$, $n = 24$, $r2 = 0.72$; $p \ll 0.001$; Fig. 4).

We found a significant relationship between the number of estimated number of grazing dairy cattle and the Starling index in 1982–2015 and no difference in the trend whether we included the period with declining grazing cattle or not (Table 2), indicating that the same pattern continued unchanged across the two periods.

4. Discussion

This study shows that the dramatic decline of breeding Starlings in Denmark during the last four decades appears related to the extent of suitably grazed grassland, which is in turn largely driven by the numbers of dairy cattle. Our results showed that Starling density in the breeding season was highly significantly correlated with numbers of dairy cows in the 13 local count areas in the mid-1990s. Nationally, it could be shown that the Starling breeding abundance index correlated with numbers of dairy cows between 1982 and 2002, and (because of the increasing trend to keeping cows indoors since then) with numbers of dairy cattle units grazing outside in fields since that date. Finally, we showed that regional differences in changes in the extent of very short grazed grassland during 2001–2014 correlated with regional changes in Starling abundance. This study therefore confirms that it is not only the extent of the grassland available to breeding Starlings that affect their relative abundance, but also that the management and consequently the quality of these grasslands that is of importance. The Starling needs grassland of short sward height to be able to benefit from access to their prey items in the upper soil horizons

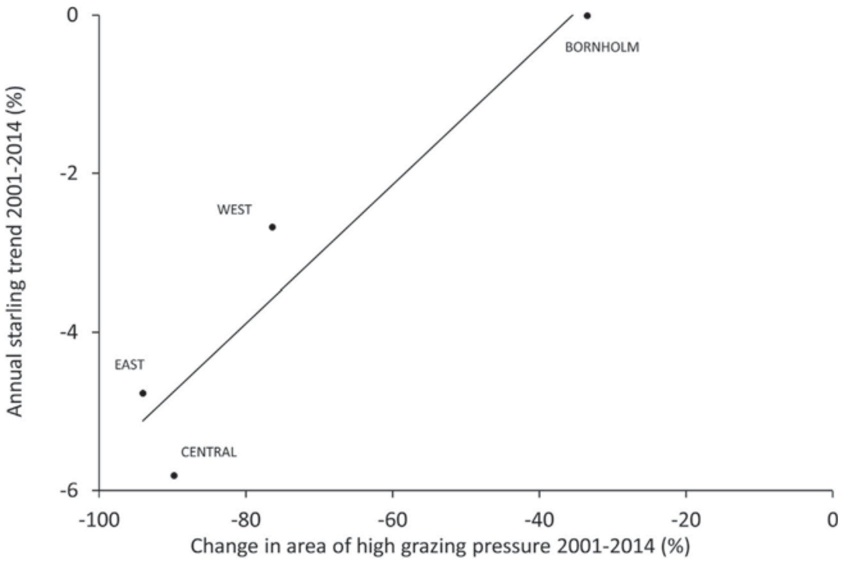

Fig. 3. Mean annual trend of Starlings (2001–2014) in four regions of Denmark (defined in Supplementary material, Fig. 3) as a function of the change in high density grazing pressure (>1) in the regions (2001–2014).

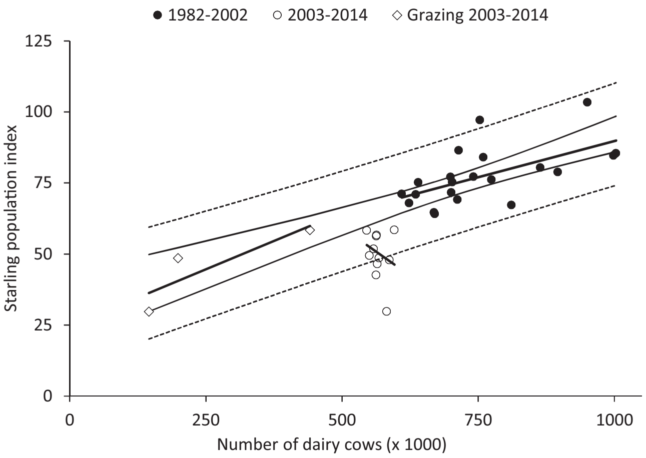

Fig. 4. The changes in the annual Danish Starling breeding population index as a function of the number of dairy cows. There is a significant linear correlation in 1982–2002 ($r^2 = 0.36$), but no such correlation in 2003–2014 ($r^2 = 0.06$). The estimated number of grazing dairy cows are also used as an alternative for 2003–2014 (see text).

(Devereux et al., 2004). Such habitat requirements are likely met by grazing cattle that continuously maintain a short sward throughout the Starling breeding season. Contemporary animal husbandry increasingly keeps dairy cattle herds indoors all year round and the expansion in the relative area of rotational silage grassland that has increasingly replaced grazed grasslands very likely contributes to the adverse effect on Starling breeding abundance.

4.1. Starling trends

We found a significant annual national decline of 2.24% in Starling abundance during 1976–2015 and significant mean annual declines of 1.7–4.5% in the three major areas during 1990–2015, in contrast to the increasing mean annual trend of 1.5% for the small population on Bornholm (Table 1).

The rate of decline amongst Starling trends in the Central and East regions of the country were more rapid than in the West. Some large local Starling populations persist in areas of grassland with grazing cattle in the East region of Denmark (own observations), showing that even in the areas showing most rapid declines, where suitable feeding conditions continue to prevail, there still remains the potential to support a healthy local breeding Starling population. The slightly higher density of Starlings in the Greater Copenhagen area compared to the rest of the East region is heavily influenced by two large Starling observations (4.7 and 7.8 times the mean of the rest) in two nature management areas retaining extensive areas of grassland grazed by cattle but is probably also a result of the areas of grazed grasslands managed to support large numbers of horses, kept for riding in the outskirts of Copenhagen (and in North Zealand), where horse densities in some Municipalities are up to 6 times the mean for the country as a whole (Danmarks Statistik, 2016). Telemetry studies of the foraging areas used by breeding Starlings provisioning young confirm that Starlings forage in horse grazed areas in the absence of grazing cows (Heldbjerg et al. in prep.).

The moderate increase in the Starling population on Bornholm is, by comparison, unusual. Bornholm is a small island, with a relatively long coastline that might provide an additional and more stable habitat for Starlings. It also differs geologically from the rest of Denmark in being rocky and hilly, which retains more marginal grazed areas and fewer biotopes modified by agriculture (Gravesen, 1996). Bornholm farms are smaller and more diverse than average for Denmark, with four times the density of cattle compared to that in the East of Denmark (Table 1), however it remains unclear why these differences should support an increase in Starling abundance, which would repay further investigation.

4.2. Starlings in relation to extent of suitably grazed grassland

The significant positive relationship between the number of dairy cows and the mean Starling density in 13 local count areas in the mid-1990s strongly suggested that the breeding density of the species depended on the extent of cattle grazing. The marked change in the significant relationship between the area of grassland and the number of dairy cows in the 98 municipalities between the 1990s and 2010 showed that the dairy farming industry has been able to support many fewer cows on the same area of grazing land in more recent years. This development has been possible by the increasing amount of indoor dairy husbandry, with fewer cows allowed to graze outside. This results in changes in the nature of the swards available to Starlings, which favour very short sward heights maintained by sequential grazing by stock. This relationship is also confirmed by the finding that changes in Starling regional abundance in Denmark correlated with regional changes in the extent of highly grazed grassland.

Grassland is largely maintained in the Danish landscape to provide cattle food. There are now strong economic reasons for keeping cattle indoors, which have major effects on the current and future management of grasslands. Grass is now largely cut for silage to feed cattle indoors, instead of being grazed. Increasingly, even non-rotational areas are cut for silage, whilst in many valley bottom grasslands grazing has been abandoned. As a result, the decline in the dairy cow population has not been associated with a change of the same magnitude in the grassland area. This can partly be explained by the extra energy intake of the dairy cows which produced 18.5% more milk in 2012 than in 2000 (Danmarks Statistik, 2016), but it is also an effect of the termination of set-aside schemes in 2007/2008 and the subsequent removal of set aside from the Danish landscape, much of which has been converted into grassland area.

Traditional grazing by dairy cows, which ensured daily heterogeneous applications of small amounts of manure and urine to grasslands, has been replaced by infrequent and uniform applications of large amounts of concentrated manure, which has likely affected invertebrate abundance and diversity and limited access to food by birds (Plantureux et al., 2005). Invertebrate

Table 2
Linear models on Starling indices and number of cattle in 1982–2015 showing estimates and *p*-values of each linear model and F and *p*-values for ANOVA's indicating if the incorporated periods are significantly different from each other (see also text).

Cattle	Period, covariate	LM		ANOVA		
		Estimate ±SE	*p*-value	F-statistic	DF	*p* value
Estimated grazing	No	6.56e−05 ± 9.08e-06	4.06e-07			
Estimated grazing	Yes	4.55e−06 ± 1.98e−05	0.821	0.053	2,21	0.821
All	No	4.64e−05 ± 1.78e−05	0.014			
All	Yes	−3.43e−05 ± 7.74e-06	0.0001	19.60	2,30	0.0001

abundance and diversity also declines with a reduction in sward diversity and structural complexity (Vickery et al., 2001). Food abundance for grassland foraging insectivore birds tends to increase with sward height but food accessibility also declines with sward height (Atkinson et al., 2004; Buckingham et al., 2004). *Tipulidae* larvae form the main food item for the Starling nestlings (Rhymer et al., 2012) but since Starling field use was inversely correlated with sward height (Fuller et al., 2003), access to food may be the critical factor (Atkinson et al., 2005).

Hence, in addition to changes in sward height caused by changes in grazing regimes, there is a possibility that changes in the contemporary management of grassland, like structural complexity and use of fertiliser may change the abundance and diversity of prey from that available in earlier forms of regularly grazed and managed grassland.

This study showed that there were regional relationships between grassland management and the population trends for breeding Starlings. These relationships are only correlative, because such species/habitat linkages are very difficult to establish but the general declines in cattle/grass coincide with declines in the Starlings. Processes at small spatial scale such as the local loss of good foraging habitat has been suggested as the main reason for the general decline in the Swedish Starling population (Smith et al., 2012) and we will have to study their foraging ecology and breeding biology in areas with different farmland management as well as different aspects of the Starlings demography to understand what causes the significant decline in Denmark which is reflected in population trends throughout much of Northern and Western Europe (BirdLife International, 2015).

5. Conclusions

This study provided evidence that developments in the dairy sector in Denmark have had major consequences for the breeding Starling in Denmark. Our results reveal that regional declines in grazing dairy cattle correlate with declines in breeding Starling abundance. Latterly, during a period of stability in managed grassland area, the increasing trend to keep dairy cows fed indoors has likely contributed to the reduction in very short grazed grassland that is most attractive to nesting Starlings. To better understand how we might investigate positive management for Starlings in the future, we need to undertake further studies to:

1. investigate effects of changes in grassland management on invertebrate abundance, diversity and accessibility to foraging adult Starlings for feeding nestlings
2. confirm the relationship between different types of grassland and grassland management and Starling reproductive success in Denmark and throughout Europe, and
3. Use the results from these to address policy needs to recognize the effects of agricultural changes on Starling populations in Denmark and throughout Europe and consider how agri-environment schemes could safeguard appropriate grazing regimes to restore the Starling to more favourable conservation status.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.05.025.

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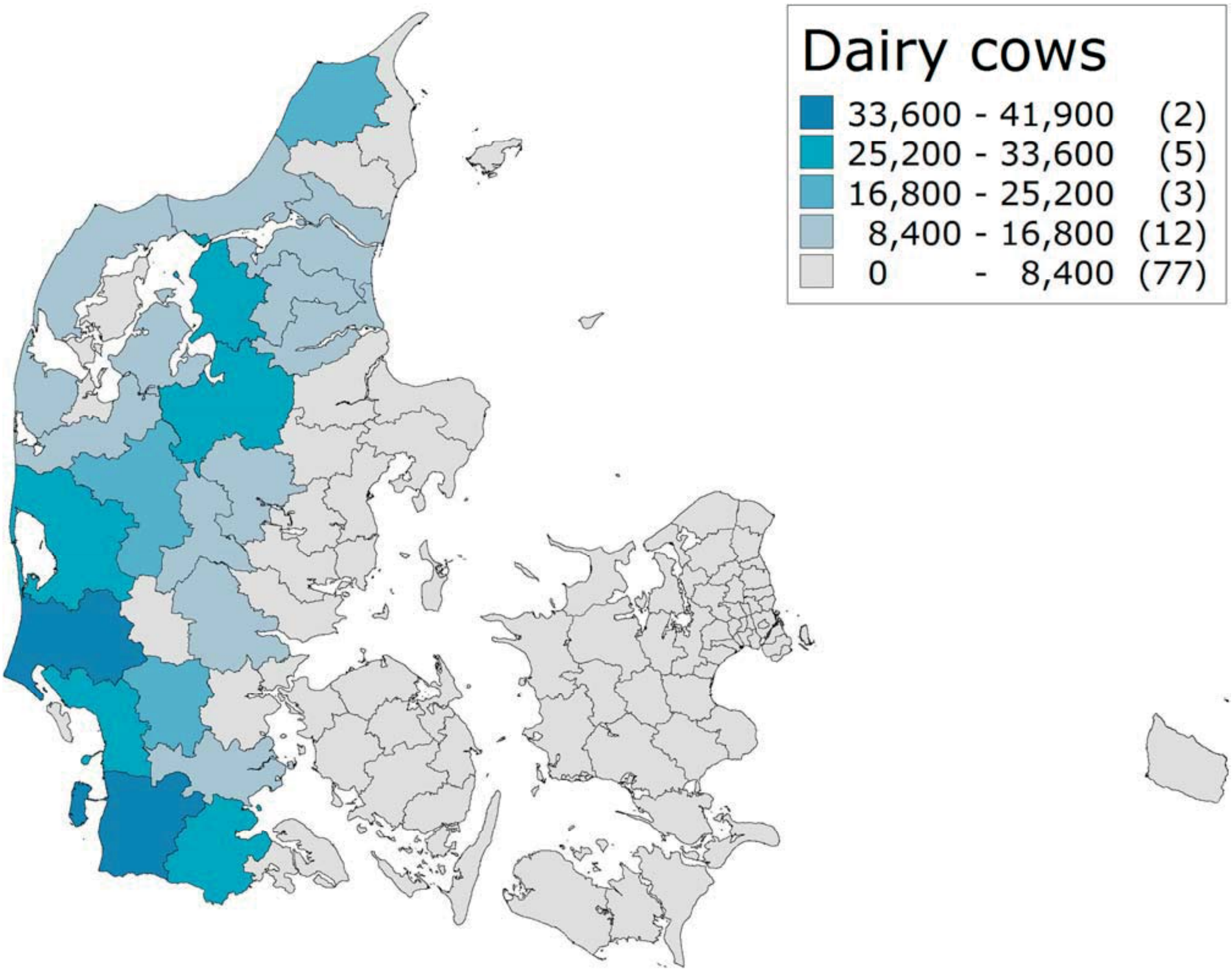
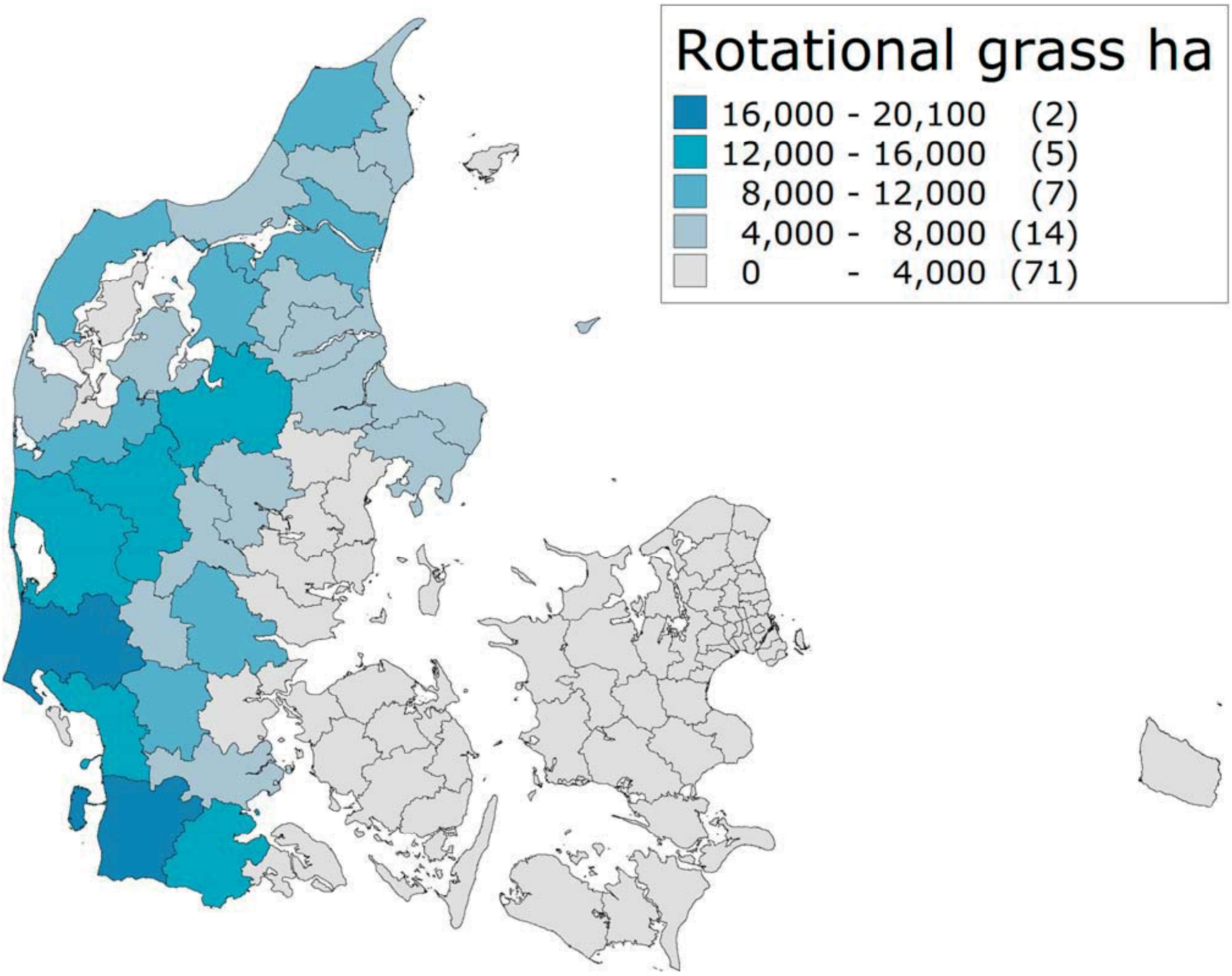
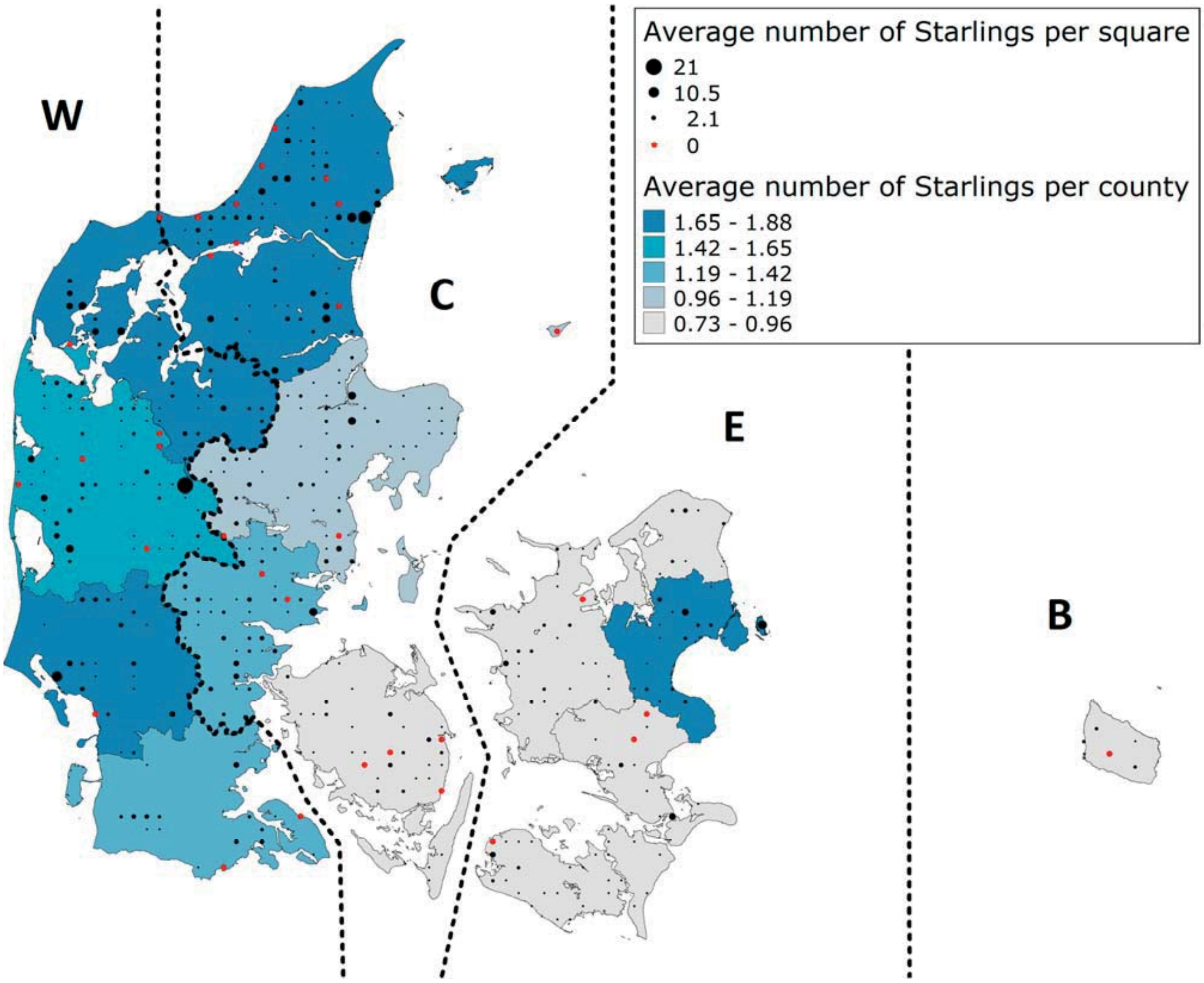
SUPPLEMENTARY MATERIAL



Supplementary material Fig 1. Number of dairy cows in the Municipalities of Denmark in 2010, data from www.statistikbanken.dk.



Supplementary material Fig 2. Hectares of rotational grassland in the Municipalities of Denmark in 2010, data from www.statistikbanken.dk.



Supplementary material Fig. 3. Relative density of Starling Sturnus vulgaris *in the mid-1990s sampled in each 5 x 5 km atlas squares and grouped into the 13 local areas. Only counts during 10-30 May have been analysed. Red dots indicate counted squares with no Starling observations. Empty squares were not counted.* Also showing the 13 local count areas and the regional divisions of Denmark used in this study. W = West, C = Central, E = East and B = Bornholm.

PAPER 5

COMMON STARLINGS (*STURNUS VULGARIS*) INCREASINGLY SELECT FOR GRAZED AREAS WITH INCREASING DISTANCE-TO-NEST

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Photo: Anthony D. Fox

RESEARCH ARTICLE

Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest

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Abstract

The abundant and widespread Common Starling (*Sturnus vulgaris*) is currently declining across much of Europe due to landscape changes caused by agricultural intensification. The proximate mechanisms causing adverse effects to breeding Starlings are unclear, hampering our ability to implement cost-efficient agri-environmental schemes to restore populations to former levels. This study aimed to show how this central foraging farmland bird uses and selects land cover types in general and how use of foraging habitat changes in relation to distance from the nest. We attached GPS-loggers to 17 breeding Starlings at a Danish dairy cattle farm in 2015 and 2016 and analysed their use of different land cover types as a function of distance intervals from the nest and their relative availability. As expected for a central place forager, Starlings increasingly avoided potential foraging areas with greater distance-to-nest: areas $\geq$ 500 m were selected > 100 times less frequently than areas within 100 m. On average, Starlings selected the land cover category Grazed most frequently, followed by Short Grass, Bare Ground, Meadow and Winter Crops. Starlings compensated for elevated travel costs by showing increasing habitat selection the further they foraged from the nest. Our results highlight the importance of Grazed foraging habitats close to the nest site of breeding Starlings. The ecological capacity of intensively managed farmlands for insectivorous birds like the Starling is decreasing through conversion of the most strongly selected land cover type (Grazed) to the least selected (Winter Crops) which may be further exacerbated through spatial segregation of foraging and breeding habitats.

Introduction

In Western and Central Europe, bird populations associated with farmland habitats have been steadily decreasing for three decades (e.g. [1–4]). These long term and large scale population declines of multiple species have been associated with 'agricultural intensification' [2,5]. However, the underlying specific, proximate causes hidden beneath such a generic explanation (which may result from multiple causes, even for a single species) often remain poorly understood. For instance, populations may decline or disappear entirely due to: (1) general

study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

deterioration in food availability, caused by intensified cultivation, (2) conversion of land cover types providing rich feeding opportunities to other cover types of less or no value and/or (3) increasing homogenisation of the agricultural mosaic (e.g. larger field units), reducing micro-habitat presence and diversity (e.g. nesting and foraging habitats) within an individual's activity range [6–8]. Although the overall process of agricultural intensification may not be reversible, the adverse effects on biodiversity components (such as species abundance) may be diminished or reversed through agri-environmental schemes or voluntary means. Such beneficial actions should include modest management targets to achieve the highest possible biodiversity benefit in a given landscape context. To achieve the best results, knowledge of a species' micro habitat requirements, which include the spatial configuration of these elements in relation to each other, are of paramount importance. To understand these requirements, predictive models of habitat suitability based on use by observed individuals relative to habitat availability, so called Resource Selection Functions (RSFs), have increasingly been used [9–11]. Ecological inference from RSFs is based on the premise that selection (i.e. the disproportionate use of a resource relative to its availability) reflects optimal behavioural decisions made by an organism in response to relative habitat quality, since relative differences in selection between habitat units are likely to be approximately proportional to their difference in quality [11–12]. The logic is that if a given habitat type, A, is used x times as often as another habitat type, B, if equally available and all other factors are held equal, then habitat A can be assumed to be approximately x times (the selection ratio or odds ratio of selection) as important as B. This is the case as long as both habitats are used for exactly the same purpose (e.g. foraging). Similarly, by simultaneously modelling several habitat variables, RSFs can estimate partial variation in habitat quality (as a proxy) as a function of individual habitat traits in a given environmental context (all other habitat factors held equal). RSFs can also quantify selection for different land cover types at different distances from the nest. Finally, maps of individual selectivity can be generated from RSFs comprising multiple predictors (e.g. effects of land cover types and distance-to-nest), which in turn can be considered as fairly reliable proxies for the relative importance of the individual area units within the studied subjects' home range [11–12].

In this study, we present a spatially explicit habitat selection model for foraging Common Starlings (*Sturnus vulgaris*, hereafter Starling) breeding in a Danish farmland landscape. We use recent developments in lightweight GPS logger technology to track foraging Starlings on a traditionally managed dairy cattle farm in southern Jutland in order to determine their habitat use in relation to land cover type (i.e. habitat) availability and distance-to-nest.

The Starling is one of Europe's most common and geographically widespread farmland birds, occupying a wide range of open habitat types, feeding on invertebrates harvested from the ground and upper soil horizons. As such, it is a perfect model species to study of how 'common' insectivorous farmland birds adapt to prevailing food conditions in farmland habitats. The Starling is a short distance migrant and a common and widespread summer visitor to Denmark, where breeding abundance has significantly declined by 2.2% per annum during 1976–2015 [13], similar to the mean annual decline of 1.9% throughout Europe during 1980–2013 [14]. During 1976–2015, Danish farmland has changed considerably through intensification and specialisation, with a major shift from spring sown to autumn sown cereals during the 1980s and 1990s and a reduction in number, an increase in mean size and an increasing concentration of dairy farms in the south and west of the country [15–16]. The extent of grazed grassland has decreased as the area of intensively managed silage grassland and maize cultivation has increased, because dairy cows are now predominantly fed indoors [4]. An earlier national study showed contrasting trends in breeding Starling abundance between Danish regions depending on the regional land use change, particularly in relation to grassland area and intensity of cattle grazing [16]. However, in the absence of data on precise habitat use by

Starlings within the farmland mosaic, it is difficult to gather more than correlational support for hypotheses regarding their population declines.

Starlings provisioning offspring become classic central-place foragers, harvesting invertebrate prey and returning to a central place (the nest site) to deliver food to their nestlings. This provides a unique opportunity to determine habitat selection at a landscape scale in relation to availability, and look at the interaction between selectivity and distance. Since prolonging foraging trip duration is both energetically costly and reduces trip frequency, we predict that habitat selection will be greater with increasing distance, increasing load size or energy content to elevate profitability [17]. For these reasons, we deployed GPS loggers on breeding male and female Starlings solely while feeding their nestlings, when habitat choice is critical to their foraging efficiency, and to their reproductive success. Since it is known that breeding Starlings select especially short sward grasslands [18–19], we were curious to see how such habitats (grazed and ungrazed, and others) were selected in the agricultural landscape by individual birds from the same colony in relation to their relative availability.

Methods

Study site

The study site was chosen at a colony on a traditional dairy farm with grazing cattle and mixed crops of spring barley, winter wheat, grass and fodder beets, owned by PVT in Hjortkær, near Esbjerg (55˚32.4077'N 8˚43.6529'E) in the area of southwest Denmark. Starlings in this part of Denmark have shown the least declines in abundance nationally [16] and hence this area was chosen because it was expected to represent birds showing least disturbed behaviour in the country. All studied Starlings bred in 27 nestboxes mounted on farm buildings or surrounding trees within 50 m of each other, 3–4 m above the ground. Breeding success at this colony has been stable since 1971 [20] and occupancy was more or less 100% until c. 10 years ago, since when the proportion has fallen to roughly 60%.

GPS loggers

We attached battery powered Gypsy 5 GPS loggers (Technosmart Europe srl., Rome) with a total mass (including Teflon harness) of c. 3.2 g (c. 3.5–4% of Starling body mass) and positional accuracy down to 2–4 metres. All loggers were set to record 1 fix/minute during the daylight period and either low frequency (1 fix /hour) or no fixes at night (night positions were not considered in this study), commencing one day after attachment to exclude eventual behavioural effects of being caught and handled. At this frequency of positional logging and a battery capacity of up to 32 hours, we re-caught tagged birds after 3–5 days to retrieve loggers to obtain as much data as possible, extracting data via a cable connection.

Capture and instrumentation

The capture and instrumenting of Starlings used in this study conforms with the Aarhus University code of practice to ensure responsible research conduct and was carried out with the expressed permission of the Ringing Centre of the Danish Natural History Museum. Breeding Starlings were caught during 5–14 May 2015 (7) and 6–14 May 2016 (10) either in nestboxes or in mist nets nearby while provisioning offspring (see S1 Table). There was very little variation in the clutch size and pairs at the colony breed highly synchronously (Thellesen in print), so the ringing/logging period was chosen to include a comparable group of adult birds with chicks at the age of 4–7 days. Hence, we consider breeding stage and brood size had little effect on individual behaviour. Individual body mass of provisioning Starlings varied by several grams per day, so mass at capture was not incorporated into the models. Starlings were fitted with a logger using a harness of 2 mm Teflon ribbon around each wing, held together by a short 4 mm Teflon ribbon in front of the sternum. Harness straps were either knotted, sewed and glued to the logger on the back of the bird (in 2015) or secured by a metal clipped loop to the logger (in 2016). For two experienced ringers the handling time was 10–20 minutes including ringing, colour ringing and attachment of the logger. Data were extracted from 17 individual first clutch breeding birds (6–32 hours of data per bird; S1 Table). Despite a potential day-to-day variation in prey availability within the c. one week per year the data were sampled, we consider the data derived from all loggers from the same year as samples of the same general conditions of prey availability in relation to habitat availability.

Starling positions and filtering the data

Each logger provided a data file (.txt) giving information on every fix until the battery runs short of energy. Each fix comprised information on time, position, speed and precision see [21] and S1 Fig.

We filtered the data to focus on habitat use only while foraging and included only precise positions. We excluded all data of birds flying (speed > 0.0) and all data with a precision less than c. 10 m (HDOP > 2.5) to maximize the number of data points assigned to foraging habitat categories. We also excluded all data between 20:00 and 05:30 local time to exclude positions related to movements to and from night roosts. Finally we excluded all data from the habitat categories buildings, gardens, forests and lakes (10.4% of total area within 1 km from the colony) since these were clearly associated with behavioural activities other than feeding (e.g. sleeping, roosting, singing, mating, drinking etc.) and were not relevant in the context of describing foraging behaviour. We only included birds/loggers with more than 50 observations which resulted in 52–382 (mean ± SE: 241 ± 25, S1 Table) positions per Starling.

Description and coding of land cover types and distance-to-nest categories

All uniform habitats out to a radius of 1 km from the capture site (in excess of the maximum distance from the nest where the Starlings foraged) were described to habitat/crop on maps within field and land parcel units, to define their relative availability to foraging Starlings. Field polygons were retrieved from the common agriculture register (GLR, "Det Generelle Landbrugsregister") maintained by the Danish AgriFish Agency [22]. For all other habitat categories (meadows, forests, etc.) we used publicly available map layers from the Danish public geographical administration data (GeoDanmark, downloaded 2012, http://download.kortforsyningen.dk). This habitat information was transferred to GIS layers by defining polygons for all registered crops.

For the statistical analyses, land cover types were condensed into five predominant crop categories available for all birds: Grazed (grazed grass, but management otherwise is unknown), Short Grass (at the time of the study), Bare Ground (new-sown maize and spring cereals), Winter Crops (autumn-sown cereals and rape) and Meadows (non-grazed/mown grassland) (Fig 1).

Habitat availability was measured as the frequency of each land cover type at different distance-to-nest categories. This was determined by superimposing a 50 m grid overlaid upon the land-use classification map covering the study area out to beyond the maximum observed Starling foraging distance from the farm. The habitats present at each grid intersection (4 ha^{-1}, hereafter referred to as relative availability points for habitat sampling, 'RAPs') were then used

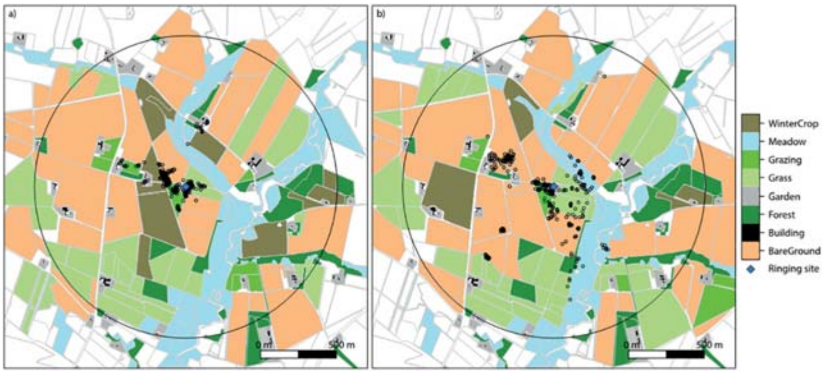

Fig 1. Positional fixes from two different foraging breeding Starlings (*Sturnus vulgaris*). The map shows positions of two different birds (left: S7, 2015 in a) and right: S9a, 2016 in b)) recorded using GPS loggers at a dairy farm in Hjortkær, Jutland, Denmark overlaid on the ringing and nest site (central blue diamond) and the surrounding fields indicating the different crops and the foraging positions of one Starling during c. 24 hours. The categories Building, Garden and Forest are only shown for clarity and were not included in the analysis. The large black circle represents the limit of habitat classification and has a radius of 1000 m (See also S1 Table and S1 Fig in Supplementary Materials for the full set of all mapped individuals).

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to generate a set of systematic habitat frequencies to describe their relative availability to Starlings in the study area.

For each recorded GPS fix (use) and RAP (availability) we assigned a habitat category and calculated the distance in metres to the colony (as a proxy for the distance to the nest and hereafter 'distance-to-nest'), using the centre of the farmyard in which the nest box colony was situated as the fixed point for all nests. In order to quantify the mean proportional use of Starlings within the various distance-to-nest distance class intervals, as well as determine their habitat selection relative to these intervals, the distance-to-nest measurements were aggregated into intervals of 100 m (i.e. 0–99 m, 100–199 m, etc.).

Analyses of distance-to-nest patterns and use of land cover types

For each Starling we calculated the average distance-to-nest and the proportion of GPS-fixes classified within the ten 100 m distance-to-nest intervals. Using individual Starlings as the observational unit, we tested whether the 17 Starlings' average distance-to-nest varied systematically between males and females and between the two study years using a simple general linear model (PROC GLM in SAS 9.4). Since there was no significant systematic variation, the mean proportion of time spent foraging in different distance-to-nest intervals was then calculated as the mean proportion of GPS fixes from each bird within a given distance interval based on simple normal statistics. As most confidence limits fell between 0 and 1, we considered it justified to base our estimates on arithmetic means rather than back-transformed values of logit-transformed means that would result in slightly low-biased estimates. To illustrate the proportional use of land cover types within each of the ten 100 m distance-to-nest intervals, we pooled data from all GPS-positions from all 17 Starlings and RAPs within each distance-to-nest interval to calculate the relative frequencies of Starling use of each habitat type relative to its availability.

We tested for sex differences in land cover use using a multinomial logistic regression model (GLIMMIX procedure in SAS 9.4 [23]) with the five land cover categories as response variable, a generalised logit link function and multinomial error distribution, sex as fixed effect and Starling ID as random effect. Habitats were equally available to all individuals (with only very minor differences between 2015 and 2016). The sex distribution between habitats was also almost identical in the two study years. Hence, the lack of systematic difference in use of land cover types between males and females could be inferred as a lack of difference in habitat selection between males and females, confirmed in the analysis (see Results). Hence, sex was not considered as factor in the subsequent analyses of habitat selection.

Analyses of habitat selection

Habitat selection was modelled as differential Starling use of habitats relative to their availability as a RSF, comparing GPS positions (representing use) with availability derived from the combined frequencies from RAPs for each Starling as observation units [9]. We used generalized linear mixed models with a logit link function and binomially distributed error terms ('logistic regression') to model the relative probability that an observation would be categorized as GPS-location (use) or as RAPs as functions of cover type and/or distance interval to the nest.

The data set consisted of all use (GPS-positions) and availability locations within the five selected land cover categories within 999 m from the colony centre for each of 17 Starlings (i.e. for each Starling a set of RAPs were entered with its ID annotated). To account for different ratios of GPS-fixes and RAPs between individuals, Starling ID was entered as a random factor. To adjust for variance inflation due to individual variation in habitat selection (which may appear as a simple result of serial dependency of consecutively recorded GPS-locations in the same field block unit), as the random effects we included interaction term(s) between Starling ID and all habitat variables entered as fixed effects [24]. All models were run in the GLIMMIX procedure in SAS 9.4 with denominator degrees of freedom estimated using the Satterthwaites approximation method [23].

As follows from RSF theory, the predicted probability provided by a RSF of an observation being a GPS-location as opposed to a RAP observation is uninformative (because the numbers of GPS-fixes and RAPs were arbitrarily chosen). However, the logistic regression coefficients describe the relative log-transformed differences in preference (which is equivalent to the relative difference in use assuming availability is constant) between habitat types when all other influencing factors were held equal in the model [9]. In the present analysis, selection for land cover types was expressed in relation to the land use category Grazed (i.e. how often the other land cover types were used relative to Grazed if equally available) and selection for distance-to-nest intervals as being relative to the 0–99 m interval.

RSFs were constructed for (i) land cover types (five categories) in isolation (i.e. ignoring variation in distance-to-nest), (ii) distance-to-nest intervals (100 m categories) in isolation (ignoring variation in composition of land cover types) and (iii) both variables combined as main effects.

Because some models failed to converge due to unbalanced data amongst individuals (e.g. because of missing observations within certain habitat categories) it was not possible to construct models that incorporated selection for land cover types as function of varying distance-to-nests (interaction terms between distance-to-nest and land cover types). Instead, selection for land cover types at different distance zones from the nest were estimated from separate RSFs constructed for sub-divisions of the data set at 0–199 m, 200–399 m and 400–999 m from the nest. To achieve model convergence, the RSF analysis from the furthest distance-to-nest zone (400–999 m) was restricted to seven Starlings with > 20 GPS locations within this interval (Loggers S2, S3, S5, S8, S9, S9a, S10, S1 Table). Also, the category Winter Crops was excluded from the analysis since no Starling was ever observed in this land cover type > 399 m from the nest. Selection coefficients (SC) for Winter Crops relative to Grazed 400–999 m from the nest were approximated for each individual Starling using the method of [25]. This calculates $SC_{WC\text{-}G} = \ln(U_{WC}/A_{WC}) - \ln(U_{GR}/A_{GR})]$, where U_{WC}/A_{WC} and U_{GR}/A_{GR} are the proportions of GPS-fixes (used = U) divided by the proportion of RAP availability points (A) from the Starling found in Winter Crops (WC) and Grazed (GR), respectively. In this case, all 0-values (i.e. no observations) of either U or A were replaced by a value equal to 0.5 count observation (so, for example if 0 out of 24 GPS-locations were found in Winter Crops, $U_{WC} = 0.5/24 = 0.021$). With normal statistics, a mean $SC_{WC\text{-}G}$, SE and 95%CI was calculated for each of the six Starlings that used Grazed at least once >399 m from the nest.

Pairwise differences in selection coefficients were estimated from different models as $\Delta B = B_1 - B_2$ (where B_1 and B_2 are estimate 1 and 2). These were tested on the basis of simple t-statistics: $t_{(df1+df2)} = (B_1\text{-}B_2)/([SE_{B1}]^2+[SE_{B2}]^2)^{0.5}$, where df_1 and df_2 are the degrees of freedom of estimates 1 and 2, and SE_{B1} and SE_{B2} are the SEs of estimates 1 and 2. This method was used to test for differences in selection coefficient estimates of land cover types from a RSF that had land cover types as the only fixed effect and a RSF that incorporated both land cover types and distance-to-nest interval as fixed effects. Similarly, the method was used to test for differences in selection coefficients of distance-to-nest intervals from a RSF that consisted of distance-to-nest intervals as the only fixed effects and a RSF incorporating land cover types and distance-to-nest interval as fixed effects.

Results

Use and selection of distance-to-nest intervals

The 17 Starlings showed individual differences in activity with distance-to-nest intervals (Fig 2A), but on average 21% (95% CI: 16–26%) of their locations fell within 99 m of the nest, 41% (32–49) within 100–199 m, 18% (11–26) within 200–299 m, 8% (4–12) within 300–399 m and 12% (4–20) >399 m from the nest. Mean activity distances (observations within land cover types included in the RSFs) were similar for males and females (240 vs. 213 m, $F_{1,16} = 0.45$, $P = 0.5$) but tended to be somewhat (although not statistically significantly) greater in 2015 than 2016 (265 vs. 188 m $F_{1,16} = 3.50$, $P = 0.08$).

Predictions for selection of distance-to-nest distance (based on 100 m-intervals) were similar for the RSF that included land cover types and distance categories and the RFS that only included distance-to-nest (Table 1). Areas within the first 199 m were selected most strongly and equally, after which distance intervals were selected increasingly less frequently relative to the use of the area within 0–99 m of the nest (Fig 2B; overall test for the ten distance intervals being equally selected: $F_{9,142} = 31.8$, $P < 0.0001$).

Use and selection of land cover types

Of all 4037 GPS fixes used in the analysis, 37% were on Bare Ground, 32% on Short Grass, 24% on Grazed, 6% on Meadows and 0.8% on Winter Crops with no difference in proportional land cover use between the sexes ($F_{4,23.1} = 0.71$, $P = 0.59$). Use, as well as availability of land cover types, varied with distance-to-nest (Fig 3).

According to both RSFs (i.e. those which only included land cover types and those which also accounted for selection within distance-to-nest intervals), at 0–999 m from the nest, Starlings strongly selected between land cover types (Table 1). The two modelling alternatives resulted in similar selection coefficients, which did not differ significantly (Table 1). Starlings selected the land cover category Grazed significantly more than all other land cover types, followed by Short Grass (selection ratio to Grazed = 1:2.6), Bare Ground (1:6) and Meadow (1:13), with Winter Crops by far the least selected cover type (1:48, Table 1, Fig 4). Hence, within cultivated fields, Bare Ground (spring sown crops) was selected eight times (95% CI: 3–18 times) more than Winter Crops (Table 1).

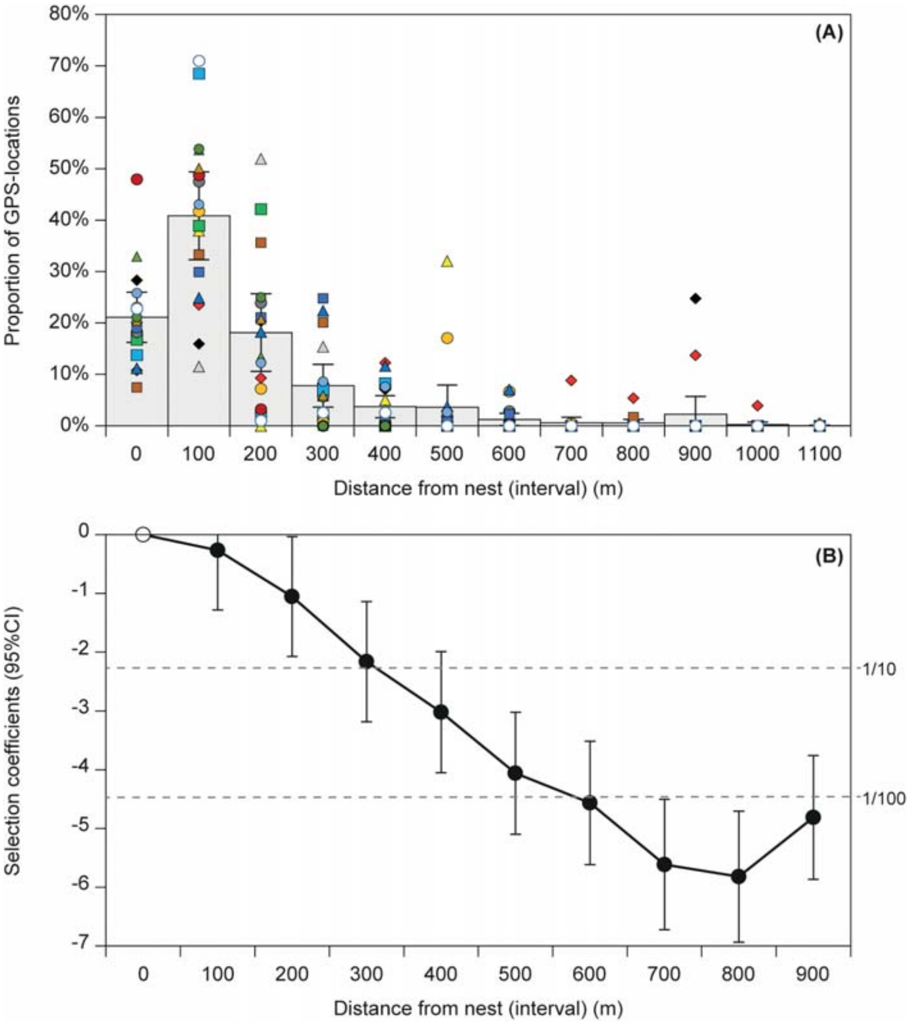

Fig 2. Foraging distance for breeding Starlings. (A) Proportion of GPS-locations of 17 foraging Starlings at different distance intervals from the nest, the different symbols indicate different birds. (B) Selection coefficients of distance intervals relative to the selection in the nearest interval (0–99 m) from RSF that also accounts for selection of land cover types. The anti-log of the coefficients indicate the approximate odds ratio by which a distance category is used relative to availability compared to 0–99 m from the nest (horizontal stippled lines indicate odds ratios of 1:10 and 1:100 as a guide).

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When RSFs were constructed for different distance-to-nest intervals, selection for land cover types varied with increasing distance to nest, as Grazed was selected significantly more than other cover types 400-999m from the nest compared to within the first 199 m from the nest (Table 2, Fig 4). Hence, while Short Grass was selected approximately equally to Grazed at 0–199 and 200–399 m from the nest, Grazed was selected significantly over Short Grass at a ratio of 9:1 further away than 399 m from the nest.

Discussion

The deployment of GPS logger units on Starlings in this study provided data with high spatial accuracy on space use and habitat selection of foraging adult breeding birds during the critical

Table 1. Model parameters of RSFs for habitat selection.

		Model = Cover type + distance					Model = Distance only					Model = Cover type only					Difference in selection coefficients				
***Fixed effects*:**		**B**	**SE(b)**	**df**	***t***	***P***	**B**	**SE(b)**	**df**	***t***	***P***	**B**	**SE(b)**	**df**	***t***	***P***	**ΔB**	**SE(ΔB)**	**df**	***t***	***P***
cover type	Grazing (ref.)	0.00	.	.	.	.						0.00	.	.	.	.	.	.	.	.	.
	Short Grass	-0.94	0.33	59.1	-2.89	0.005						-1.56	0.32	50.0	-4.9	<0.0001	-0.62	0.46	109	-1.35	0.18
	Bare Ground	-1.83	0.32	58.4	-5.64	<0.0001						-2.10	0.32	49.7	-6.6	<0.0001	-0.27	0.46	108	-0.60	0.55
	Meadow	-2.55	0.33	65.2	-7.66	<0.0001						-3.01	0.33	53.8	-9.2	<0.0001	-0.46	0.47	119	-0.98	0.33
	Winter Crop	-3.87	0.43	107	-8.97	<0.0001						-4.48	0.37	91.6	-12	<0.0001	-0.61	0.57	199	-1.06	0.29
	Overall effect of cover type: $F_{4,77.7} = 54.10$, P<0.0001											$F_{4,\ 56.8} = 42.4$, P<0.0001									
Distance	0–99 m (ref)	0.00	.	.	.	.	0.00	.	.	.	.						.	.	.	.	
	100–199 m	-0.27	0.51	119	-0.52	0.604	-0.57	0.56	126.3	-1.02	ns						-0.31	0.76	245	-0.40	0.69
	200–299 m	-1.05	0.51	120	-2.04	0.043	-1.95	0.56	126.8	-3.47	0.0007						-0.90	0.76	247	-1.18	0.24
	300–399 m	-2.16	0.52	123	-4.18	<0.0001	-2.96	0.56	128.2	-5.25	<0.0001						-0.80	0.76	251	-1.05	0.29
	400–499 m	-3.02	0.52	126	-5.81	<0.0001	-3.55	0.57	130.9	-6.27	<0.0001						-0.53	0.77	257	-0.69	0.49
	500–599 m	-4.06	0.52	130	-7.74	<0.0001	-3.98	0.57	131.3	-7.01	<0.0001						0.08	0.77	261	0.11	0.92
	600–699 m	-4.57	0.53	136	-8.61	<0.0001	-4.99	0.58	139	-8.67	<0.0001						-0.42	0.78	275	-0.54	0.59
	700–799 m	-5.61	0.56	172	-9.99	<0.0001	-6.13	0.60	168.9	-10.14	<0.0001						-0.51	0.83	340	-0.62	0.53
	800–899 m	-5.82	0.56	175	-10.3	<0.0001	-6.34	0.61	174.9	-10.41	<0.0001						-0.52	0.83	350	-0.63	0.53
	900–999 m	-4.81	0.53	138	-9.03	<0.0001	-5.28	0.58	142.6	-9.12	<0.0001										
	Overall effect of distance category: $F_{9,142} = 31.8$, P <0.0001						$F_{9,144.5} = 28.1$, P <0.0001														
Random effects (covariance parameters)																					
Starling ID		0.32	0.26	∞	1.24	0.22	0.45	0.25	∞	1.77	0.11	0.10	0.11	∞	0.95	0.34					
Starling ID*Distance		2.13	0.29	∞	7.36	<0.0001	2.60	0.34	∞	7.70	<0.0001	.	.		.	.					
Starling ID*Cover type		0.78	0.16	∞	4.75	<0.0001	.	.				0.82	0.17	∞	4.74	<0.0001					

Model parameters and overall statistical significance (type-III effects) of variables of Resource Selection Functions for habitat selection by GPS-tagged Starlings 0–999 m from the nest site.

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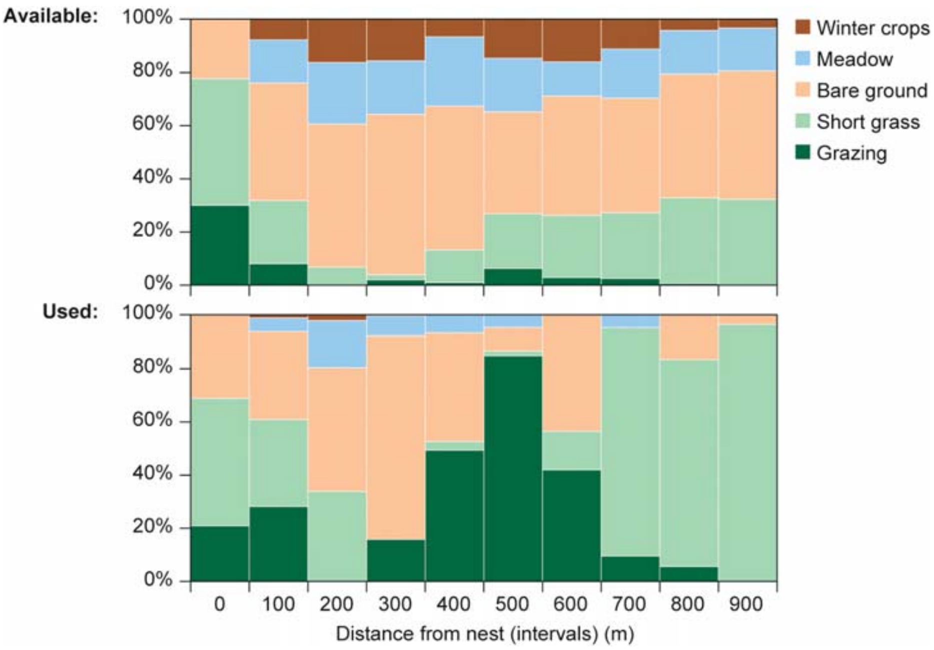

Fig 3. Availability and use of land cover types by 17 GPS-tagged Starlings. The availability and use of land cover types is shown at different distance intervals from the nest (all fixes in a given distance interval pooled across individuals).

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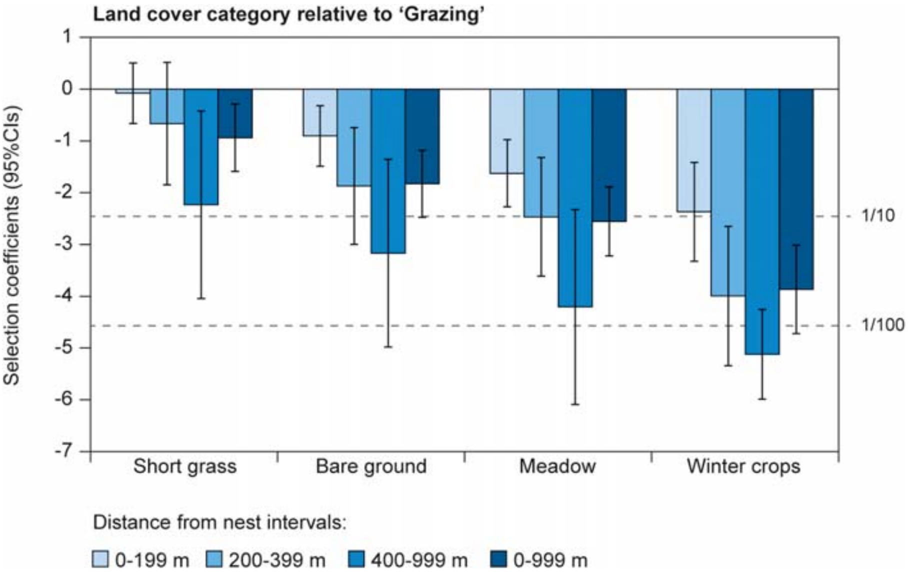

Fig 4. Selection for land cover types. Selection for land cover types is shown relative to "Grazing" by 17 GPS-tagged Starlings at different distance-to-nest intervals (within which selection for 100 m distance intervals are accounted for unless otherwise stated). The anti-log of the coefficients gives the approximate odds ratio to the frequency by which a land cover category is used relative to grazed areas if availability is the same (horizontal stippled lines indicate odds ratios of 1:10 and 1:100 as a guide).

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Table 2. Selection of land cover types.

Distance intervals	Selection coefficients for land cover types relative to "Grazed"																				Test for overall selection		
	Short Grass					Bare Ground					Meadow					Winter Crops							
	B	SE (b)	df	*t*	*P*	B	SE (b)	df	*t*	*P*	B	SE (b)	df	*t*	*P*	B	SE (b)	df	*t*	*P*	*F*	df	*P*
A: 0–199 m	-0.08	0.29	38.9	-0.27	0.79	-0.90	0.29	38.7	-3.13	0.003	-1.62	0.32	59.5	-5.01	<0.0001	-2.37	0.48	93.1	-4.93	<0.0001	12.7	4,52	<0.0001
B: 200–399 m	-0.67	0.59	83.9	-1.12	0.27	-1.87	0.57	71.7	-3.31	0.002	-2.47	0.57	76.4	-4.29	<0.0001	-4.00	0.68	88.0	-5.90	<0.0001	13.9	4,63.5	<0.0001
C: 400–999 m	-2.23	0.87	21.3	-2.56	0.02	-3.17	0.87	21.3	-3.64	0.002	-4.21	0.92	26.1	-4.59	<0.0001	-5.12	0.43	5.0	-11.9	<0.0001	7.92	3,23	0.0008
difference: A-B	0.59	0.66	122.8	0.89	0.38	0.97	0.63	110.3	1.52	0.13	0.84	0.66	135.9	1.28	0.20	1.63	0.83	181	1.96	0.051			
difference: B-C	1.57	1.05	105.2	1.49	0.14	1.30	1.04	93.0	1.25	0.21	1.74	1.08	102.4	1.61	0.11	1.12	0.80	93.0	1.40	0.16			
difference: A-C	2.16	0.92	60.2	2.35	0.02	2.27	0.92	60.0	2.47	0.002	2.58	0.97	85.6	2.66	0.009	2.75	0.64	98.1	4.27	<0.0001			

Coefficients for selection of land cover types relative to “Grazed” and F-statistics for test for overall selection of land cover types for analyses split on different distance-to-nest intervals from the nest for GPS-tagged Starlings.

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period when they seek to maximise food provisioning. The results clearly showed Starlings foraged at distances more than 500 m from the nest more than 100 times less frequently than within 100 m and selected Grazed grassland over all other habitat category types in the farmland landscape. These novel results provide three key implications for agri-environmental management schemes.

Firstly, this study quantified the differences in use by foraging Starlings between common available crops in a Danish farmland landscape and illustrated how some crops were clearly avoided by Starlings foraging to provision their offspring. The strong selection for Grazed areas confirmed the importance of grazing livestock (in this case cattle) for maintaining short-grazed high quality foraging habitats for Starlings. Grazed areas were selected 2.6 times more than ungrazed (at the time of the study) Short Grass and six times more than Bare Ground. It seems likely that food items should be equally accessible in these crops (relative to their density) for foraging Starlings, implying that Grazed habitats host a higher density of available prey compared to cut Short Grass and Bare Ground (i.e. ploughed cultivated fields for spring crops). Grazed grassland was selected 13 and 48 times more than Meadow and Winter Crops, while Bare Ground (i.e. new sown spring crops) was selected by a factor of 8 over Winter Crops, indicating the relative profitability of foraging between these habitats. If we assume that microhabitat selection coefficients from RSFs reflect differences in habitat quality, then the behaviour of the tagged breeding Starlings supports the hypothesis that long term population declines in Starling populations in Denmark and other western European countries are causally linked to the transformation of actively grazed pastures to managed silage swards and cultivated crops. It therefore follows that the conservation of actively grazed areas is one of the main key actions likely to guard against further loss of foraging habitats for Starlings and other ground feeding insectivorous farmland birds in order to safeguard these populations from further declines in the future [26].

Secondly, the shape of the activity and selection patterns for distance-to-nest intervals indicate that areas further than 200 m from the nest increasingly lose foraging value with increasing distance, a pattern that undoubtedly relates to increasing travelling costs between nest and foraging sites. In practice, this means that disconnection of breeding sites (i.e. safe nesting cavities in buildings or holes in trees) from foraging habitats at scales beyond a few hundred metres is likely to reduce the quality of potential foraging habitats because increased commuting costs reduce foraging time and elevate flight energy expenditure [27].

Thirdly, the selection increased with foraging distance. Starlings became increasingly selective in their habitat choice the longer they flew, i.e. the more they invested in the foraging trip. Starlings were thus able to compensate to some extent for more widely distributed resources in the landscape by concentrating on exploiting the most profitable patches. Starlings breeding in modern agricultural landscapes (i.e. with large fields and long commuting distances between nest and foraging sites) will profit more by access to limited patches of very high foraging value (e.g. cattle grazed pastures) than larger areas of modest foraging quality (e.g. grass or open land), which fail to balance the energetic costs of commuting to and from the nest site.

Land cover types and the significance of habitat quality

Starlings showed strong preferences for Grazed over Bare Ground and Short Grass, avoiding Meadows and Winter-crops. These significant differences between habitat types likely mirror food accessibility. Starlings mainly prey on larvae of crane flies (*Tipulidae*) but also those of butterflies, moths and beetles [28]. We were unable to study prey availability in the different crops at our study site but [29] found greater prey abundance in pasture and other permanent grass than in cereal fields in South Sweden and we see no reason why this pattern should be different at our study site. The abundance and density of invertebrates is also lower in intensive grassland monocultures than in extensively managed grassland [30]. As well as density, prey availability is likely affected by vegetation height [19,31–32], because the least preferred tall Winter Crops such as rape or winter wheat reach vegetation heights of c. 150 cm and 40–50 cm, respectively, during the Starling breeding season. In contrast, spring sown crops such as maize (common in the area), fodder beet (rare) and spring sown cereals (mainly barley, which is relatively common) show such late season growth that extensive Bare Ground remains between growing plants during the Starling breeding season, providing additional foraging opportunities for Starlings. Grazed grassland seems to provide the most optimal combination of high prey density and easy access to prey.

At the study site, Grazed grass was available in abundance immediately adjacent to the nest colony, which could explain the consistently high breeding density of Starlings here. The local composition of crops has remained largely unchanged during 1971–2016, during which time there has been no significant change in the mean production of nestlings produced per pair [20]. In order to obtain a better understanding of what influences density and accessibility of the prey, we would also need to consider the variation in mechanical and chemical treatment of the fields as well as determining the effect the presence of grazing cattle has *per se*, but such investigations were beyond the scope of this study.

Activity distance and the significance of resource dispersion

Ninety-two percent of foraging positions recorded from 17 Starlings of both sexes in two years were within 500 m of the nest, indicating the importance of foraging areas close to nest sites. Wiersma *et al.* [33] showed that daily flight times increased 4-fold with a 3-fold decline in food availability to caged Starlings, increasing daily energy expenditure by 43%. Starlings make up to 250 feeding roundtrips per day [28], so an increase from 100 m to 200 m will increase the total daily travelled distance from 50 km to 100 km. At a mean flight speed of 10 m per second (close to the optimal flight speed at minimum metabolic power of 9.4 W [34]) this would increase daily energy expenditure from 47 kJ to 94 kJ. Starling nestlings consume c. 40 g fresh food per day [35] or c. 160 *Tipula* larvae (mean wet weight c. 0.25 g and an energy content of c 4 kJ/g; [28, 35]); corresponding to a daily energy demand of c. 160 kJ per nestling. In this way, adding an additional 100 m to the foraging distance equates to c. 30% of the daily energy requirements of one nestling. Thus, extending foraging trips will adversely affect breeding success, reflected in the negative relationship between nestling feeding frequency and adult foraging distance [18], which may reduce nestling survival.

Increased selection with increasing foraging distance

As far as we are aware, few avian studies (e.g. Ring-billed Gulls *Larus delawarensis* [17] and Cinereous vulture *Aegypius monachus* [36]) have demonstrated an increase in habitat selection with distance-to-nest. In this study, we analyse the importance of distance and habitats, and combine them to analyse the relative importance of the different habitat types at different distances from the Starlings nesting site. The significance of Grazed grass for foraging Starlings in the agricultural landscape was further supported by the fact that the selection for this habitat type became more pronounced with increasing distance.

This result conforms to expectations, since the area within each additional 100 m wide circular distance bands away from the nest is increasing, thus providing a greater number of foraging opportunities if and when the Starling invests in longer foraging trips. However, this requires greater habitat selection to compensate for the increasing energetic costs associated with flying longer distances.

Nesting Starlings are classic central place foragers (as shown by aviary studies, e.g. [37] and in the field, e.g. [28]) and our new approach clearly demonstrated increasing habitat selection with distance-to-nest, confirming results from radio-transmitter studies [18]. It seems likely that this is the case for many other species for which such patterns have yet to be demonstrated. Improving telemetry technology offers exciting opportunities to improve our understanding of animal–habitat relationships at finer scales by incorporating interactions to the distance components of RSFs [38].

The 'Starling landscape' and conservation implications

The Starling is highly dependent on two important landscape elements, 1) nest site and 2) foraging areas, as is the case for many other species. Our results show that both resources must be available in close proximity within the 'Starling landscape'. Within Denmark, the extent of actively grazed grasslands has fallen in recent years as more cattle remain indoors throughout the year [16]. Given these trends and the propensity of Starlings nesting on adjacent farms to commute 500–700 m to forage on selected habitat adjacent to the study farm, it is easy to understand how loss of grazed grassland may have contributed to the observed Starling population declines. Such changes in the agricultural landscape have occurred nationally, as well as at a Western European scale, which may contribute to explaining the differences between declining trends here compared to stable and increasing trends in Eastern Europe [39]. The decline in grazed areas is also known to have an important effect on the populations of Little Owl (*Athene noctua*), another declining species that hunts insect prey in open farmland [40–41].

Summer Starling densities correlated with numbers of grazing cattle and changes in regional Starling breeding abundance correlate with changes in grazing intensity across Denmark [16]. However, even in parts of Denmark with very few cattle, Starlings can persist where a single local farm retains grazing cattle (own observations). Despite a farmland 'ocean' of unsuitable habitats within the agricultural mosaic, Starlings can persist if they can find 'islands' of nesting and foraging areas in sufficiently close proximity to provide safety from predators and sufficient food to provision nestlings to fledging. Such a habitat matrix is more frequent in western Denmark (where the more dominant dairy farming provides grazed grassland), where Starling densities remain highest and declines have been of least magnitude. In the arable dominated farmland in eastern Denmark, with little or no preferred Grazed or Grassland, the 'Starling landscape' is far more restricted and commuting distances are extended to relatively few distant 'islands' in far greater 'oceans' of unsuitable habitat for the Starling. Smith & Bruun [42] found that both breeding density and production of Starling young per nest was positively related to the availability of pasture close to the breeding colony.

Away from the study farm, loss of actively grazed grassland has presumably caused Starlings nesting in traditionally suitable areas to forage further and further from suitable nesting habitat, to a point where it is no longer energetically profitable to provision offspring at such long distance. This potentially supports the contention that the reduction of pasture in modern agricultural landscape may explain the declining Starling population, as cited by [42]. Elevating Starling breeding abundance can probably better be facilitated by establishing 'islands' of high quality Starling habitat across the farming landscape rather than by large areas of modest quality. Future studies should focus on the relationship between provisioning flight distance, foraging profitability and habitat selection in other farmland mosaics, where the distance and availability of habitats contrast the more favourable ones studied here and should also include urban areas and open woodland areas where Starling breed and also show declining trends. Comparisons should also be sought at larger spatial scales. For instance, comparing other parts of Denmark or other countries with less favourable agricultural landscape mosaics for Starlings with central or eastern parts of Europe, where locally breeding Starling numbers are either stable or increasing. The GPS-logger technology provides valuable information on for instance flight distances and home-range sizes e.g. [43] and we have here shown the value of deploying such devices on a species as small as a Starling for the first time, which illustrates the potential for similar studies on a larger number of species.

Supporting information

S1 Fig. Maps of the ringing site and the surrounding fields indicating the different crops and the foraging positions of 17 different tagged Starlings tracked during May 2015 and 2016.
(PDF)

S1 File. Data set used for analyses of use and selection of habitat categories of GPS-tagged Starlings.
(XLSX)

S1 Table. Information about the 17 loggers/Starlings showing year, logger, sex, start and length of each logger period, number of foraging positions and registered mean and max distance.
(DOCX)

Acknowledgments

Thanks to the Bird Ringing Centre, Natural History Museum of Denmark for permitting deploying loggers on the Starlings, to Michael Fink Jørgensen, 'Mikkel' Torben Mikkelsen and Karin Thellesen for valuable help with fieldwork and Carlo Catoni, Techno Smart for technical and practical advice all throughout both field seasons. Finally thanks to Jeroen Minderman and an anonymous referee for detailed and valuable comments to an earlier version of the manuscript.

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Henning Heldbjerg, Anthony D. Fox, Peder V. Thellesen, Lars Dalby & Peter Sunde

Common Starlings (*Sturnus vulgaris)* increasingly select for grazed areas with increasing distance-to-nest
Plos One (2017)

(Short title: Distance dependent habitat selection among Common Starlings)

Electronic supplementary material

Table S1. Information about the 17 loggers/Starlings showing year, logger, sex, start and length of each logger period, number of foraging positions and registered mean and max distance. Each logger provides a data file (txt) giving information on every fix until the battery runs short of energy. Each fix comprises the following information: Date (dd/mm/yyyy), Time (hh:mm:ss), Latitude, Longitude, Altitude, Instantaneous speed ground (km/h), Number of satellites, Horizontal Dilution of Precision (HDOP, a value which describes the geometric strength of satellite configuration on GPS accuracy; lower values indicate higher accuracy) and GSV Value (a measure of satellite reception power, higher values indicating better satellite reception; see [17].

Year	Logger	Sex	Data start	Data time (dd:hh:mm)	All Positions	Mean distance	Max distance	Selected Positions	Ring
2015	S3	M	05-05-2015 08:11	00:13:10	114	380	995	113	8A42334
2015	S2	M	06-05-2015 06:33	01:01:34	206	455	1101	195	8E03440
2015	S5	M	12-05-2015 06:03	01:03:36	313	194	586	302	8E03442
2015	S7	F	12-05-2015 06:31	00:23:36	210	160	463	193	8E03443
2015	S8	F	12-05-2015 06:45	00:14:46	259	187	466	254	8E03444
2015	S9	M	13-05-2015 06:00	01:05:49	382	256	830	374	8E03447
2015	S10	F	13-05-2015 06:33	01:02:16	245	302	620	237	8E03446
2016	S4a	F	07-05-2016 00:01	01:06:08	352	222	706	351	8E03626
2016	S9a	F	07-05-2016 00:05	01:04:21	245	294	804	241	8E03622
2016	S1	F	07-05-2016 00:20	01:06:13	174	234	891	174	8E03627
2016	S11	M	08-05-2016 00:00	01:05:06	337	169	450	337	8E03618
2016	S12	F	08-05-2016 00:00	00:05:59	52	210	333	52	8E03632
2016	S13	M	08-05-2016 00:00	00:16:19	52	145	293	52	8E03628
2016	S14	M	08-05-2016 00:00	01:05:49	185	175	336	185	8E03629
2016	S17	M	08-05-2016 00:00	01:07:59	280	182	653	280	8E03630
2016	S4b	F	15-05-2016 00:00	01:06:13	328	125	262	328	8E03634
2016	S9b	F	15-05-2016 00:00	01:06:54	369	100	245	369	8E03621

Supporting information for the paper:

Common Starlings (Sturnus vulgaris) increasingly select for grazed areas with increasing distance-to-nest
Henning Heldbjerg, Anthony D. Fox, Peder V. Thellesen, Lars Dalby & Peter Sunde.
Plos One (2017)

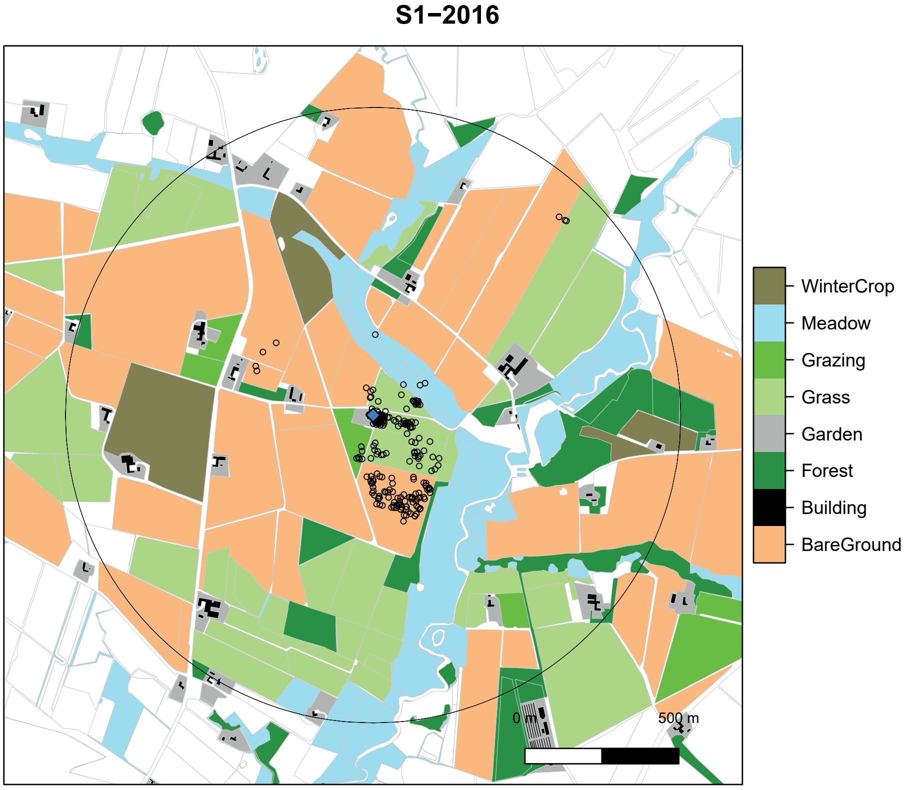
Data set used for analyses of use and selection of habitat categories of GPS-tagged Starlings:

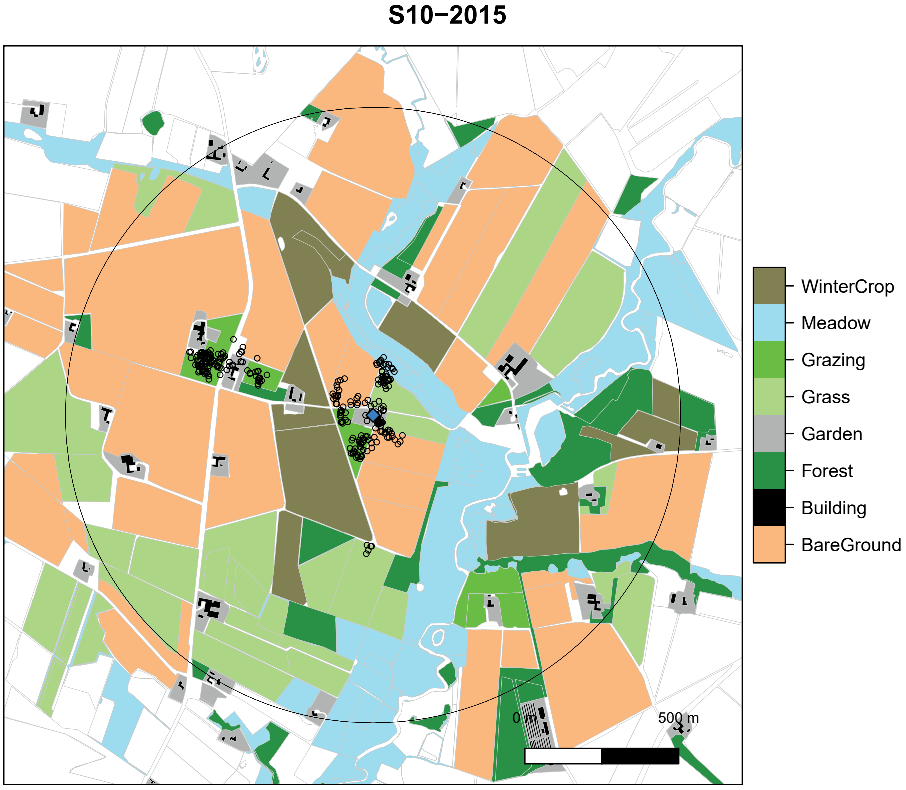
Variable name	Explanation
LoggerID	Logger (starling) Identity (17 starlings in total)
Sex	Gender of starling: F=Female, M= Male
Year	Study year
U_A	1=use (GPS location), 0=availability point (one for every 50 m in grid)
Distance	Distance from nest (centre of colony) in m
dist_int100	100-m distance from nest: 0-99, 100-199, …. 900-999}
dist_int200_3cat	Distance intervals (3 categories): 0-199m, 200-399m, 400-999m
landcover	Landcover type: Selected for the analysis:{Grazed, Grass, Bareground, Meadow, WinterCrop}, deselected: {NA, Forest; Bulding, Garden}
PolyID	Idendity of GIS-polygon
selected	1= observation selected for the analyses (< 1000 m from the nest, landcover = {Grazed, Grass, Bareground, Meadow, WinterCrop}, 0 = observation not included in analysis (shaded)
Data set	23029 records available at http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0182504#sec018

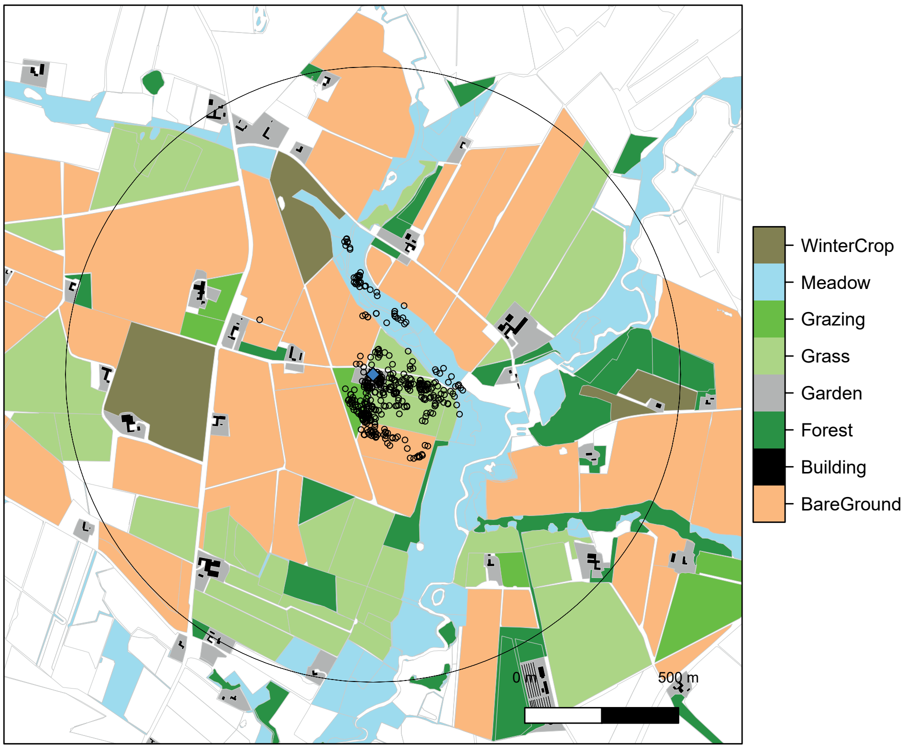
Supporting information for the paper: Starlings (*Sturnus vulgaris*)

Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest
Henning Heldbjerg, Anthony D. Fox, Peder V. Thellesen, Lars Dalby & Peter Sunde.
Plos One (2017).

This document contains maps of the ringing site and the surrounding fields indicating the different crops and the foraging positions of 17 different tagged Starlings tracked during May 2015 and 2016.







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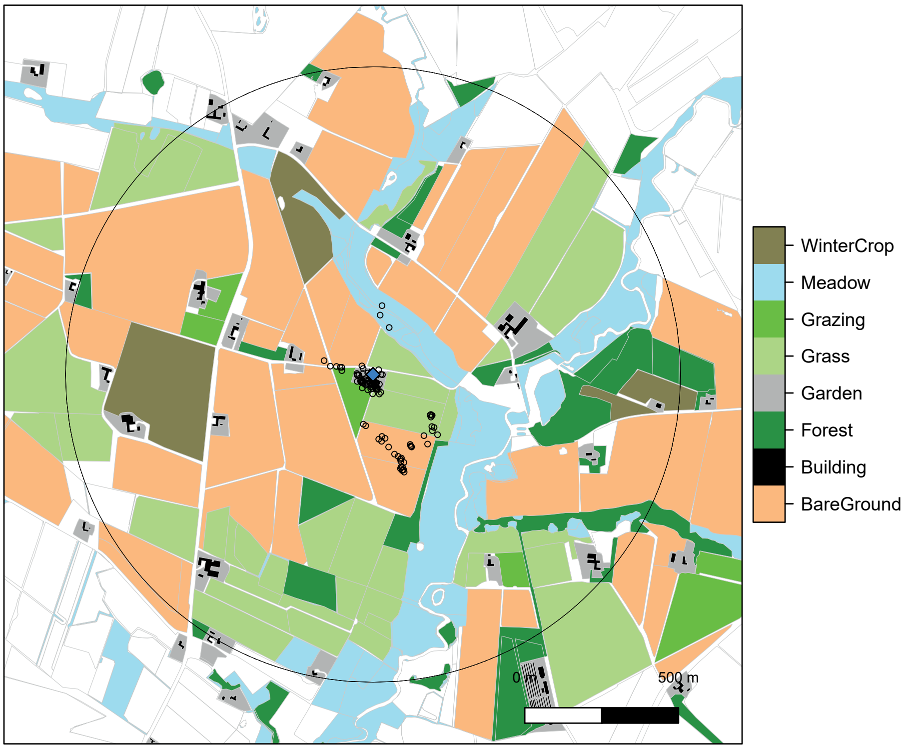
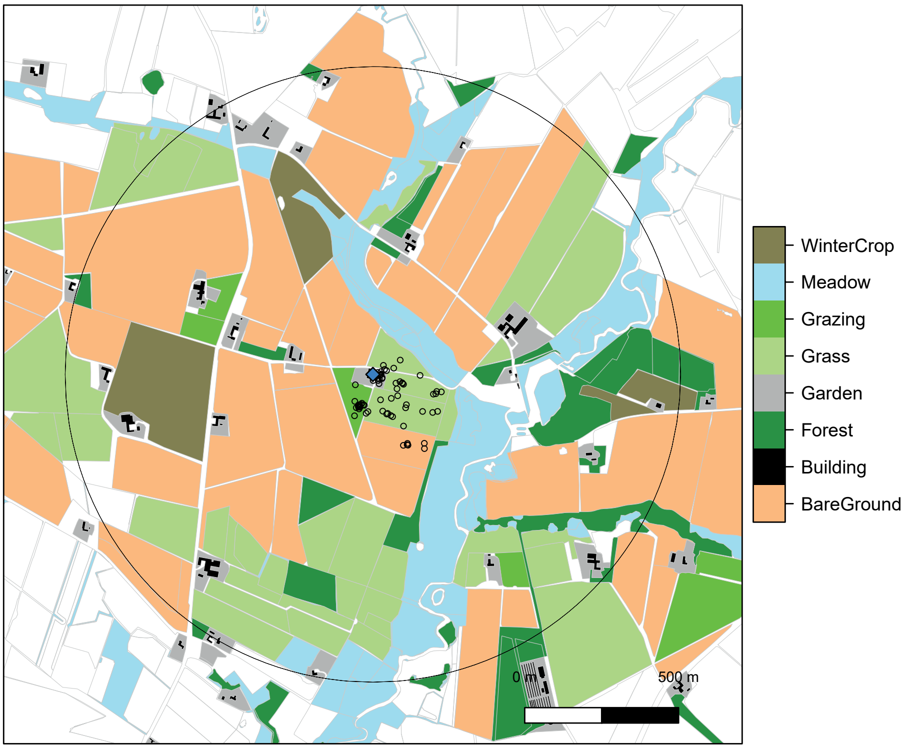


S12−2016

S13−2016



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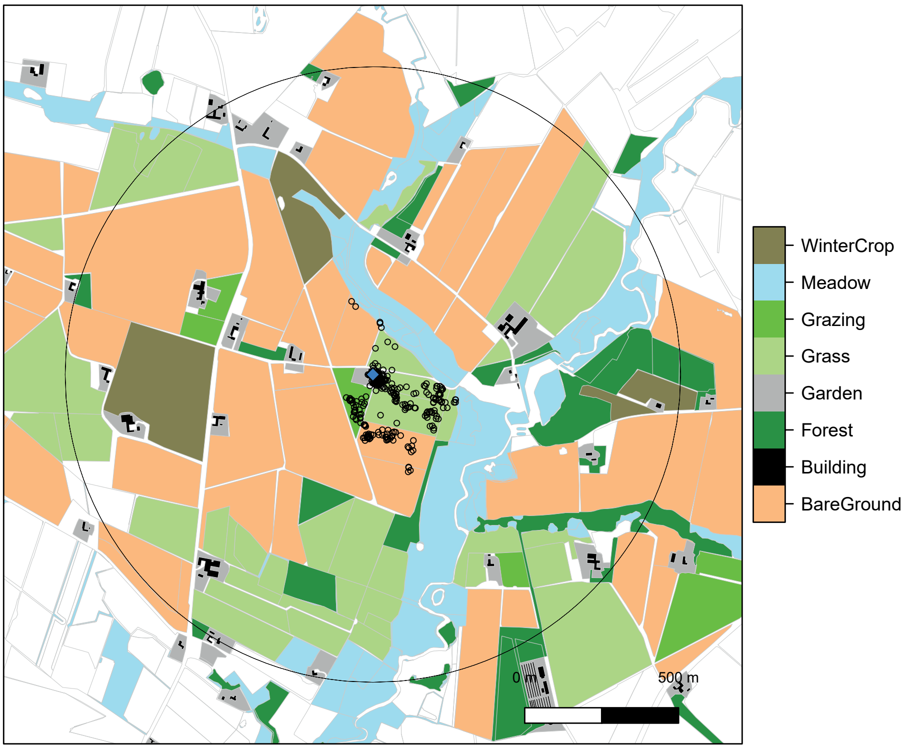

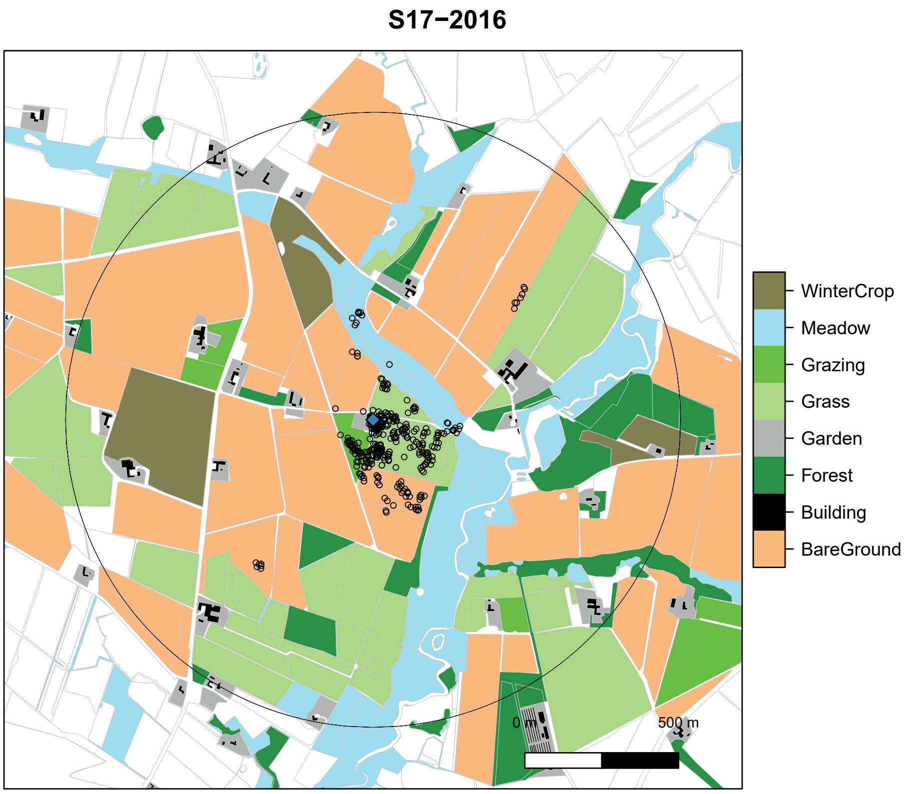
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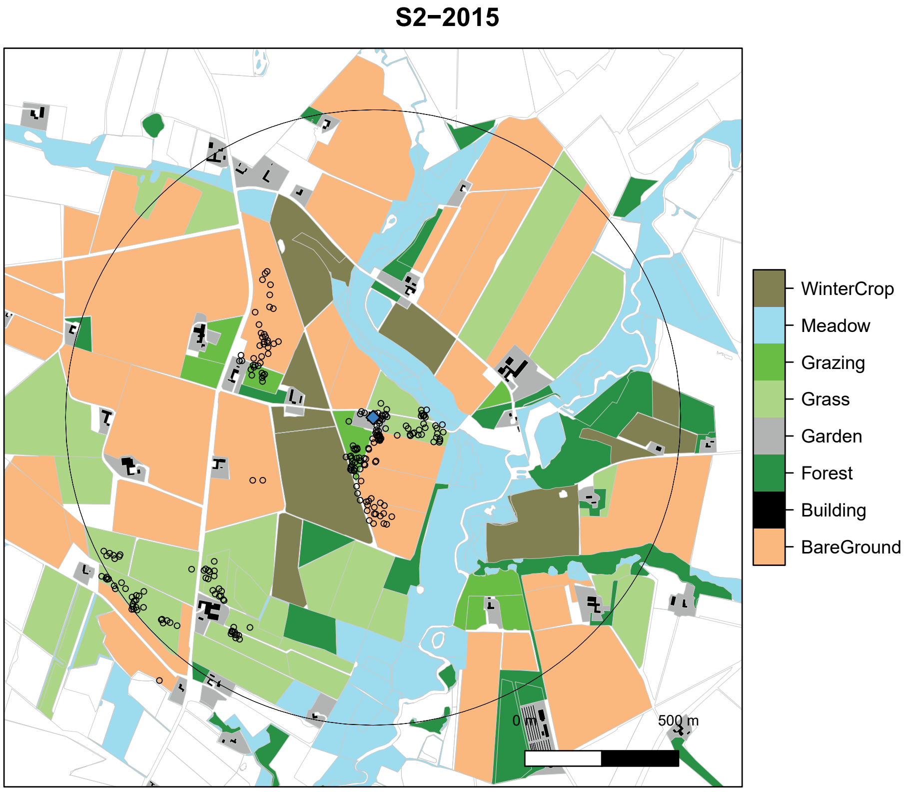
WinterCrop
Meadow
Grazing
Grass
Garden
Forest
Building
BareGround
0 m
500 m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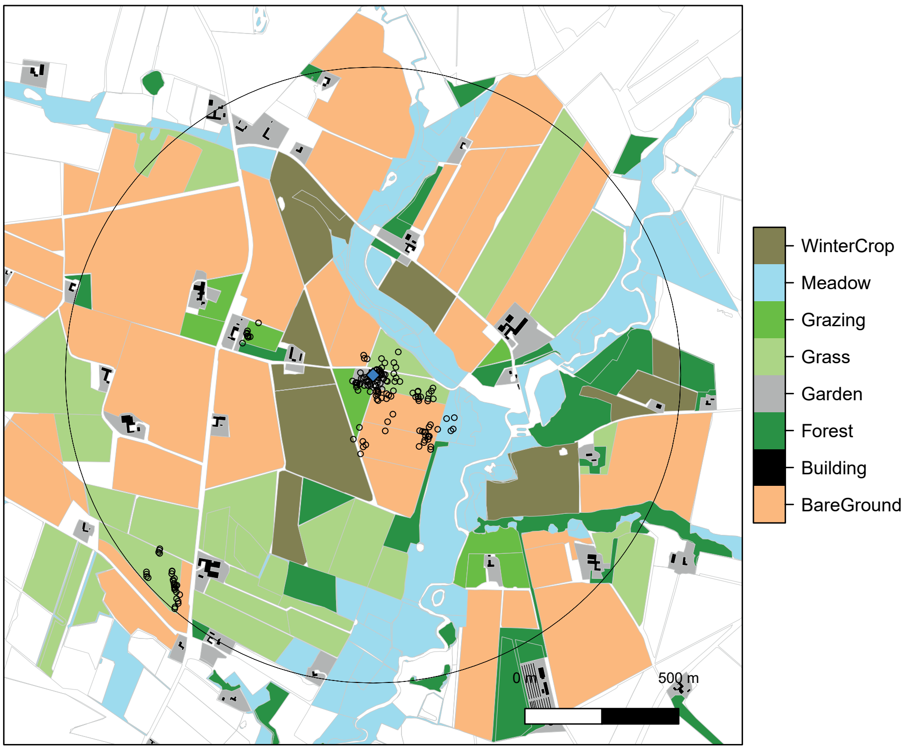
WinterCrop
Meadow
Grazing
Grass
Garden
Forest
Building
BareGround
0 m
500 m



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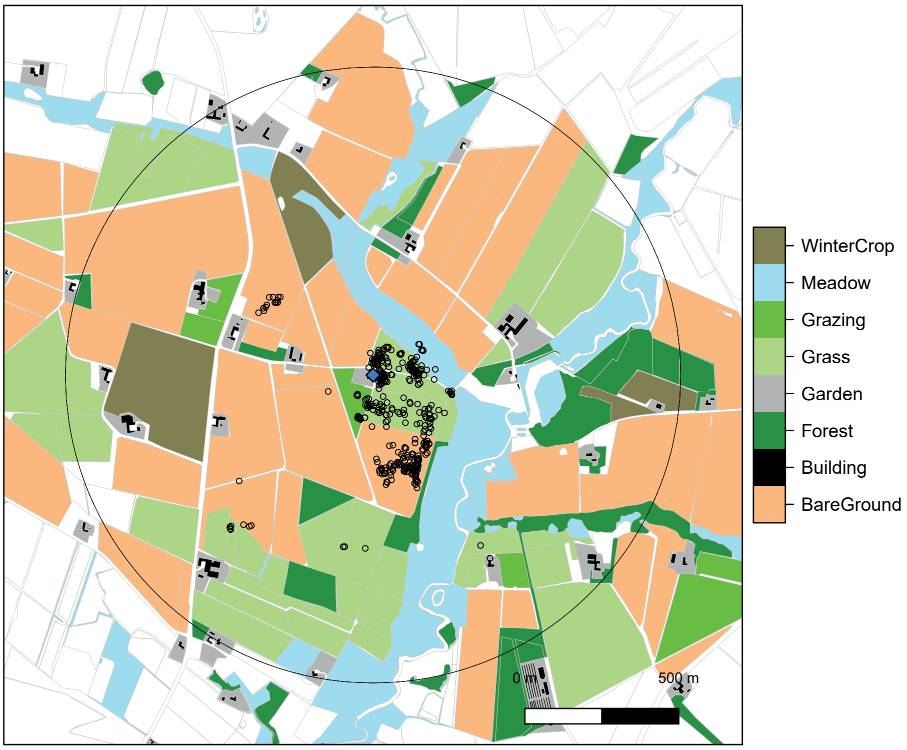

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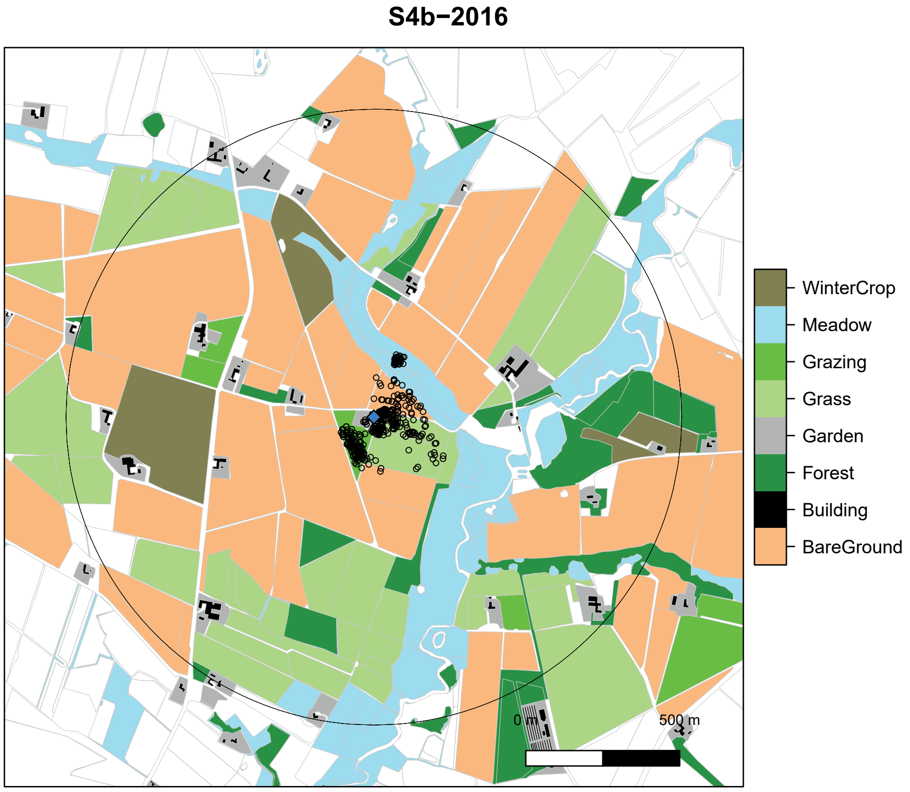
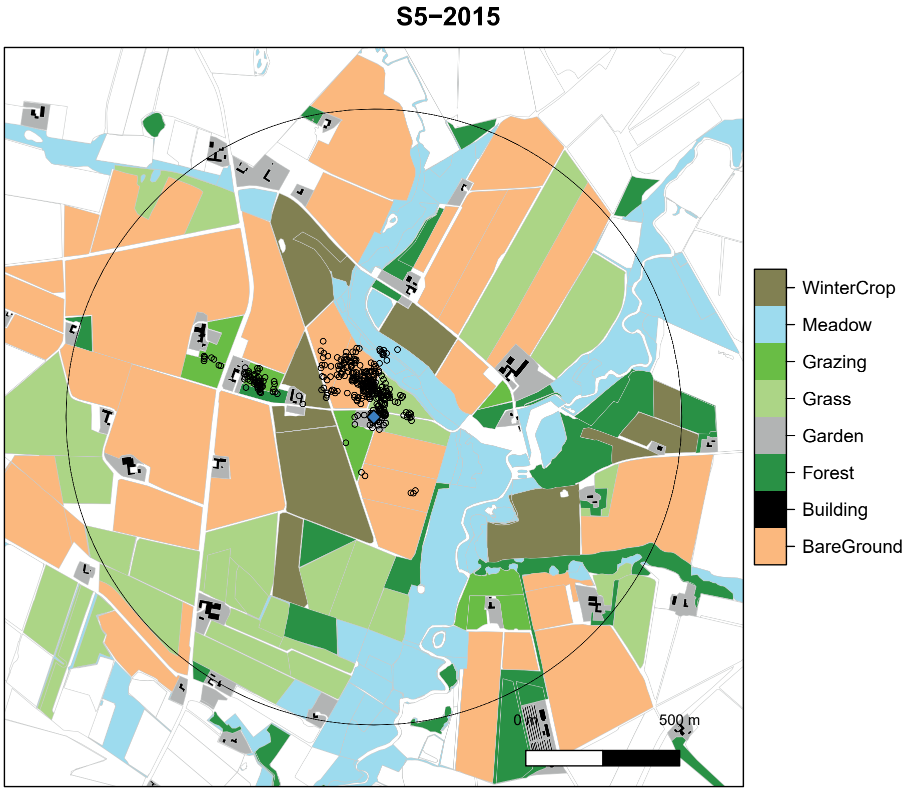

S4b−2016
WinterCrop
Meadow
Grazing
Grass
Garden
Forest
Building
BareGround
0 m
500 m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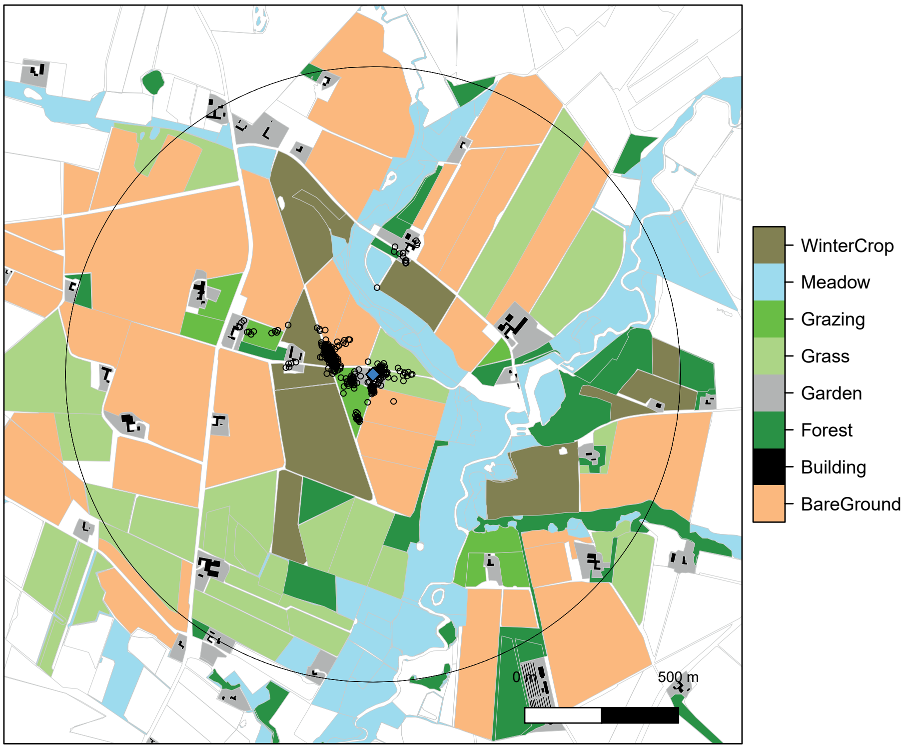
Meadow
Grazing
Grass
Garden
Forest
Building
BareGround
0 m
500 m

S7−2015



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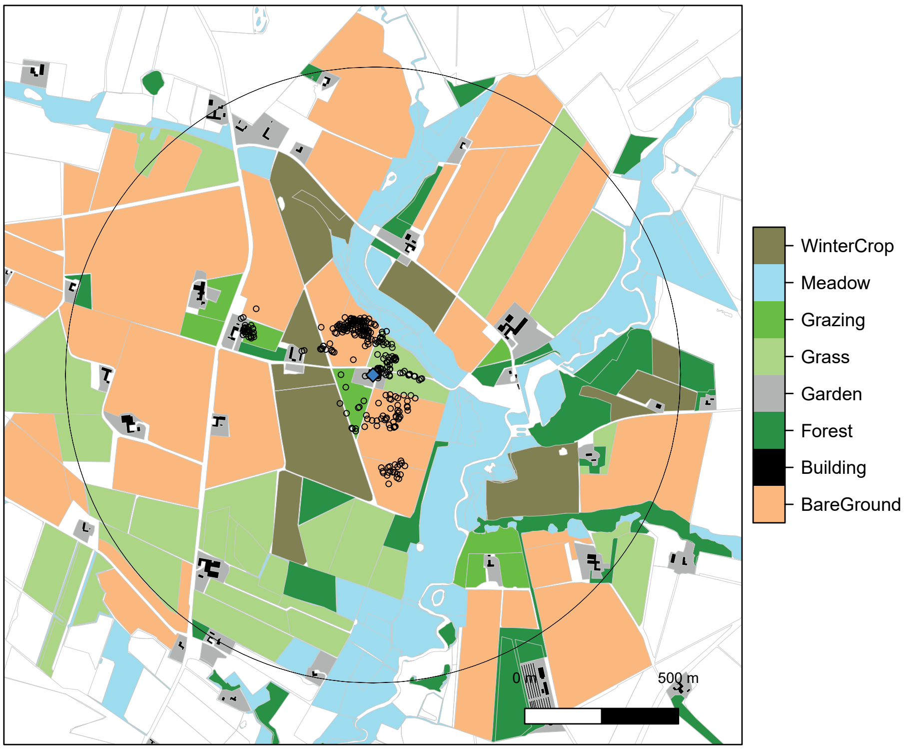
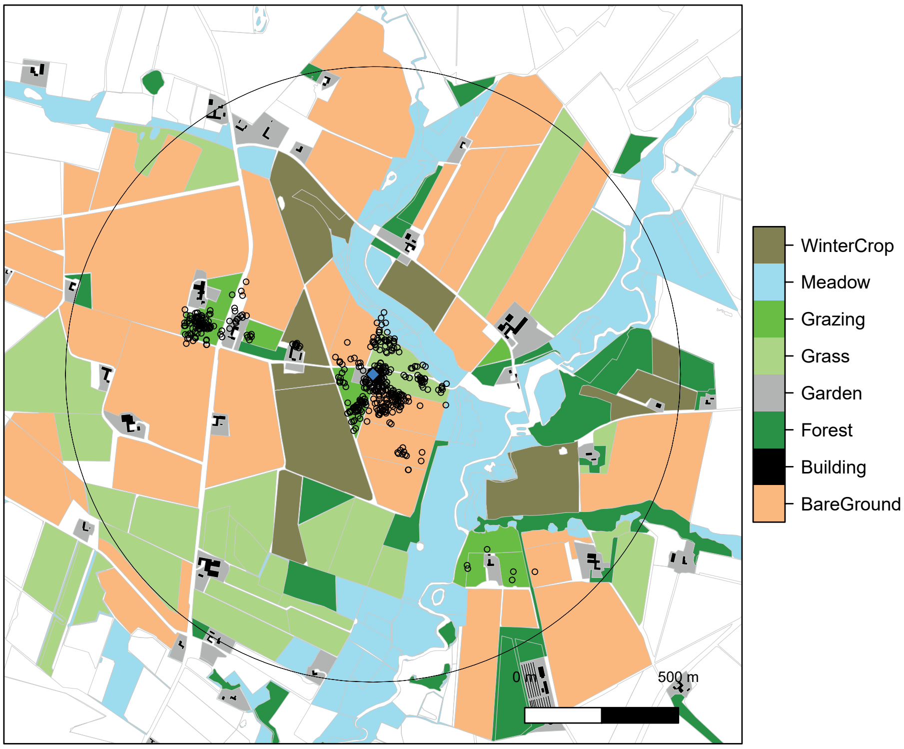
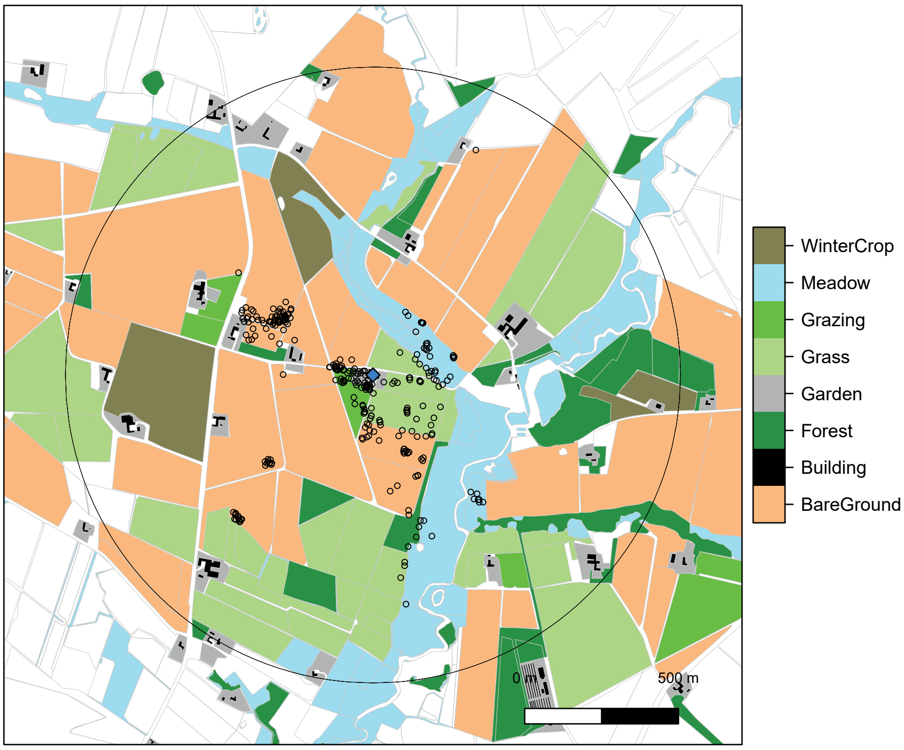
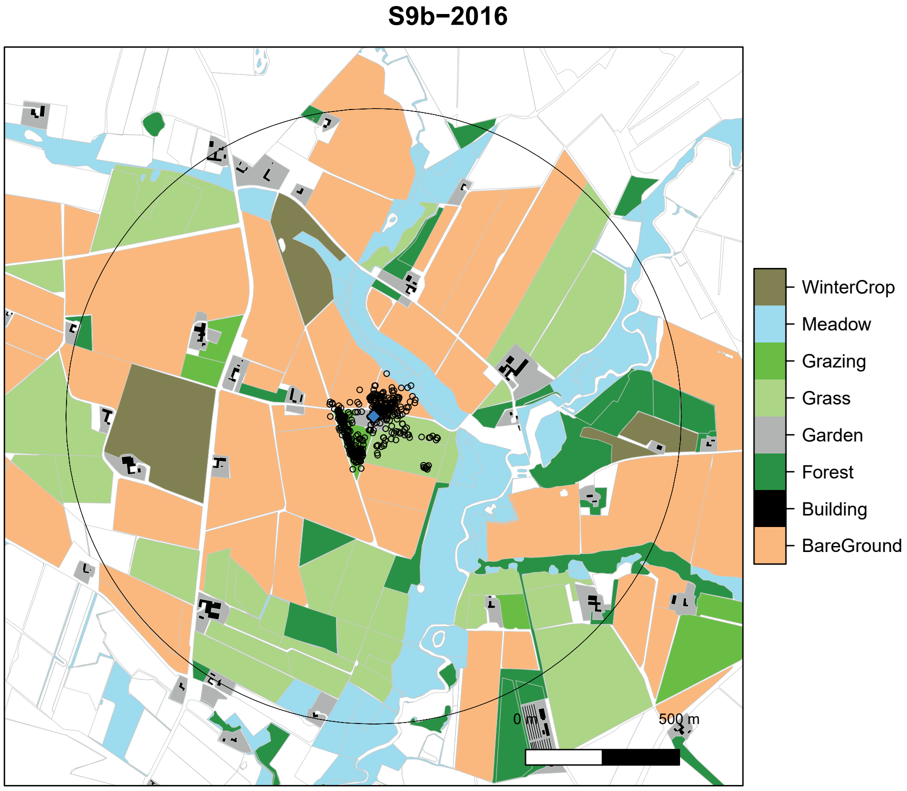


S9−2015



S9a−2016




S9b−2016
WinterCrop
Meadow
Grazing
Grass
Garden
Forest
Building
BareGround
0 m
500 m

PAPER 6

LARGE-SCALE CLIMATIC DRIVERS OF REGIONAL WINTER BIRD POPULATION TRENDS

Aleksi Lehikoinen[1]*, Ruud P.B. Foppen[2,3], Henning Heldbjerg[4,5], Ake Lindstrøm[6], Willem van Manen[2], Sirke Piirainen[1], Chris A.M. van Turnhout[2,3] and Stuart H.M. Butchart[7,8]

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Diversity and Distributions A Journal of Conservation Biogeography

BIODIVERSITY RESEARCH

Large-scale climatic drivers of regional winter bird population trends

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ABSTRACT

Aim Changes in climate and land use practices have been found to affect animal populations in different parts of the world. These studies have typically been conducted during the breeding season, whereas the non-breeding season (hereafter 'winter') has received much less attention. Changes in regional winter abundances could be caused by changes in overall population sizes and/or redistribution of populations. We tested these mechanisms for terrestrial winter bird population changes in Northern Europe and explored the role of climate change and species habitat preference.

Location The Netherlands, Denmark, Sweden, Finland.

Methods We used winter bird counts from four countries conducted annually between 15 December and 20 January in 1980/1981–2013/2014. We report national population trends for 50 species for which a trend could be calculated in at least three of the countries. We analysed country-specific population growth rates in relation to species' climatic summer and winter niches, habitat preference and migratory behaviour.

Results Species breeding in colder (typically northern) areas showed more negative winter population trends than species breeding in warmer areas. Regional winter population trends were negatively correlated with characteristics of their winter climatic niche: populations in the colder part of their winter distribution increased in abundance, whereas populations in the warmer part of their winter distribution decreased. Woodland species tended to do better than farmland species. Migratory behaviour did not explain variation in population trends.

Main conclusions The generally decreasing winter population trends of cold-dwelling breeding species probably reflect the general decline in population sizes of these species. In contrast, increasing winter population trends for populations in the colder parts of the winter distribution indicate a redistribution of wintering individuals towards the north-east. Both these patterns are likely caused by climate change.

Keywords
farmland, forest, global warming, management actions, monitoring, spatio-temporal changes.

INTRODUCTION

An increasing number of studies has shown that distributions and population dynamics of animals are affected by climate change and human land use practices (Parmesan *et al.*, 1999; Fahrig, 2003; Parmesan, 2006; Jetz *et al.*, 2007; Butchart *et al.*, 2010; Chen *et al.*, 2011). Such distribution and population changes have most frequently been studied during the reproductive season (Jonsson & Jonsson, 2009; Brommer & Møller, 2010; Breed *et al.*, 2012; Walsh *et al.*, 2015). Spatio-temporal population changes during other parts of the annual cycle have received much less attention. It is widely acknowledged that climate change influences the phenology of migratory species, affecting the occurrence of

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species in space and time (Parmesan, 2006; Lehikoinen & Sparks, 2010). However, long-term changes in abundances during the non-breeding season (hereafter 'winter') have rarely been examined, especially at large spatial scales and for a large number of species. It is important to understand what influences distribution and abundance outside the reproductive season, as processes during winter have a large impact on survival and thus general population dynamics (Newton, 1998; Jørgensen *et al.,* 2016).

One in five of all bird species are migratory, and this proportion is greater at high latitudes (Kirby *et al.*, 2008; Newton, 2008). Birds are one of the few taxonomic groups for which large-scale, long-term and multispecies datasets are available (Pearce-Higgins & Green, 2014). This makes birds excellent species to study the effect of increasing winter temperature on winter distribution. In North America, the centre of wintering abundances of 254 bird species has shifted northwards *c.* 1 km per year due to increasing winter temperature during 1975–2004 (La Sorte & Thompson, 2007; La Sorte & Jetz, 2012). Furthermore, some wader and duck species in Europe have shifted the centre of their winter distribution towards the north-east (Austin & Rehfisch, 2005; Maclean *et al.*, 2008; Lehikoinen *et al.*, 2013a; Pavón-Jordán *et al.*, 2015). Nevertheless, these studies have not investigated what factors are correlated with the species-specific variation in population trends. To our knowledge, the only multi-species study on wintering populations that examined the impact of climate change and human land use changes simultaneously is from Finland (Fraixedas Nuñez *et al.*, 2015a). This study showed that population sizes of wintering water birds have increased on average, due to increasing temperature, while increasing population sizes in urban bird species and declines in forest bird species are likely driven by human land use changes. Nevertheless, to draw broader conclusions on which factors are influencing trends of wintering populations, such patterns should be investigated at larger spatial scales, taking regional variation into account.

We investigated which factors have driven the winter population trends of 50 bird species of terrestrial habitats over 34 years in four countries spanning more than 2000 km along a north-east–south-west latitudinal gradient in Northern Europe. We concentrate here on land-birds, as large-scale studies on wintering terrestrial bird species are largely lacking (but see La Sorte & Thompson, 2007; La Sorte & Jetz, 2012).

Regional winter population trends may be driven by at least two major processes: i) changes in the overall population size, which will lead to an increase or decrease in the regional winter population size; and/or ii) redistribution of the winter population, as a result of increases in some regions and decreases in others. To investigate these two alternatives, we studied the national winter population trends in relation to species' traits linked to general population drivers, that is climate and land use, during breeding and non-breeding season. A change in overall population size is known to be linked with migratory behaviour (Laaksonen & Lehikoinen, 2013; Vickery *et al.*, 2014; Jørgensen *et al.,* 2015). However, redistribution of the winter population is also connected with migratory behaviour because of a change in the proportion of individuals that migrate, and/or a reduction in the distance that individuals travel, possibly as a response to milder winters (Austin & Rehfisch, 2005; Maclean *et al.*, 2008; Visser *et al.*, 2009; Lehikoinen *et al.*, 2013a).

To evaluate drivers of overall population size, we first investigated whether characteristics of the climatic niche during the breeding season was associated with population trends, as more northern and cold-dwelling species have declined in North Europe compared to southern species (Devictor *et al.*, 2008; Jiguet *et al.*, 2013; Laaksonen & Lehikoinen, 2013; Lindström *et al.*, 2013). Our first hypothesis was that cold-dwelling birds will on average show more negative winter trends than more southerly breeding species, simply because cold-dwelling species are expected have suffered more from warmer summers.

Second, we evaluated the potential impacts of human land use changes on wintering birds by adding habitat preference as a covariate. We hypothesize that birds breeding and wintering in woodland would fare better than farmland birds, as farmland biodiversity has declined severely in Europe in recent decades (Donald *et al.*, 2001; Warren *et al.*, 2001; Gregory *et al.*, 2005, 2007). However, there could be spatial differences in land use changes throughout our study area, and thus, an interaction between country and habitat could reveal local differences. For instance, many wintering forest birds have declined in Finland (Fraixedas Nuñez *et al.*, 2015a). If forest management has had more negative impacts in the north of Europe, we would expect a significant negative interaction between region and habitat.

Third, in contrast to drivers of overall population change, we hypothesize that regional winter trends are affected by the climatic niche of each species during winter. With warmer winters in northern Europe [European Environment Agency (EEA), 2012], we expect more positive trends in winter population sizes in the colder parts of the winter distribution, and more negative trends in the warmer parts of the winter distribution (Jiguet *et al.*, 2010a,b; Lehikoinen *et al.*, 2013a). To evaluate this, we developed and applied a 'species winter temperature index' for European land-birds (cf. Devictor *et al.*, 2008, and see Materials and Methods).

Finally, we examined the impact of migratory behaviour *per se*, as this has been shown to be associated with species' population trends (Vickery *et al.*, 2014; Jørgensen *et al.,* 2015; Gilroy *et al.*, 2016) and also to impact the redistribution of wintering populations (Fraixedas Nuñez *et al.*, 2015a). We hypothesize that winter populations of partial migrants increased more than residents. Partial migrants can benefit from favourable circumstances during the breeding and non-breeding season, and/or from a shift of wintering ranges towards the north because of more favourable winter conditions (Brommer, 2008; Meller *et al.*, 2016; Välimäki *et al.*, 2016).

MATERIAL AND METHODS

Study area and census data

The study area includes four mainly northern European countries: the Netherlands, Denmark, Sweden and Finland. These countries are situated along a south-west–north-east climatic gradient spanning *c.* 2000 km between 51° and 70°N (Fig. S1). In all countries, winter populations have been systematically monitored annually at least since winter 1980–1981 (hereafter winter 1981), and our study period covers the winters 1981–2014 (34 years). The national schemes each use somewhat different methods (explained below in more detail), but this does not influence the results of our study, as the primary analysis is a comparison between national temporal trends, which are largely independent of census methods (e.g. point counts, line transects and territory mapping, see Gregory *et al.*, 2005).

In the Netherlands, the winter counts consist of free-choice point-count routes, which are surveyed once during mid-winter, in the period between 15 December and 1 January (Boele *et al.*, 2008). Each route consists of 20 points, separated by at least 500 m, at which all birds heard or seen are counted during exactly 5 min. The counts started in 1978. The annual number of routes counted averaged 376 (range 143–464) during the study period. The routes are distributed over the entire country (Fig. S1). In all countries, all routes counted at least twice are included in the analyses.

The Danish Common Winter Bird Monitoring programme is based upon free-choice point counts censused in the period 20 December–20 January. Each route consists of 10–20 points. At each point, all birds seen and heard, regardless of distance from observer, are registered and recorded in a 5-min observation window (Heldbjerg, 2005; Nyegaard *et al.*, 2015). The number of routes increased from around 100 at the start and has been relatively stable around 280 since 1988 (mean 244, range 104–324 in the whole period). The routes are distributed over the entire country (Fig. S1).

In Sweden, the winter counts consist of free-choice point-count routes, which are surveyed either five times per winter or once during mid-winter (Green & Lindström, 2015). For the present analysis, we only used data from the more numerous midwinter counts (19 December–8 January). The average annual number of mid-winter counts was 347 (range 246–505). Each route consists of 20 points, separated by at least 300 m, at which all birds heard or seen are counted during exactly 5 min. Most routes have been surveyed in the southern half of Sweden, in and around the most human-populated regions. On the few winter counts that are carried out in the northern half of Sweden, normally very few individuals of a small number of species are observed (Fig. S1).

In Finland, monitoring of winter birds since the 1950s is based on a free-choice line-transect method. Annual abundances of wintering bird populations have been monitored on 4000 transect routes, the average length of which is about 10 km. Observers repeat the same route by either walking or skiing and count all birds recorded (see Lehikoinen *et al.*, 2013b; Fraixedas Nuñez *et al.*, 2015a). There are three census periods in winter, but for this study, we only used the mid-winter counts from 25 December to 7 January because this maximizes survey effort and this period overlaps with those in the other countries. The annual mean number of routes was 530 (range 455–602). The majority of the census sites are carried out in the south and central part of the country (Fig. S1; Fraixedas Nuñez *et al.*, 2015a). In all countries, all routes counted at least twice are included in the analyses.

Selection of species

We included all land-bird species that had reliable trend data (data from at least 29 of 34 winters) from at least three of the four countries. In most of the cases (> 93%), data covered all years. Altogether, our analyses included 50 species. The country-specific sample sizes are shown in Table 1.

Temperature data

To evaluate temporal and spatial trends in winter temperatures, we calculated mean temperatures from each country during December–February. For the Netherlands, we used the referential weather station from De Bilt, provided by the Dutch Royal Meteorological Institute (KNMI) (https://data.knmi.nl/portal/KNMI-DataCentre.html#_). For Denmark, we used the mean Danish temperature provided by the Danish Meteorological Institute (http://www.dmi.dk/vejr/arkiver/maanedsaesonaar/). For Sweden, we used monthly mean data from the Swedish Meteorological and Hydrological Institute (SMHI, www.smhi.se, data were sent on request). Data from approximately 300 weather stations around Sweden were interpolated to a 4 × 4 km grid, using geo-statistic interpolation (Johansson, 2000). We averaged data from all grid stations S of 61°N, from where the vast majority of all bird data originate. For Finland, weather data interpolated in 10 km grids was obtained from the Finnish Meteorological Institute (www.fmi.fi, Venäläinen *et al.*, 2005). We used data between 59°50′N and 68°N, which covers > 95% of the census sites.

Explanatory variables

We used four explanatory variables for the national trends. First, we used the Species Temperature Index during the breeding season (first variable, hereafter STIs) to describe the general temperature niche of the species during their breeding season (derived from Devictor *et al.*, 2008). The STIs are the mean temperature in April–August (1961–2008, www.worldclim.org) of the breeding distribution of the species in Europe (Hagemeijer & Blair, 1997). Typically, cold-dwelling species that have more northerly breeding distributions have lower

Table 1 Species-specific population trends (annual rate of change including standard errors) of study species over the period 1981–2014 with mean annual sample sizes (*N*) in Finland (FIN), Sweden (SWE), Denmark (DK) and the Netherlands (NL).

Species	FIN slope ± SE	FIN *N*	SWE slope ± SE	SWE *N*	DK slope ± SE	DK *N*	NL slope ± SE	NL *N*
Grey Partridge *Perdix perdix*	−0.010 ± 0.009	147	**−0.046 ± 0.021**	32	**−0.041 ± 0.010**	173	**−0.043 ± 0.004**	280
Northern Goshawk *Accipiter gentilis*	0.001 ± 0.003	66	**−0.018 ± 0.006**	26	0.001 ± 0.009	15	**0.021 ± 0.004**	63
Eurasian Sparrowhawk *Accipiter nisus*	**−0.005 ± 0.002**	93	**−0.016 ± 0.004**	51	**−0.013 ± 0.004**	85	**−0.010 ± 0.002**	202
Common Buzzard *Buteo buteo*	**0.061 ± 0.013**	7	**0.006 ± 0.002**	257	**0.015 ± 0.002**	639	**0.023 ± 0.001**	1979
Rough-legged Buzzard *Buteo lagopus*	–	–	**−0.017 ± 0.005**	41	**−0.053 ± 0.006**	50	**−0.037 ± 0.007**	18
Common Kestrel *Falco tinnunculus*	–	–	**−0.020 ± 0.007**	24	**−0.009 ± 0.004**	146	**−0.009 ± 0.001**	598
Common Wood Pigeon *Columba palumbus*	–	–	**0.023 ± 0.006**	888	**0.030 ± 0.002**	5964	0.002 ± 0.002	51712
Eurasian Collared Dove *Streptopelia decaocto*	−0.001 ± 0.012	31	−0.025 ± 0.013	42	**−0.029 ± 0.006**	218	−0.001 ± 0.002	2090
European Green Woodpecker *Picus viridis*	–	–	−0.003 ± 0.003	113	**−0.035 ± 0.010**	13	**0.044 ± 0.004**	102
Black Woodpecker *Dryocopus martius*	**0.032 ± 0.002**	120	0.001 ± 0.003	126	**−0.021 ± 0.010**	19	−0.004 ± 0.004	53
Great Spotted Woodpecker *Dendrocopos major*	**0.020 ± 0.001**	2009	−0.000 ± 0.001	830	**0.011 ± 0.002**	417	**0.026 ± 0.002**	859
Eurasian Skylark *Alauda arvensis*	–	–	−0.043 ± 0.051	12	−0.003 ± 0.016	96	**−0.013 ± 0.004**	2030
Winter Wren *Troglodytes troglodytes*	–	–	**0.030 ± 0.004**	128	**0.018 ± 0.002**	440	**0.010 ± 0.001**	1450
Bohemian Waxwing *Bombycilla garrulus*	0.006 ± 0.009	14247	**0.047 ± 0.009**	1319	**0.101 ± 0.038**	229	–	–
Meadow Pipit *Anthus pratensis*	–	–	0.007 ± 0.017	36	0.009 ± 0.020	75	−0.002 ± 0.004	1115
European Robin *Erithacus rubecula*	**0.059 ± 0.011**	13	**0.037 ± 0.005**	66	0.005 ± 0.003	183	**0.014 ± 0.001**	1254
Common Blackbird *Turdus merula*	**0.062 ± 0.002**	1053	**0.021 ± 0.002**	1087	**0.004 ± 0.001**	3039	**0.010 ± 0.001**	6372
Fieldfare *Turdus pilaris*	−0.007 ± 0.010	16256	0.003 ± 0.005	8328	0.002 ± 0.004	4393	**−0.015 ± 0.003**	15508
Redwing *Turdus iliacus*	–	–	0.061 ± 0.038	102	**0.044 ± 0.011**	253	**−0.013 ± 0.003**	3229
Goldcrest *Regulus regulus*	**−0.025 ± 0.001**	3049	**−0.030 ± 0.002**	1584	**−0.022 ± 0.002**	1325	**−0.032 ± 0.002**	1517
Long-tailed Tit *Aegithalos caudatus*	**0.058 ± 0.004**	555	0.007 ± 0.004	323	**−0.025 ± 0.005**	301	**0.007 ± 0.002**	1656
Willow Tit *Poecile montanus*	**−0.032 ± 0.001**	4555	**−0.031 ± 0.002**	763	–	–	**−0.041 ± 0.002**	288
Marsh Tit *Poecile palustris*	–	–	**−0.027 ± 0.002**	781	**−0.007 ± 0.003**	350	0.005 ± 0.003	265
European Crested Tit *Lophophanes cristatus*	**−0.009 ± 0.001**	1103	**−0.008 ± 0.002**	327	**−0.019 ± 0.004**	160	**−0.013 ± 0.002**	408
Coal Tit *Periparus ater*	**0.004 ± 0.001**	845	**−0.015 ± 0.002**	356	−0.000 ± 0.003	375	**−0.046 ± 0.003**	289
Eurasian Blue Tit *Cyanistes caeruleus*	**0.063 ± 0.001**	12796	**0.022 ± 0.001**	3313	0.001 ± 0.002	1657	−0.001 ± 0.001	3774
Great Tit *Parus major*	**0.013 ± 0.001**	29040	**0.003 ± 0.001**	5841	**−0.009 ± 0.001**	4094	**−0.006 ± 0.001**	6742
Eurasian Nuthatch *Sitta europaea*	−0.001 ± 0.012	12	**0.014 ± 0.001**	1320	**0.019 ± 0.002**	446	**0.041 ± 0.002**	625
Eurasian Treecreeper *Certhia familiaris*	0.003 ± 0.002	418	**−0.013 ± 0.002**	188	−0.006 ± 0.004	89	–	–
Great Grey Shrike *Lanius excubitor*	**0.018 ± 0.004**	34	−0.000 ± 0.005	32	−0.009 ± 0.010	11	**0.027 ± 0.007**	19
Eurasian Jay *Garrulus glandarius*	**0.012 ± 0.001**	1089	**−0.005 ± 0.002**	802	−0.001 ± 0.002	655	**0.009 ± 0.001**	1682
Common Magpie *Pica pica*	**−0.003 ± 0.001**	9875	**−0.004 ± 0.001**	3499	−0.002 ± 0.002	1868	**−0.028 ± 0.001**	5149

Table 1 Continued.

Species	FIN slope ± SE	FIN *N*	SWE slope ± SE	SWE *N*	DK slope ± SE	DK *N*	NL slope ± SE	NL *N*
Western Jackdaw *Corvus monedula*	**0.051 ± 0.002**	8817	**0.006 ± 0.002**	10317	**0.016 ± 0.003**	4312	−0.002 ± 0.001	31009
Rook *Corvus frugilegus*	**−0.084 ± 0.039**	12	**0.029 ± 0.005**	1084	−0.003 ± 0.003	4610	**−0.030 ± 0.002**	13469
Hooded/Carrion Crow *Corvus corone*	**−0.009 ± 0.001**	13501	**−0.015 ± 0.001**	9547	**−0.006 ± 0.002**	6960	−0.000 ± 0.023	19058
Northern Raven *Corvus corax*	**0.032 ± 0.002**	897	**0.013 ± 0.002**	1257	**0.116 ± 0.010**	122	**0.025 ± 0.009**	53
Common Starling *Sturnus vulgaris*	−0.006 ± 0.010	78	**0.063 ± 0.020**	113	0.014 ± 0.011	512	−0.004 ± 0.002	77336
House Sparrow *Passer domesticus*	**−0.043 ± 0.001**	17421	**−0.022 ± 0.003**	1062	**−0.030 ± 0.003**	1450	**−0.021 ± 0.001**	5656
Eurasian Tree Sparrow *Passer montanus*	**0.089 ± 0.003**	2831	**−0.009 ± 0.002**	1914	**0.013 ± 0.003**	1619	**−0.039 ± 0.002**	2598
Common Chaffinch *Fringilla coelebs*	0.002 ± 0.002	231	0.004 ± 0.005	390	**−0.005 ± 0.002**	3055	**0.010 ± 0.002**	10614
Brambling *Fringilla montifringilla*	**−0.014 ± 0.007**	178	−0.017 ± 0.019	13947	**−0.012 ± 0.006**	1548	**−0.030 ± 0.005**	1033
European Greenfinch *Carduelis chloris*	**0.045 ± 0.001**	17698	−0.004 ± 0.002	3969	−0.006 ± 0.003	1788	**0.036 ± 0.004**	1809
European Goldfinch *Carduelis carduelis*	**0.075 ± 0.006**	269	**0.019 ± 0.009**	121	**0.018 ± 0.008**	323	**0.031 ± 0.004**	929
European Siskin *Carduelis spinus*	**0.046 ± 0.005**	2837	**−0.024 ± 0.004**	3390	**−0.012 ± 0.003**	2434	**−0.012 ± 0.002**	4500
Twite *Carduelis flavirostris*	–	–	−0.036 ± 0.025	57	−0.008 ± 0.018	254	**−0.097 ± 0.012**	231
Common Redpoll *Carduelis flammea*	**−0.006 ± 0.002**	13515	**−0.024 ± 0.004**	2950	−0.034 ± 0.009	661	−0.000 ± 0.001	424
Hawfinch *Coccothraustes coccothraustes*	–	–	**0.021 ± 0.007**	142	**0.021 ± 0.010**	50	**0.034 ± 0.008**	57
Red Crossbill *Loxia curvirostra*	**−0.031 ± 0.005**	1223	**−0.016 ± 0.006**	742	**0.003 ± 0.005**	648	**0.033 ± 0.008**	303
Eurasian Bullfinch *Pyrrhula pyrrhula*	**−0.021 ± 0.001**	7761	**−0.006 ± 0.001**	2742	0.002 ± 0.003	586	**0.006 ± 0.003**	268
Yellowhammer *Emberiza citrinella*	**−0.012 ± 0.001**	30586	**−0.021 ± 0.002**	7104	**−0.029 ± 0.003**	2441	**0.029 ± 0.004**	762

Significant trends are shown in bold. '–' means that there was not enough data to calculate trends.

STIs. The methodology is described in detail by Devictor *et al.* (2008).

We also calculated Species Temperature Index values for winter distributions (hereafter STIw) using distribution data from BirdLife International and NatureServe (2015). STIw values were calculated using species' winter distribution in Europe and Africa, excluding parts of the distribution where the species occurs year round south of the Sahara, because such populations are unlikely to influence winter population trends in Europe. For Common Buzzard *Buteo buteo*, we excluded the sub-Saharan wintering distribution because this relates to a different subspecies (*vulpinus*) which largely breeds in Asia (Forsman, 1999). We used climate data from worldclim (www.worldclim.org; Hijmans *et al.*, 2005), more specifically the monthly mean temperature for December, January and February in the second half of the 20th century (the time period is presented as 1950–2000). The climate data were in ESRI-format and had a cell size of 30-arc seconds (*c.* 1 km). The bird distribution data were used to calculate the mean winter mean temperatures for each species. We first converted the species range polygons into raster format, overlaid these rasters with the climate raster and then counted the overall mean of all the overlapping raster cells. When converting the species distribution polygons to raster, the cell size was set to be the same as for the climate data, which matched the output raster. The same procedure was conducted on all the three winter months. Finally, the mean winter temperature was counted as the average of the monthly means. All the geographical information system (GIS) analyses were conducted with ArcMap 10.3.1, Redlands, California, USA.

Once species-specific STIw values were estimated, we calculated the relative winter thermal niche for each species in each country (second variable, regional STIw, hereafter rSTIw) by calculating how much the winter temperature in the study region (see above) differed from the STIw of the species. Negative values mean that a population is situated in the colder part of the species' winter distribution (typically to the north), where the population would be expected to increase due to climate change. Conversely, positive values mean that the population is situated in the warmer (typically southerly) part of the distribution and is thus expected to decline if the temperature increases.

We classified species based on their main winter habitat (third variable, acronym 'Hab') using two main habitat categories: woodland and farmland (for classification based on habitat preference in winter bird counts, see Boele *et al.*, 2008; Fraixedas Nuñez *et al.*, 2015a).

For each country, we classified the species' migratory behaviour (fourth variable, acronym 'Mig') into three categories: (1) resident, for which only a minimum of migration movements is known; (2) partial migrant, where a substantial part of the population migrates, or the winter population consists of both resident breeding birds and migrants from the north; and (3) migrant, where a majority of the population leaves a country, or the species is present in the country only during non-breeding season (Fransson & Pettersson, 2001; Bønløkke *et al.*, 2006; Fransson & Hall-Karlsson, 2008; Fransson *et al.*, 2008; Saurola *et al.*, 2013; Valkama *et al.*, 2014).

The explanatory variables used were not strongly correlated (using the criteria of 0.5 correlation max; Booth *et al.*, 1994). The highest collinearity was found between STIs and migratory behaviour ($r = 0.32$): birds with high STIs in general were more often residents. In the rest of the cases, $|r| < 0.22$. Species-specific classifications are shown in Table S1.

Statistical analyses

We used log-linear Poisson regression (program TRIM, Pannekoek & Van Strien, 2004) to calculate annual population growth rates for each combination of species and country. TRIM imputes missing values and takes serial autocorrelation and over-dispersion into account. We used the annual growth rates calculated by TRIM as a response variable in the final model. We aimed to explain the variation in country-specific growth rates of species with the explanatory variables using linear mixed effect models.

We used the Deviance information criterion (DIC, similar to AIC, Akaike information criterion see Burnham & Anderson, 2002) in model selection, which was carried out in two steps. First, we investigated which phylogenetic structure fits best with the full model (all fixed factor predictors including interactions), using ten different combinations of phylogeny, downloaded from www.birdtree.org (Table S2). The model with the best fit based in DIC values (tree #7) (Table S2) was used in the second step of the analyses. In all cases, the models were within 2 DIC-value, so the variation in the phylogeny was not very large.

In the second step of the model selection, we built models using all combinations of variables (STIs, rSTIw, Hab, Mig) as main effects. Then, we included the corresponding models where rSTIw was interacting with Hab and Mig. Both STIs and rSTIw values were centralized (mean zero) before analyses. The best phylogenetic structure was used in all model combinations. Altogether, we analysed 26 models (Table 2).

All the analyses were carried out in program R version 3.2.2 (R Development Core Team, 2015).

RESULTS

The Netherlands had the lowest proportion of increasing population trends (29%) and the largest proportion of declining trends (40%), whereas the pattern was opposite in Finland (43% and 33% of the species increased and declined, respectively; Table 3). The species-specific growth rates in each country are shown in Table 1.

Annual mean temperatures in December–February did not increase significantly during the study period in any of the countries (all Ps > 0.15; see Table 4). However, in all countries, there was a tendency towards a warmer winter climate, although there were two cold winters at the very end of the study period (Table 4; Fig. 1). The top ranked model included STIs, rSTIw and habitat, and this model was clearly better than other models ($\Delta\text{DIC} \geq 2$; Table 2). Based on coefficients of the variables of the top ranked model, STI values were positively associated with population trends (Table 5, Fig. 2a), meaning that (summer) warm-dwelling species had on average higher growth rates than cold-dwelling species. Common Buzzard, Common Blackbird *Turdus merula*, Goldfinch *Carduelis carduelis* and Hawfinch *Coccotraustes coccotraustes* are examples of warm-dwelling species with increasing population trends, whereas Rough-legged Buzzard *Buteo lagopus*, Willow Tit *Poecile montanus*, Brambling *Fringilla montifringilla* and Twite *Carduelis flavirostris* are examples of cold-dwelling (northern) declining species. Furthermore, rSTIw values were negatively associated with growth rates, meaning that populations situated on the cold side of their wintering distribution increased compared to populations that were situated on the warm side of their distribution (Table 5, Fig. 2b). In addition, woodland species tended to have more positive population trends than farmland species ($P = 0.06$; Table 5).

DISCUSSION

Most winter populations of common land-birds in Northern Europe have changed significantly in size during the last three decades. This is likely driven both by changes in the overall population size and by redistribution of wintering populations, suggesting shifts in densities towards the north-east. Our analyses revealed that cold-dwelling species (species with low STIs), which on average have more northern breeding distributions, are doing worse compared with more southerly species. This supports previous findings that climate change has affected cold-dwelling species negatively (Hill *et al.*, 2002; Virkkala & Rajasärkkä, 2011; Jiguet *et al.*, 2013; Laaksonen & Lehikoinen, 2013; Lindström *et al.*, 2013), often leading to an overall decline in population size

Table 2 The explanatory power of different linear mixed-effects models in explaining the population trends of wintering bird population in four countries. Variables included were species' summer temperature index (STIs), regional species' winter temperature index (rSTIW), habitat (Hab), migration strategy (Mig) and order (Ord). Phylogeny structure (Tree2 in Table S1) was a random factor in all models. Deviance information criteria (DIC) and difference to the top ranked model (ΔDIC) are shown.

Nr	Model	DIC	ΔDIC
9	rSTIw + STIs + Hab	−821.60	0.00
12	rSTIw + STIs + Hab + Mig	−819.45	2.15
15	rSTIw + STIs + Hab + Hab*rSTIw	−819.43	2.17
6	rSTIw + STIs	−818.04	3.56
22	rSTIw + STIs + Hab + Hab*rSTIw + Mig	−817.89	3.71
23	STIs + Hab	−817.67	3.93
26	STIs + Hab + Mig	−816.57	5.03
10	rSTIw + STIs + Mig	−816.30	5.30
20	rSTIw + STIs + Hab + Mig + Mig*rSTIw	−815.72	5.88
3	STIs	−814.72	6.88
18	rSTIw + STIs + Hab + Hab*rSTIw + Mig + Mig*rSTIw	−813.60	8.00
24	STIs + Mig	−813.02	8.58
16	rSTIw + STIs + Mig + Mig*rSTIw	−812.41	9.19
7	rSTIw + Hab	−807.82	13.78
13	rSTIw + Hab + Hab*rSTIw	−806.58	15.02
11	rSTIw + Hab + Mig	−806.32	15.28
21	rSTIw + Hab + Hab*rSTIw + Mig	−805.43	16.17
2	rSTIw	−804.58	17.02
8	rSTIw + Mig	−804.38	17.22
19	rSTIw + Hab + Mig + Mig*rSTIw	−802.88	18.72
17	rSTIw + Hab + Hab*STIw + Mig + Mig*rSTIw	−801.78	19.82
4	Hab	−801.33	20.27
14	rSTIw + Mig + Mig*rSTIw	−800.85	20.75
1	Gen (Base model)	−798.10	23.50
25	Hab + Mig	−798.02	23.58
5	Mig	−797.00	24.60

Table 3 Number of study species in each country (*N*) and proportion of species with significantly increasing or decreasing population trends.

Country	*N*	Increased, %	Decreased, %
Finland	39	43	33
Sweden	50	30	36
Denmark	49	41	39
The Netherlands	48	29	40

Table 4 Change in mean winter temperature (December–February) in the four study countries during 1981–2014, as tested by linear regression.

Country	*B* ± SE	*F*-value	*P*-value
Finland	0.0504 ± 0.0379	1.76	0.19
Sweden	0.0427 ± 0.0430	0.99	0.33
Denmark	0.0385 ± 0.0359	1.15	0.29
The Netherlands	0.0391 ± 0.0296	1.75	0.20

and/or distribution. In contrast, warmer winters may improve the survival of warm-dwelling species (species with high STIs, but also populations with low rSTIw), leading to increased population sizes, as has been demonstrated in recent studies concerning both residents and short-distance migratory species, including partial migrants (Jørgensen *et al.*, 2015; Pearce-Higgins *et al.*, 2015). Several studies have shown that winter temperatures in general show a long-term increase especially in Fennoscandia, and that in general, there has been a decreasing frequency of extreme cold temperatures (EEA, 2012; Mikkonen *et al.*, 2015). This is in line with the temperature development in our study period (although with no significant increase). Although the fact that the linear increase in temperatures was statistically non-significant during our study period, the general tendency of an increase of 1.3–1.7 degrees in regional temperatures can have biological significance.

Furthermore, our results indicate that regional population trends increased in the colder part of winter distributions and decreased in the warmer parts. This indicates that the mean centres of winter abundances of the species have shifted towards the north along their winter climate niche, probably due to climate change (La Sorte & Thompson, 2007). Climate-driven poleward shifts of populations have previously been documented both during breeding and wintering season (Parmesan *et al.*, 1999; Parmesan, 2006; La Sorte & Thompson, 2007; Brommer & Møller, 2010; Pearce-

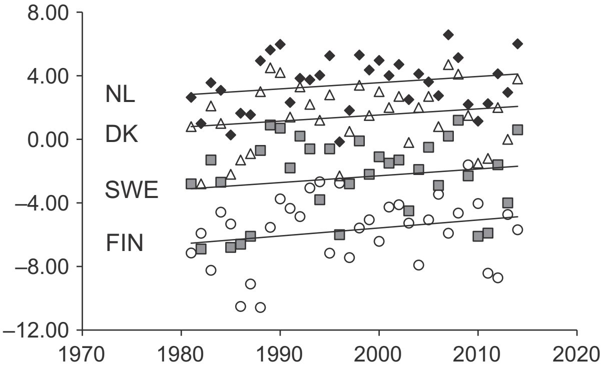

Figure 1 Annual winter temperatures (December–February) in the Dutch (NL), Danish (DK), Swedish (SWE) and Finnish (FIN) study areas (see details in text). The lines represent linear least-square regression lines.

Table 5 Coefficients (*B*), their 95% confidence intervals and *P*-values of the variables in the top ranked model. Variables included were species' summer temperature index (STIs), regional species' winter temperature index (rSTIW) and habitat (Hab).

Variable	*B* [95% CI]	*P*-value
Intecept	−0.0137 [−0.0397 to 0.0099]	0.28
STIs	0.0053 [0.0024 to 0.0080]	< 0.001
rSTIw	−0.0011 [−0.0020 to −0.0080]	0.02
Habitat	0.0117 [−0.0005 to 0.2392]	0.06

Higgins & Green, 2014). Based on our knowledge, our findings are the first to show large-scale redistribution of wintering land-bird populations in Europe. However, similar abundance shifts of wintering water-birds have been documented elsewhere (Austin & Rehfisch, 2005; Maclean *et al.*, 2008; Lehikoinen *et al.*, 2013a; Pavón-Jordán *et al.*, 2015; but see Fox *et al.*, 2016).

Interestingly, we could not detect any significant interactions between the factors examined, other than a general increase in population trends towards the north. This suggests that climate change is likely the key driver of winter population trends in this region, and that it uniformly affects common wintering land-birds, including both migratory and resident species. Nevertheless, the mechanisms of impact could be different between these groups. In migratory species, a decrease in migration distances could cause shifts in abundance towards breeding areas (Visser *et al.*, 2009; Lehikoinen *et al.*, 2013a,b), although this does not seem to be the case in all migratory populations (see Potvin *et al.*, 2016). Resident species, however, do not migrate, so other mechanisms must explain the pattern. Northern populations are likely to be more physiologically constrained by cold climate than southern populations of the same species (Root, 1988), and thus, increased winter temperature could especially enhance wintering survival of northern populations compared with southern populations of a species (Pearce-Higgins *et al.*, 2015; Jørgensen *et al.*, 2016). In addition, the spatial difference in population trends of resident species could be influenced by changes during the breeding season, such as climate-driven improved breeding success (Pearce-Higgins *et al.*, 2015). Alternatively, southern populations of a species could be more influenced by interspecific interactions, such as competition or host–parasite interactions (Marcogliese, 2008; Braustein *et al.*, 2010; Pearce-Higgins & Green, 2014; Dale & Andreassen, 2016). Populations of a given species that are situated at the colder end of its distribution have a more positive growth rates than populations that are situated at the warmer end of the distribution (Jiguet *et al.*, 2010a,b).

Importantly, we found that species wintering in woodlands had on average more positive trends than species wintering in farmlands. These findings support previous studies, which have shown strong declines in the abundance of breeding farmland birds in large parts of Europe in recent decades, compared with woodland species (Donald *et al.*, 2001; Gregory *et al.*, 2005, 2007). Despite the local population declines of forest birds at least in the northern part of our study area (Fraixedas Nuñez *et al.*, 2015a,b), farmland birds tended to do even worse than woodland species. Intensified agriculture has also lead to declines of British butterfly populations, masking the positive effects of climate change which should benefit most of the population at the same time (Warren *et al.*, 2001).

Our results add to the growing body of evidence that recent climate change and habitat suitability have a substantial impact on biodiversity, including winter bird

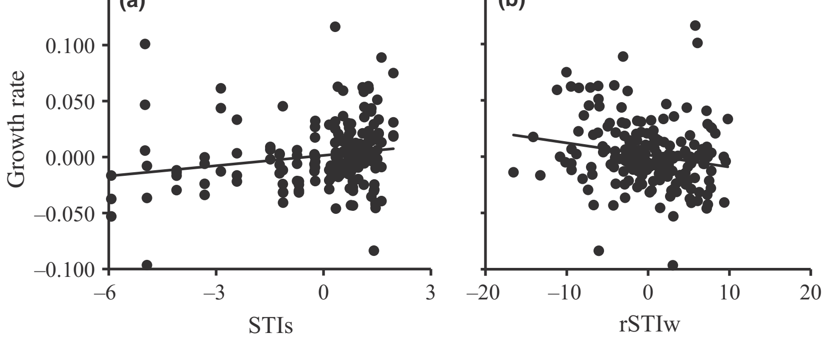

Figure 2 Population trends of species in different regions in relation to (a) species' summer temperature index (STIs) and (b) regional species' winter temperature indices (rSTIw) (both indices are centralized to zero, see Materials and Methods). The lines represent linear least-square regression lines.

communities. Moreover, our study illustrates that when investigating population trends during the non-breeding season, it is important to consider the factors influencing the overall size of populations, as well as their spatial redistribution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Classifications of species according to their order, family, species' temperature index in summer and winter, winter habitat preference and migratory behaviour in different countries.

Table S2. Comparison of the full models with different phylogenetic structures obtained from www.birdtree.org.

Figure S1. Location of the census sites in Finland, Sweden, Denmark and the Netherlands.

BIOSKETCH

Aleksi Lehikoinen is leading the research group of the Helsinki Lab of Ornithology (Finnish Museum of Natural History). He is interested in understanding how climate change and land use changes affect different aspects of the ecology and population dynamics of species. This international project was a collaboration within the network of the European Bird Census Council (EBCC), an organization focussing on collecting and analysing bird monitoring and distribution data across Europe to improve the knowledge of the population changes of birds in Europe.

Author contributions: A.L., R.P.B.F, H.H., Å.L. and C.A.M.T. conceived the study. A.L., H.H., Å.L., W.M., S.P. and S.H.M.B. gathered the data. A.L. analysed the data and interpreted the results. A.L. wrote the article, with a significant input from other authors.

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Supplementary Material

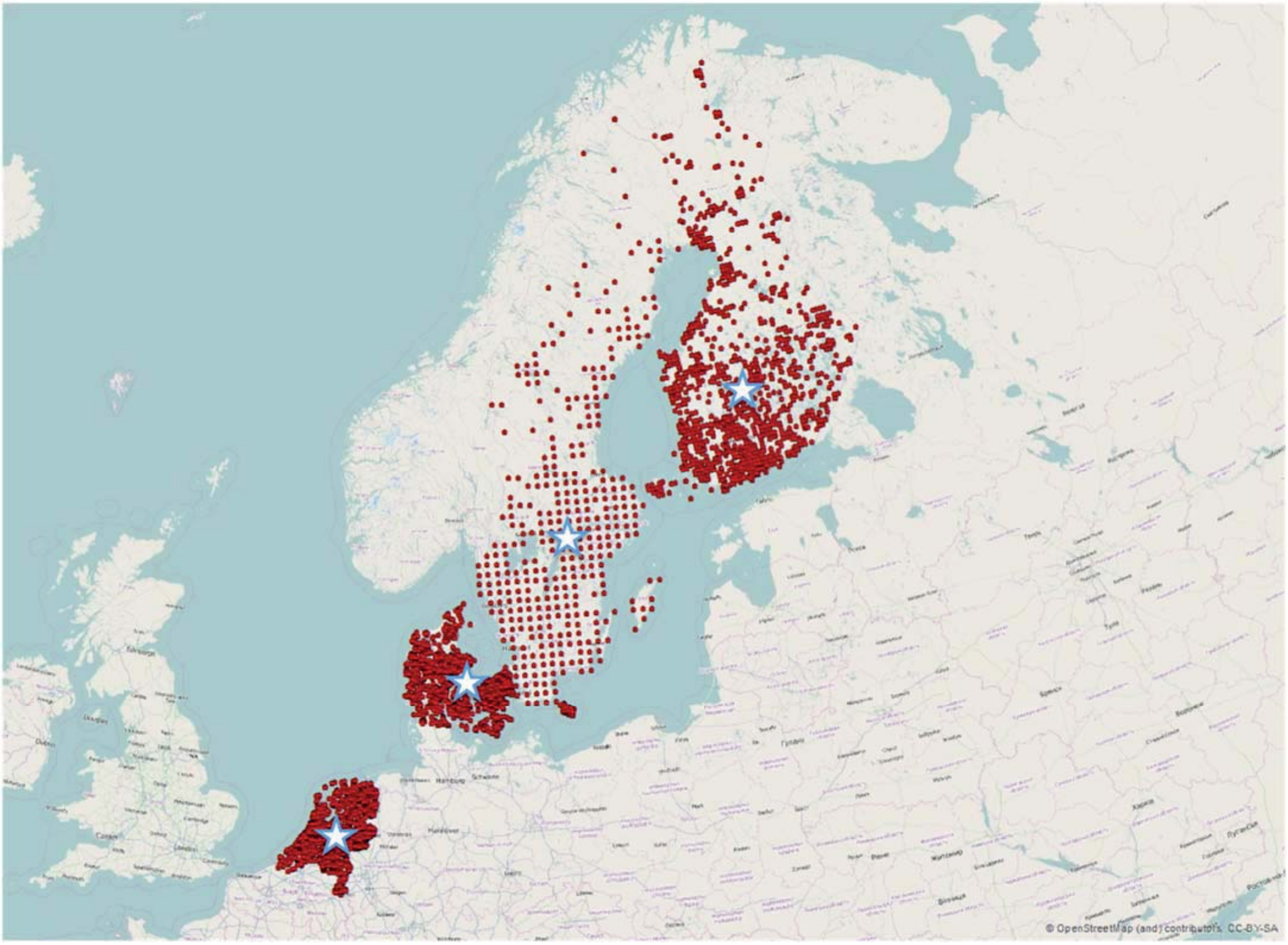
Table 1. Species' temperature index in summer (STIs) and winter (STIw), winter habitat preference (1 = mainly woodland, 0 = mainly farmland) and migratory behaviour in different countries (1 = resident, 2 = partial migrant, 3 = migrant). Species with up to five missing years were grey partridge *Perdix perdix* (Sweden), common buzzard *Buteo buteo* (Finland), skylark *Alauda arvensis* (Sweden, Denmark), meadow pipit *Anthus prantensis* (Denmark), winter wren *Troglodytes troglodytes* (Finland), Bohemian waxwing *Bombycilla garrulus* (Denmark), Eurasian robin *Erithacus rubecula* (Finland), redwing *Turdus iliacus* (Sweden), Eurasian nuthatch *Sitta europeae* (Finland), rook *Corvus frugilegus* (Finland), starling *Sturnus vulgaris* (Finland), and twite *Carduelis flavirostris* (Sweden).

Species	STIs	STIw	Habitat	Mig FIN	Mig SWE	Mig DK	Migr NL
Grey Partridge	14.84	-5.45	0	1	1	1	1
Northern Goshawk	13.8	-6.36	1	2	1	1	1
Eurasian Sparrowhawk	13.85	2.89	1	3	3	2	2
Common Buzzard	14.65	1.24	0	3	2	2	2
Rough-legged Buzzard	7.46	-3.23	0	-	3	3	3
Common Kestrel	14.36	4.09	0	-	3	2	2
Common Wood Pigeon	14.16	4.60	1	-	3	2	2
Eurasian Collared Dove	14.81	-3.22	0	1	1	1	1
European Green Woodpecker	14.73	-2.86	1	-	1	1	1
Black Woodpecker	13.16	-7.64	1	1	1	1	1
Great Spotted Woodpecker	14.1	-5.82	1	1	1	1	1
Eurasian Skylark	14.16	2.73	0	-	3	3	2
Winter Wren	14.08	-0.76	1	-	3	2	1
Bohemian Waxwing	8.4	-6.21	0	3	3	3	-
Meadow Pipit	11.9	5.45	0	-	3	3	2
European Robin	13.93	3.93	1	3	3	3	2
Common Blackbird	14.48	2.21	1	2	2	2	2
Fieldfare	12.16	-2.68	0	3	3	3	3
Redwing	10.52	3.13	1	-	3	3	3
Goldcrest	12.7	-4.39	1	2	2	2	2
Long-tailed Tit	14.51	-4.76	1	1	1	1	1
Willow Tit	12.26	-7.47	1	1	1	-	1
Marsh Tit	14.21	-2.65	1	-	1	1	1
European Crested Tit	13.59	-5.87	1	1	1	1	1
Coal Tit	13.73	-5.30	1	1	1	1	2
Eurasian Blue Tit	14.64	-3.11	1	2	2	2	2
Great Tit	14.29	-5.02	1	2	2	2	2
Eurasian Nuthatch	14.72	-5.28	1	1	1	1	1
Eurasian Treecreeper	13.14	-6.94	1	2	2	1	-
Great Grey Shrike	13.15	6.86	0	3	3	3	3
Eurasian Jay	14.41	-5.32	1	1	1	1	1
Common Magpie	14.12	-5.82	0	1	1	1	1
Western Jackdaw	14.89	-1.17	0	2	2	2	2
Rook	14.8	-1.20	0	3	2	2	2
Hooded Crow	14.08	-5.42	0	2	2	2	1
Northern Raven	13.71	-5.93	1	1	1	1	1
Common Starling	13.79	2.17	0	3	3	3	2
House Sparrow	14.21	-3.00	0	1	1	1	1
Eurasian Tree Sparrow	15.01	-4.19	0	1	1	1	1
Common Chaffinch	14.23	1.55	1	3	3	2	2
Brambling	9.28	9.28	1	3	3	3	3
European Greenfinch	14.53	-1.28	0	2	2	2	2
European Goldfinch	15.34	2.77	0	3	2	2	2
European Siskin	12.25	0.01	1	3	2	3	3
Twite	8.46	-1.14	0	-	3	3	3
Common Redpoll	10.07	-7.41	1	3	2	3	2
Hawfinch	14.93	0.01	1	-	2	2	2
Red Crossbill	10.97	-7.90	1	2	2	3	3
Eurasian Bullfinch	12.65	-4.88	1	2	2	2	2
Yellowhammer	13.55	-5.41	0	2	2	1	1

Supplementary Table 2. Comparison of the full models with different phylogenic structures obtained from www.birdtree.org (footnotes available here: http://onlinelibrary.wiley.com/wol1/doi/10.1111/ddi.12480/suppinfo).

Phylogeny	DIC	ΔDIC
TREE 7	-813.8566	0
TREE 8	-813.7827	0.0739
TREE 9	-813.6474	0.2092
TREE 6	-813.3408	0.5158
TREE 3	-813.1538	0.7028
TREE 1	-812.7635	1.0931
TREE 4	-812.7187	1.1379
TREE 5	-812.4698	1.3868
TREE 10	-812.2857	1.5709
TREE 2	-812.0990	1.7576

Supplementary Fig. 1. Location of the census sites in Finland, Sweden, Denmark and the Netherlands. The sites are truncated in 10 km grids in Finland and 25 km grids in Sweden. Stars show the central gravity of the census sites.



PAPER 7

DISENTANGLING THE EFFECTS OF MULTIPLE ENVIRONMENTAL DRIVERS ON POPULATION CHANGES WITHIN COMMUNITIES

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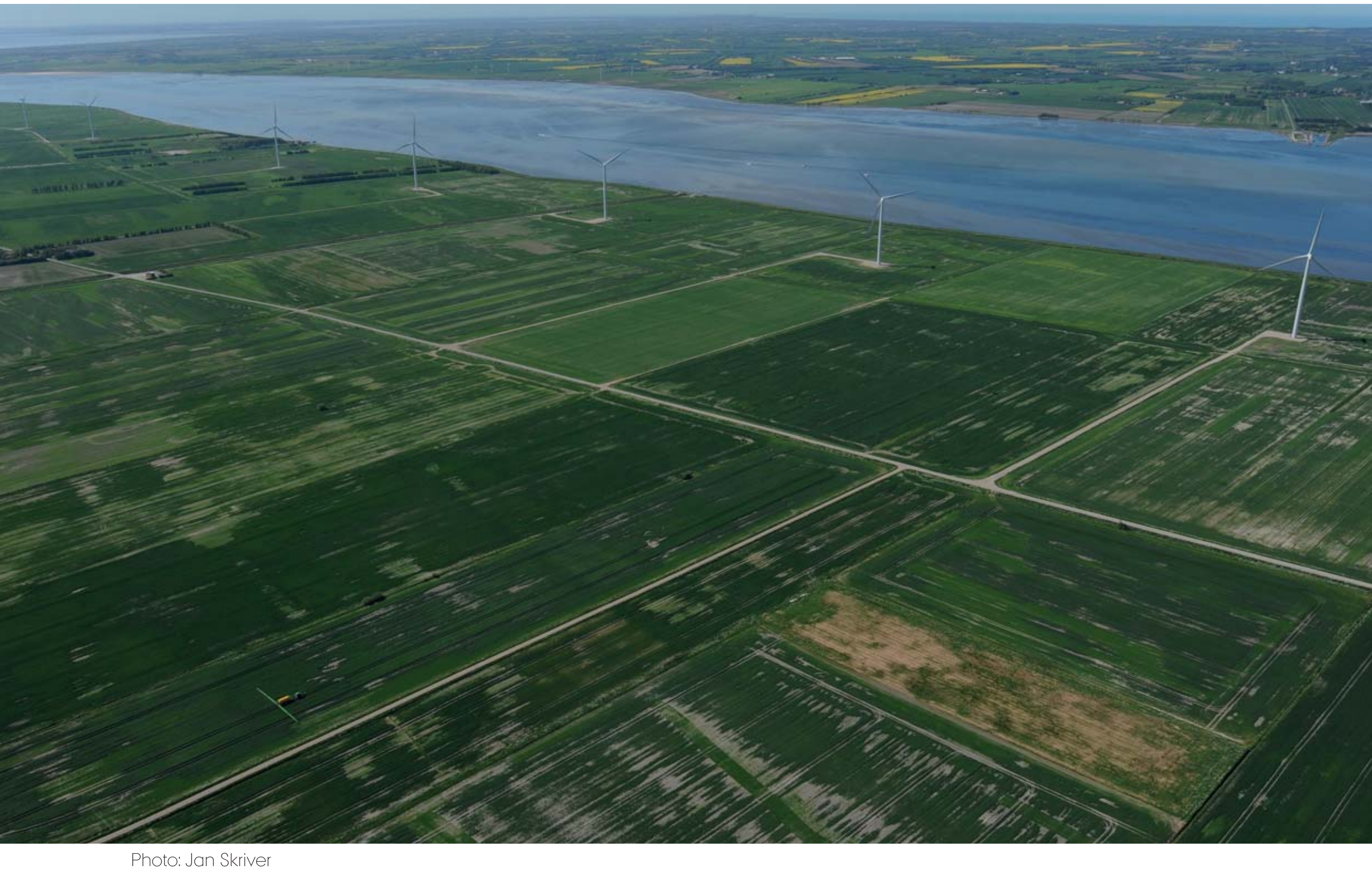

Photo: Jan Skriver

DISENTANGLING THE EFFECTS OF MULTIPLE ENVIRONMENTAL DRIVERS ON POPULATION CHANGES WITHIN COMMUNITIES

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Abstract

1. The effects of different environmental drivers on population abundances can be difficult to disentangle since they often act simultaneously. Researchers have built statistical models that include environmental variables (such as annual temperature), or species attributes (such as a species' temperature preference), which are assumed to detect the impacts of specific drivers (such as climate change). However, these approaches are often applied separately or, even if combined, not explicitly compared.
2. We show the complementary insights gained by applying both these approaches to a community dataset on Danish terrestrial birds. We use our analysis to compare the relative importance of climate change and agricultural land-use change for changes in abundances within the community between 1983 and 2013.
3. Population models were fitted to the community data of species' annual abundances with predictors comprising: species attributes, environmental variables, or both. Relationships between species' abundances and environmental variables were used to identify the drivers associated with average abundance changes of species in the community. Relationships between species' abundances and their attributes were used to understand the drivers causing interspecific variation in abundance changes.
4. Warmer winters were positively associated with community-level abundances, and warm-adapted species had more positive abundance changes than cold-adapted ones. Agricultural area was negatively associated with community-level abundances, and birds using a high proportion of meadow and habitat specialists had more negative abundance changes than birds using other habitats and habitat generalists. Effect sizes of environmental variables were larger for agricultural land-use change while those for species attributes were larger for climate change.
5. The environmental-data approach suggested that agricultural land-use change has decreased the average abundances of species in the community, affecting total community size while the species-attribute based approach suggested that climate change has caused more variation in species abundance, affecting community composition. We show that a combined approach, which draws on the mechanistic link supplied by environmental data and the generality supplied by species attribute data is most useful to understand how communities have changed in the past and how they might change under further environmental change.

Key words: Climate change; Community ecology; Land-use change; Population trends; Species attributes; Trait-based approach

Introduction

Understanding the causes of changes in species' population abundances is essential for effective conservation management and policy development (Butchart *et al.* 2010; Díaz *et al*. 2015; Gamero *et al.* 2016; Stephens *et al*. 2016). Much of the change in abundances since the 1970s can be attributed to broad-scale direct anthropogenic drivers (Díaz *et al*. 2015), especially climate change and agricultural land-use change (Stoate *et al.* 2001; Pereira, Navarro & Martins 2012; WWF 2014; Burns *et al.* 2016). As populations have simultaneously been subjected to these different drivers, teasing apart their relative importance for species abundances is a challenge. To isolate the impact of a particular environmental change, such as climate change, studies have taken different approaches. Ecologists have either related population abundances directly to measured environmental change, e.g. annual temperature (Saether *et al.* 2000) (hereafter "environmental-data" approach) or have related interspecific variation in abundance trends to species attributes, e.g., temperature preference (Jiguet *et al.* 2010, Buckley & Kingsolver 2012) (hereafter "species attribute-based" approach). Few studies have recognized the relative contributions and value of each approach. In this paper, we combine the strengths of both approaches into one framework to identify drivers of past population change in species' communities.

Most commonly, the effect of environmental change has been studied by relating summary variables of environmental change, such as of climate or land-use change, to species' population abundances in statistical models. Climate change can be summarized in a myriad of different ways but monthly or seasonal mean temperatures are often used in models (Eglington & Pearce-Higgins 2012; Pearce-Higgins *et al.* 2015a). For instance, Sæther et al. (2000) related inter-annual changes in the size of the White-throated Dipper (*Cinclus cinclus*) population to mean winter temperature, and from this inferred the likely impacts of climate change. Models of bird population dynamics have also included annual cereal yield or indices of the number of cattle and sheep as proxies of agricultural land-use change and found that these proxies could explain long-term decreases in abundance (Eglington & Pearce-Higgins 2012). The "environmental-data" approach is usually applied to study the responses of single species but it can also be applied to community datasets to determine whether there are any average or common relationships between abundances and environmental conditions across species in a community. Roy et al. (2001) found positive associations between temperatures, especially during previous summer, and abundances across various species in a butterfly community.

Rather than identifying the most predictive environmental variables of abundance changes, some studies have focused on explaining the interspecific variation of abundance changes using a species trait- or attribute-based approach as a way to infer environmental change impacts. Variation in species' long-term population trends have been related to a range of species attributes (i.e., traits measurable on individuals as well as other variables, such as niche, measured more often on populations), such as their ecological preference, life history traits, physiology and morphology (Lemoine *et al.* 2007a; Williams *et al.* 2008; Jiguet *et al.* 2010; van Turnhout *et al*. 2010). Of course, many species attributes, such as habitat and temperature preferences, are inferred using environmental data but the attributes are assumed to be intrinsic species characteristics and not to change over years. For example, bird species regarded as 'farmland birds' (i.e., using farmland as a preferred breeding habitat) have declined while others have not (Lemoine *et al.* 2007a; Jorgensen *et al.* 2016), which has been taken as an indicator of the impacts of agricultural intensification. Similarly, positive relationships between species' temperature preferences and the population trends of birds and butterflies, representing relative increases of warm-adapted species over cool-adapted species, have pointed towards the effects of climate change (Jiguet *et al.* 2010; Devictor *et al*. 2012).

Recent studies have begun to combine both species attributes and environmental variables in statistical models of community dynamics (Pearce-Higgins *et al.* 2015b; Jorgensen *et al.* 2016). However, these studies have not explicitly compared the roles of species attributes versus environmental variables for explaining changes in species' abundances within communities. The environmental-data and attribute-based approaches ask subtly different questions (Fig. 1). The environmental-data approach estimates how much, and in what direction, species' abundances change with environmental change (Fig. 1 left). When the environmental-data approach is applied to a community dataset, rather than that of a single species, for instance by modelling species differences as only random effects, it can be used to ask whether there are average or consistent abundance changes across species, which would affect total community abundance. In contrast, the attribute-based approach focuses on the variation of species responses and informs rather on impacts on community composition (Fig. 1 right). If all species in a community are similar (in their niche, tolerances or traits) and therefore respond similarly (positively or negatively) to a specific environmental driver, then environmental variables may show non-zero average effects on the community; and species attributes are likely to be weak predictors. In contrast, when there is greater species variation and some species respond positively and others negatively, the aver-

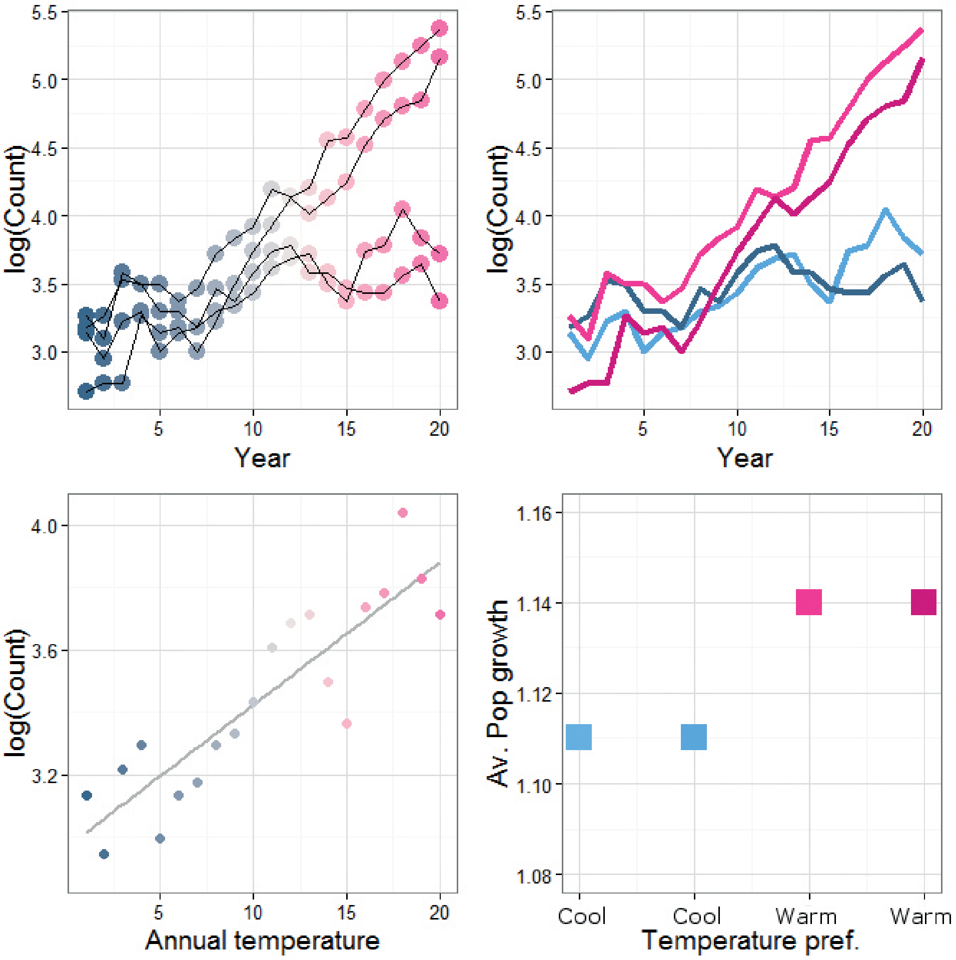

Figure 1. Comparison of the environmental data versus species attribute-based approach on a community dataset. Environmental change causes two types of variation in a community – variation in abundance between years that may be explainable by year-to-year variation in environmental variables (top left showing time series for four hypothetical species – a change from cool to warm ambient temperatures over years is represented by the shift from blue to pink colours) and variation in abundance among species that may be explainable by species attributes (top right showing the same – with cool-adapted species coloured blue and warm-adapted species coloured pink). In the context of climate change, increasing abundance over years (top left) is caused by increasing annual temperatures and an average positive effect of temperature on species' abundances (bottom left). Increasing relative abundance of warm-adapted species over cool-adapted species (top right) is caused by species with warmer temperature preferences having higher population growth rates in response to the rising temperatures (bottom right). A similar framework can be applied to other environmental change in which a relevant environmental variable could be agricultural area and the associated relevant species attribute as species farmland use.

age effect of environmental variables in the community may not differ from zero and species attributes have the potential to be better predictors. Thus, both approaches provide complimentary information – specifically on the mean and variance of species' abundance changes – that help determine how environmental changes affect total community size and community composition.

Results from both approaches have already highlighted the impacts of environmental change and climate change on the recent dynamics of European bird populations. Using population data from terrestrial birds recorded by the Danish common breeding bird survey, we extend previous analysis by explicitly comparing the conclusions of both approaches, specifically on the mean and variance in species' changes, to understand the implications for total community size and composition. Birds are an excellent study group to test hypotheses about the relative influence of different environmental drivers and the influence of species attributes because they are well-sampled, with well-known attributes, and play important roles in ecosystems. Although our methodology applies to any type of environmental change, we focused this study on climate change and land use change. For land use change, we focused specifically on agricultural land-use change because agricultural land was the dominant land cover and farmland was a significant part of the habitat of many species in the community. Land-use change, especially of farmland, has clearly played, and continues to play, a major role in species popula-

Table 1. The species attributes and environmental variables that are hypothesized to relate to climate and agricultural land-use change impacts on species' population abundances. The sign in brackets indicates the hypothesis regarding the direction of the effect (i.e., / means the environmental variable/species attribute is positively/negatively associated with species' abundances.

Environmental change (Hypothesis #)	**Environmental variable (1)**	**Species attribute (2)**	**Combined: Interactions (3)**
Climate change	Temperatures (+) Precipitation (+)	Temperature preference (+) Migration (–)	Temperatures x Preference (+) Temperatures x migration (–)
Agricultural land-use change	Agricultural yield and area (–)	Arable land use/ meadow use (–)	Agricultural Yield/area * use (–)
Environmental change (climate or land-use)	–	Habitat breadth (+)	Temperatures * Habitat breadth (+) Yield/area * Habitat breadth (+)

tion trends for bird communities within Europe (Julliard, Jiguet & Couvet 2004; Eglington & Pearce-Higgins 2012); however, it may be decelerating in some regions (Gingrich *et al.* 2015). Some recent studies suggest that climate change could be becoming as important as land-use change for population trends (Lemoine *et al.* 2007b; Jorgensen *et al.* 2016). Danish breeding bird populations have been shown previously to be affected by land-use changes (Fox 2004; Eskildsen, Larsen & Heldbjerg 2013; Heldbjerg, Sunde & Fox 2017) but the impact of climate change has so far not been assessed.

We tested the hypotheses that: (1) species' abundances, on average, increased after years with warmer temperatures (Pearce-Higgins *et al.* 2015b) and decreased with increasing agricultural land-use use change (Eglington & Pearce-Higgins 2012) (environmental data approach, Table 1: hypotheses 1); (2) temperature preference and habitat breadth/farmland specialisation explain variation in the abundance changes of different species, leading to relative increases of warm-adapted species and habitat generalists (Jiguet *et al.* 2010; Davey *et al.* 2012) (species attribute-based approach Table 1: hypotheses 2). To explain variation in species' responses to each environmental variable, we additionally tested (3) whether temperature preferences mediated (i.e., interacted with) species' population responses to a climatic variable (Pearce-Higgins *et al.* 2015a); whether habitat breadth/preference mediated species' responses to an agricultural land-use variable (Jorgensen *et al.* 2016) and whether migratory strategy determined species response to changing temperatures (Møller *et al.* 2008) (combined approach, Table 1: hypotheses 3). Moreover (4), we expected that the effects sizes of environmental variables or species attributes associated with agricultural land-use change were greater than the effect sizes of variables associated with climate change on the assumption that year-to-year changes in land-use have been stronger than that of climate (Eglington & Pearce-Higgins 2012). Finally (5), we expected that more variation in the community data would be explained by species attributes than by environmental data alone because of the broad range of species in the dataset that were expected to respond differently to environmental change.

Materials and Methods

Data

We analysed the annual national population indices of 77 terrestrial species made publically available online by DOF-Birdlife Denmark (http://www.dof.dk/), selected by exclusion of species that had been affected by culling or hunting, and freshwater species associated with open water (SOM A shows species that were included). These indices are based on annual point count surveys that now involves c. 370 routes across the country monitored in the period 1st May – 15th June (Nyegaard *et al.* 2015). Most routes consist of 10–20 marked 'points' at which all birds seen and heard are recorded in a 5-min observation period (Heldbjerg 2005). All routes are counted in at least two years by the same observer, at the same time of year (± 7 days), same time of day (± 30 min) and under good weather conditions. The annual national abundance indices for each species had been calculated by DOF-Birdlife Denmark by fitting a log linear regression model to the point count data with Poisson error terms using the software TRends and Indices for Monitoring data (TRIM) (Pannekoek & van Strien 2004). In this model, the count at a given route in a given year is assumed to be the result of a route and a year effect, accounting for overdispersion and temporal autocorrelation. Because these abundance data are indices and not true counts, we used the log of the annual indices as our response variable.

Environmental data were compiled on climate and agricultural land-use. Daily mean temperature and precipitation amount data were extracted from the portion of the E-OBS dataset (Haylock *et al.* 2008) that overlapped with the Danish boundary. These data were used to calculate mean daily temperature values and monthly precipitation totals for each season (winter: Dec to Feb; spring: Mar to May; summer: June to Aug; autumn: Sept to Nov) of each year, averaged across the country. We focused on these seasons as they represent the extremes, as well as conditions during the breeding season, and were expected to be most important. Annual national land-use data were extracted from databases of the FAO (http://www.fao.org/faostat; annual cereal, barley and wheat yield) and Statistics Denmark (www.dst.dk; annual areas of grassland, winter wheat, spring barley and maize). We focused on land-use variables related to agriculture as this is the dominant land-use in Denmark.

Species attribute data were compiled from different sources. Species' temperature preferences were calculated by overlaying species distribution data (BirdLifeInternational & NatureServe 2012) with average (1969–1990) daily mean temperature maps from an E-OBS map delimitated to Europe. Because some species were trans-Saharan migrants and therefore not in Europe all year, we only used the breeding distribution and spring (March to May) temperature data. However, our aim was only to create a variable that put species on a gradient from cool to warm temperature preferring. Using the temperature data of climatic grid cells intersecting with each species distribution, unimodal response curves were fitted using the eHOF package (Jansen & Oksanen 2013) and the optimum temperature (i.e., peak of the curve) was extracted for each species, but similar results were obtained using only the average temperature over the range. Data on species' relative habitat uses (classified for coniferous forest, deciduous forest, arable land, meadow, bog/marsh, heath, dunes/shore, lake and urban) across Denmark were taken from the appendix of Larsen et al. (2011). Using the point counts of the Danish breeding bird survey, Larsen et al. (2011) had calculated species' relative habitat uses as the abundance of a species in a particular habitat relative to the abundance of this species in all other habitats. Here, we focused on species' habitat uses of "meadow use" and "arable-land use" – these were continuous variables reflecting how much each species is specialised on each of these habitats (Larsen, Heldbjerg & Eskildsen 2011). Although not all of these bird species are traditionally regarded as 'farmland birds', all used farmland to some extent over their range in Denmark (Larsen, Heldbjerg & Eskildsen 2011). As a measure of habitat breadth, we used the coefficient of variation of species' relative uses (Julliard *et al.* 2006) across all nine different habitats listed above; this was multiplied by –1 so that species using similar proportions of different habitats (i.e., generalists) would have higher values, while species mostly using one habitat (i.e., specialists) would have low values. Finally, species were classified as trans-Saharan migrants or otherwise (sedentary, partial migrant and short distance migrants were combined) based on ringing recovery data (Bønløkke *et al.* 2006).

Because some of the environmental data only began in 1983, we fitted the statistical models to data from this year onwards to 2013. Hypotheses for the effects of the species attributes and environmental variables, and their links to environmental change are found in Table 1.

Statistical modelling

Our analysis was designed to test whether variation in species' abundances in a community can be explained by annual environmental data, species attributes, and/or their interaction (Fig. 1). In general, our model was a standard autoregressive model (of order 1) of the following form:

$$x_t = a + \rho x_{t-1} + b_1\,Var\_1 + \ldots + b_n\,Var\_n + \varepsilon$$

where $_t$ is the logged national population index () of a species in year *t*. *Var_n* is either a species attribute or an environmental variable. is the intercept; is the autocorrelation term, and are the coefficients of each attribute/variable (usually slopes as all variables/attributes were continuous apart from migration), which are estimated by the model. The model was fit to the community dataset comprising all 77 species so additional random effects (independent and identically distributed) were added for year and for species (on and).

We ran three sets of models using different types of predictors:
(1) *Environmental data*: annual climatic (temperatures and precipitations in each season), annual agricultural area (maize, winter wheat) and annual agricultural yield (cereal, wheat and barley) variables were included in the model to test hypothesis (1). All data were taken for the year prior to the census except winter temperature that also included the winter immediately preceding the census. We also considered temperatures in the previous year to this as well as cumulative lagged effects for the climatic variables using rolling means of the previous two years. In addition to the general model described above, species-level variation was modelled by including species-specific random slopes of the effects of each environmental variable.

Many of the land-use variables were strongly correlated (Fig. S1). Hence, we first tested the strength of each variable's association with species' population abundance in separate regression models. We highlight the two strongest associated variables (assessed by the z-score of each coefficient) from each of the three aforementioned groups, which were combined (when uncorrelated) into a multiple regression model of the form below.

$$x_t = a + \rho x_{t-1} + b_1\, \mathit{Environ\_1} + \ldots + b_n \mathit{Environ\_n} + \varepsilon$$

(2) *Species attributes*: temperature preference, habitat uses (meadow, arable – on a continuous scale and logged because of skew), habitat breadth and migration (trans-Saharan migrant or not) were included in the model to test hypothesis (2). Because species attributes used in the analysis were not strongly correlated (all r<0.7), they were included in the same multiple regression model. Initially, the effects of attributes on population abundance changes were assumed to be constant over time (i.e. tested by an attribute X year interaction term, meaning that the attribute affects species' long-term population trends), as has been done previously (Jorgensen *et al.* 2016). However, we also built random walk models in which the effects of species attributes were allowed to vary between years. The general model was of the form:

$$x_t = a + \rho x_{t-1} + f(\mathit{Year}, \mathit{Attr\_1}) + \ldots f(\mathit{Year}, \mathit{Attr\_n}) + \varepsilon$$

(3) *Combined approach*: In the third set of models, we asked whether we could link the effects of species attributes to specific environmental changes to test hypothesis (3). Using the environmental variables and species attributes that were statistically significant in previous models, we tested interactions in a multiple regression model according to our hypotheses (Table 1).

$$x_t = a + \rho x_{t-1} + b_1\, \mathit{Environ\_1} * \mathit{Attr\_1} + \ldots + b_n\, \mathit{Environ\_n} * \mathit{Attr\_n} + \varepsilon$$

Models were fit using R-INLA (Rue, Martino & Chopin 2009). All variables were standardized to units of standard deviation prior to analysis so regression coefficients represent standardized effect sizes (Schielzeth 2010). For the effects of the environmental variables on abundances', we also compared the effect sizes that accounted for the long-term in each variable (i.e., effect size of each environmental variable in its original units [e.g., log abundance change $^{\circ}C^{-1}$] multiplied by its long–term trend [e.g., $^{\circ}C\ y^{-1}$], giving an effect size of comparable units of log abundance change y^{-1}). We used the effect sizes to compare the relative importance of land-use change and climate change to test hypothesis (4). We calculated the variance explained by the fixed effects of the models (species attributes and/or environmental variables) to test hypothesis (5). Significant effects were identified as those with 95% confidence intervals not overlapping zero. For all multiple regression models, insignificant terms were removed to obtain the final simplified model and the effect sizes of the significant variables; the insignificant terms were then added one-by-one to the final model to also obtain their effect sizes. All analysis was conducted using R (R Core Team 2013) and a sample script is provided in SOM B.

Results

Environmental changes

We found evidence that both the climate and agricultural land-use has changed over time (Fig. 2; further trends are shown in Fig. S2 and Table S1). Out of the climatic variables, winter and spring temperatures increased the most. Agricultural intensification began in the 1980s, but some changes, such as maize area, increased more during the 00s.

Environmental data approach

In the first set of models, we used environmental variables to model the changes in species' population abundances between years at the community-level (species-level variation was only included as random effects). In simple regression models, the most important climatic variables were winter (averaged over 2 years)

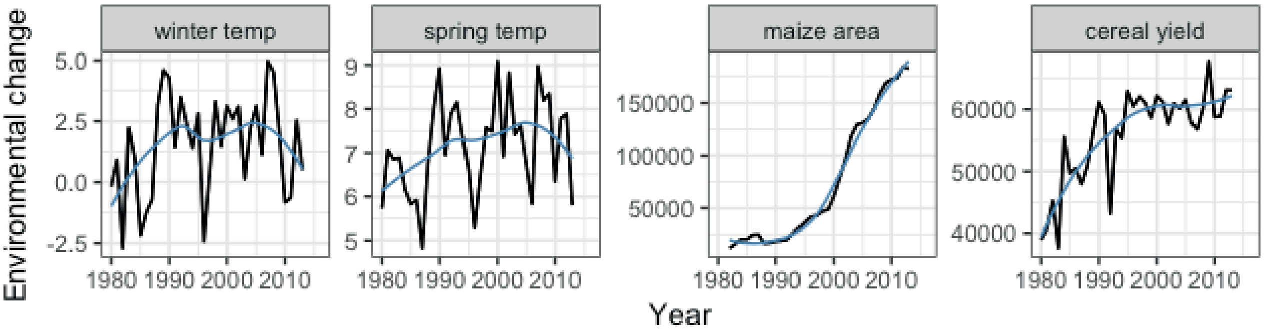

Figure 2. Time series of environmental variables (temperatures in ºC; maize area in ha and yield in Hg ha^{-1}) for Denmark since 1980. The blue line is a loess smoother to highlight the trend.

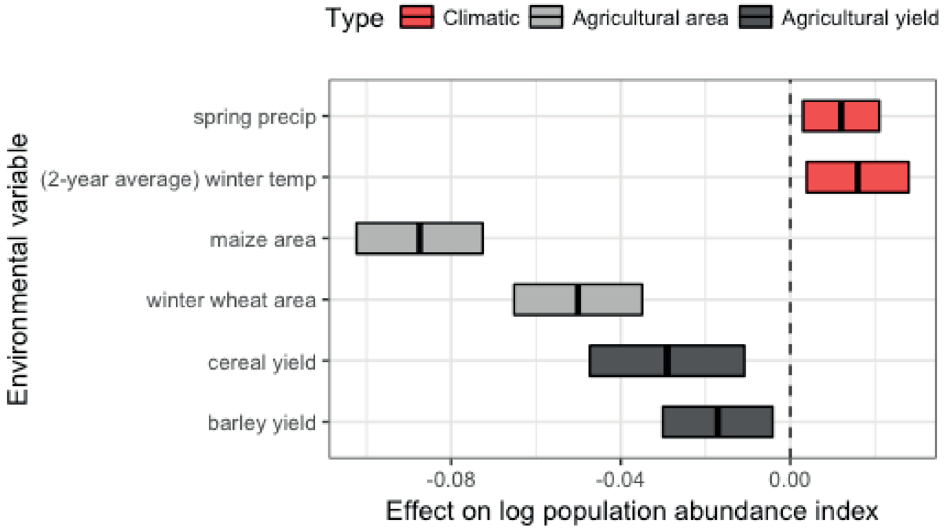

Figure 3. Effects (mean effect size ± 95% confidence intervals) of environmental variables on the log of species' population abundance indices. All variables were tested separately on the community data in regression models, with species included as random terms (intercept and slopes) and an autocorrelation term. Shown are the best two variables for each environmental variable type (climatic, agricultural area or yield) as inferred from the z-score of each coefficient. Effect sizes for all other variables tested are shown in Table S2.

and spring precipitation, which were positively associated with population abundance (Fig. 3, Table S2). The most important agricultural area and yield variables were maize and winter wheat area, and barley and cereal yield, respectively, which were negatively associated with population change (Fig. 3). Thus, our findings supported our hypothesis (1). The effect sizes for the agricultural area variables tended to be greater than the climatic variables, supporting hypothesis (4). A similar pattern was obtained when standardizing the effect sizes by the long-term trend in each (Fig. S3), because the land-use variables had stronger trends than the climatic variables. When combining the best uncorrelated variables from each group (correlations among them shown in Fig. S1), only winter temperature and maize area retained significant effects. The fixed effects of the environmental variables in this best model (i.e., population average effects for winter temperature plus maize area) explained only 2% of the variation in the data.

Species attribute-based approach

In the second set of models, we used species attributes to model the changes in species' population abundances. Temperature niche had the largest effect on changes in abundance: warm-adapted species increased in abundance over years relative to cool-adapted species (Fig. 4). Species using a higher proportion of meadow tended to decrease in relative abundance over time. In contrast, arable land use was associated with a slight positive effect on abundance. Habitat breadth was positively associated with changes in abundance, reflecting relative increases of generalists over specialists, (Fig. 4) and it had a stronger effect than either meadow or arable land-use. Trans-Saharan migrants also had more negative changes in abundance than other species (effect size = -0.11, 96% CI = -0.0013, -0.021). Thus, apart from the surprising positive effect of arable land use, our findings supported hypothesis (2). Contrary to our hypothesis (4), the effect size for temperature niche reached greater

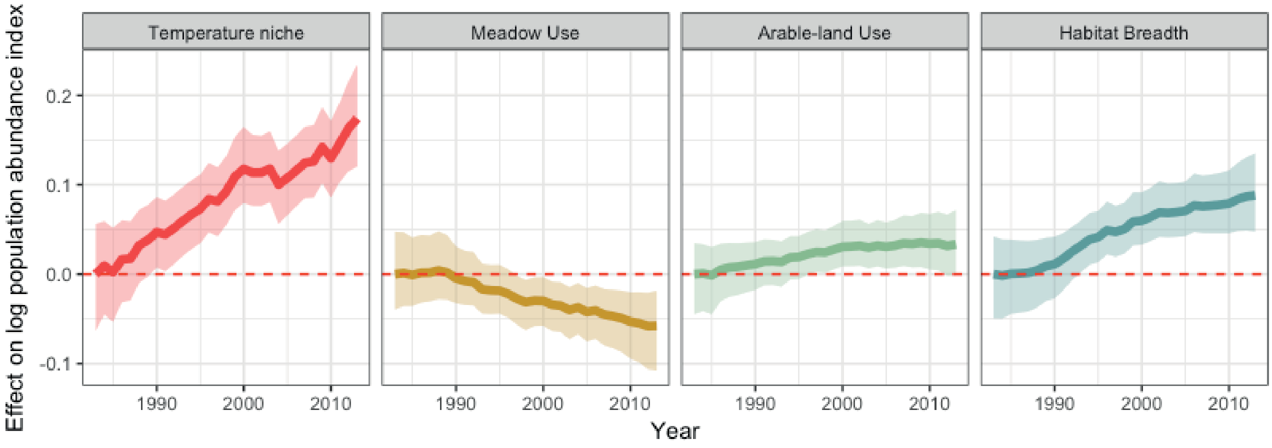

Figure 4. Cumulative effects (i.e., effect of the attribute on the log population abundance index from the first year: 1983) and 95% confidence intervals of species attributes on the changes in species' population abundances over years (obtained from a random walk model).

values than the effect sizes for the other attributes. Mostly similar results were obtained assuming attributes had temporally constant effects and only influenced species long-term population trends, but the effect of arable-land use was not statistically significant (Fig. S4, Table S3). The fixed effects of the model (species attributes X year effects) explained 12% of the variation in the data. Thus, our results were consistent with hypothesis (5) as more variation was explained by the species attributes compared with the average effects of the environmental variables (12% versus 2%).

Combined approach: testing interactions

Finally, we built models that included both the environmental variables and species attributes, and tested their interactions. We only tested interactions based on *a priori* hypotheses (Table 1; all tested interactions are shown in Fig. 5). These interactions showed that relative increases of warm-adapted species over cold-adapted species were associated with warmer winters (Fig. 5). The abundances of trans-Saharan migrants were more negatively associated with warmer springs than the abundances of non-trans-Saharan migrants. The abundances of species using a high proportion of meadow were more negatively associated with increasing maize area. In contrast, the negative effect of maize area of species abundances was weaker for habitat generalists. There was no evidence that habitat breadth affected species response to winter or spring temperatures. Apart from the lack of link between habitat breadth and a land-use variable, our hypothesis (3) was supported. Effects of the attributes and environmental variables together explained 14% of the variation in the data.

Discussion

Different analytical approaches can be used to study the response of species to environmental change. Directly relating environmental variables to changes in species' population abundances can be the most useful approach for single-species studies (Saether *et al.* 2000) but the findings cannot be necessarily extended to other species. Analysing the effects of species attributes on species' abundance changes can be a community-level indicator of environmental change but only informs on the variation in abundance response among species. Here we applied both approaches to a community dataset of Danish breeding birds to understand how environmental changes have affect the mean and variance of species' abundance changes, which have consequences for total community size and composition. By comparing these approaches, we can extend previous analysis and show the contrasting information that each supplies: agricultural land-use change has most likely had stronger mean effects on species' abundance changes (environmental data approach) while climate change has most likely had stronger effects on the variance in species' abundance changes (species attribute based approach).

Using the environmental-data approach, we could ask whether there were any average or community-level relationships between environmental variables and population abundances. Since we found both significant climatic and agricultural variables, many species appeared to be responding in the same direction to environmental change, which means that environmental change has affected the total size of the community. Across species in the community, abundances generally increased

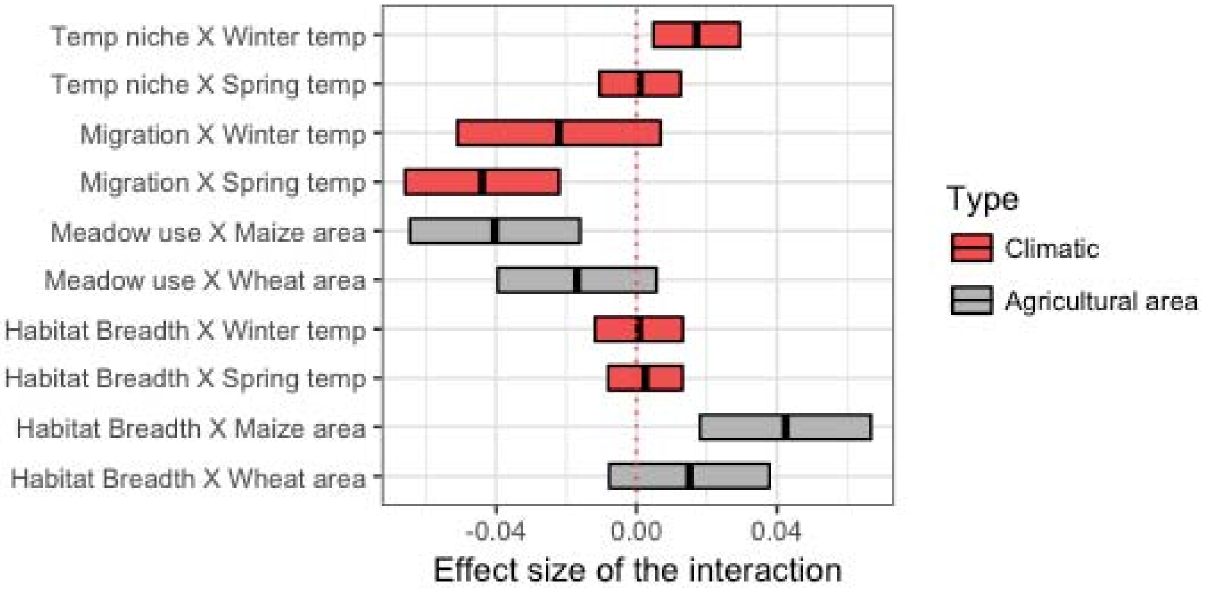

Figure 5. Interactions (mean ± 95% confidence intervals) between species attributes and environmental variables on the log population abundance indices. All variables were continuous standardized variables except migration, which was a categorical variable: non-trans-Saharan migrant or trans-Saharan migrant.

after years with warmer winters, perhaps by reducing overwinter mortality (Robinson, Baillie & Crick 2007; Lehikoinen *et al.* 2016). However, the average negative effect sizes of the land-use related environmental variables were larger than the positive effect sizes of the climatic variables. This suggests that the negative effects of land-use change have outweighed any direct benefits from warmer winters due to climate change on species' abundances, which is consistent with the overall decline of bird abundances in this community. The most strongly related agricultural land-use variable in our analysis was maize area, which has markedly increased since 1990, more recently than other features of agricultural change (e.g., the shift from spring to winter cereals, which occurred in the 1980s). Many Danish breeding birds are insectivores and maize cultivation (used for livestock fodder) rapidly forms dense biomass that provides no feeding resources for them (Engel, Huth & Frank 2012; Sauerbrei *et al.* 2014). Unfortunately, we had no information on species-specific maize use to explore this with the attribute-based approach. Because many environmental variables, especially for land-use change, show similar directional changes over time (Robinson & Sutherland 2002; Fox 2004; Heldbjerg *et al.* 2016), it is difficult to confidently determine the most important component of land-use change. Thus, we cannot determine whether maize area itself or associated changes were the main driver – most likely it was a combination. Nonetheless, our results suggest agricultural change has had large and detrimental repercussions for the terrestrial bird community leading to lower abundances of the bird community.

Using the species-attribute based approach, we asked whether signals of climate change and land-use change were also visible on the interspecific variation in abundance changes. We found the strongest evidence for relative increases of warm-adapted species and habitat generalists over cold-adapted species and habitat specialists (Devictor *et al*. 2012). As temperature niche had the largest effect size on abundances out of all the species attributes, climate change has potentially been most responsible for causing variation in abundance changes among species, which would change community composition. However, land-use change has likely also caused changes in community-composition. The most important habitat use affecting species' abundances appeared to be meadow use and probably relates to changes in grassland management. This is probably because dry grasslands are grazed less, as more livestock are kept indoors, and reseeded swards are instead intensively managed to maximise silage production, which reduces suitability for species such as the Starling, *Sturnus vulgaris* (Heldbjerg *et al.* 2016). In addition, many wet marginal grasslands that are important for more specialised breeding bird species have been abandoned for grazing (e.g. Lapwing *Vanellus vanellus*, Redshank *Tringa totanus* and Curlew *Numenius arquata*) (Heldbjerg *et al.* 2016). The slight positive effect of arable land-use was unexpected, although few species were specialists of arable land (Larsen, Heldbjerg & Eskildsen 2011), and the effect may be due to temporary positive effects of set-aside schemes on species such as the Corn Bunting, *Miliaria calandra* that showed a high association with arable land.

Potentially the effects of species attributes are mediated by unstudied environmental drivers, or correlations between these species attributes and unstudied species attributes or traits. However, the interactions between species attributes and environmental variables give weight to the inference that the effects of temperature niche on species' abundances were due to temperature change, and the effects of habitat breadth were due to land-use change. The community shift to warm-adapted species could be linked to the effects of increasing winter temperatures (Prince & Zuckerberg 2015), as shown by the significant interaction between winter temperature and temperature preference. The positive effect of warming spring temperatures on abundances was lower for migratory species, which may be linked with a growing mismatch between their timing of breeding and the peak timing of food supply (Both *et al*. 2006; Møller *et al*. 2008). There is widespread evidence for communities becoming more dominated by generalist species, which could be hypothesized to be a consequence of either climate change or habitat change (van Turnhout *et al*. 2010; Davey *et al.* 2012; Pearce-Higgins *et al.* 2015a; Thomsen *et al.* 2016). In our dataset, the increased relative abundance of habitat generalists, compared with specialists, could be better explained by agricultural intensification than by temperature change because habitat breadth only significantly interacted with a land-use environmental variable and not a climatic one.

Our analysis shows the knowledge that can be gained from combining species attributes and environmental variables together in a single analysis. The combined model only explained slightly more variation in the data than the attribute-based approach alone (14% vs 12%), probably because the 'year' effect in the attributes model captured the directional trends in the environmental variables. However, as shown above, in the combined model, we could test hypotheses about which environmental variables interacted with which species attributes. On their own, both approaches have their own merits and supply different information on the impacts of environmental change. The attribute-based approach can be most useful when local environmental data are not readily available but community data on species occurrences/abundances are. Ecological data are increasingly better organized and accessible; however, we still often lack data on environmental variables (apart from climatic data), especially at an annual resolution, from regions of population surveys. Species attribute data can be easier to obtain; thus, species attribute (or trait-based) approaches can be useful and practical shortcuts to identify whether an environmental change has affected the abundances of species in a community. The findings of the attribute-based approach are also potentially generalizable across different species, with predictions of abundance changes being possible for a species, even if there is no population data, given sufficient information on its attributes (Williams *et al.* 2008).

A short-coming of inferring the impacts of environmental change from species attributes is that any links may be due to multiple drivers and correlated species attributes/traits. Thus, the environmental-data approach can always be regarded as superior if the most relevant components of environmental change can be identified and relevant data obtained. Then, the advantage is that the statistical model includes some of the mechanisms through which environmental change affects populations, which enables projection of abundances to other scenarios, on the basis of environmental data. However, the major challenge to this approach is to identify the most relevant environmental variable(s); aspects to consider include the environmental variable (e.g., temperature or aridity); the time period and spatial scale of data to be integrated (lagged or not) and the summary parameter (e.g., mean or maximum) (van de Pol *et al.* 2016).

We show how a combined analysis of environmental and species attribute data can disentangle the effects of environmental change on communities. Analysis of the effect of species attributes on changes in species' abundances shows which types of species are increasing relative to others, helping to understand changes in the species composition of communities. However, the inclusion of environmental variables is essential to link the changes in abundance with the actual environmental change and understand the consequences for changes in absolute population and community size. We suggest that this combined approach, which draws on the mechanistic link supplied by environmental data and the generality supplied by species attribute data will be potentially most useful to project how communities might change under further environmental change.

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Author contributions

DB conceived the idea, performed the analysis and wrote the first draft; HH provided data. HH, AF and KB contributed to hypothesis development and interpretation of the results. All authors contributed to the drafts and gave final approval for publication.

Data accessibility

The bird population data is freely available from the DOF website:
http://www.dof.dk/fakta-om-fugle/punkttaellingsprojektet/indeks-og-tendenser

Web links to other data sources are found within the SOM.

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SOM A

Species included in the analysis: *Accipiter gentilis, Accipiter nisus, Acrocephalus palustris, Acrocephalus schoenobaenus, Acrocephalus scirpaceus, Aegithalos caudatus, Alauda arvensis, Anthus pratensis, Anthus trivialis, Apus apus, Buteo buteo, Carduelis cannabina, Carduelis carduelis, Carduelis chloris, Carduelis flammea, Certhia familiaris, Circus aeruginosus, Coccothraustes coccothraustes, Corvus corax, Corvus monedula, Cuculus canorus, Delichon urbicum, Dendrocopos major, Dryocopus martius, Emberiza citrinella, Emberiza schoeniclus, Erithacus rubecula, Falco tinnunculus, Ficedula hypoleuca, Fringilla coelebs, Garrulus glandarius, Haematopus ostralegus, Hippolais icterina, Hirundo rustica, Lanius collurio, Locustella naevia, Loxia curvirostra, Luscinia luscinia, Miliaria calandra, Motacilla alba, Motacilla flava, Muscicapa striata, Numenius arquata, Oenanthe oenanthe, Parus ater, Parus caeruleus, Parus cristatus, Parus major, Parus palustris, Passer domesticus, Passer montanus, Phoenicurus ochruros, Phoenicurus phoenicurus, Phylloscopus collybita, Phylloscopus sibilatrix, Phylloscopus trochilus, Picus viridis, Prunella modularis, Pyrrhula pyrrhula, Regulus regulus, Riparia riparia, Saxicola rubetra, Sitta europaea, Streptopelia decaocto, Strix aluco, Sturnus vulgaris, Sylvia atricapilla, Sylvia borin, Sylvia communis, Sylvia curruca, Tringa totanus, Troglodytes troglodytes, Turdus merula, Turdus philomelos, Turdus pilaris, Turdus viscivorus, Vanellus vanellus*

SOM B

```
#####################################################################

#Data sources - all data is freely downloadable from the web

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#Bird population data is obtainable from:
#http://www.dof.dk/fakta-om-fugle/punkttaellingsprojektet/indeks-og-tendenser

#Climatic data is available from:
#http://www.ecad.eu/download/ensembles/download.php

#Agricultural yield and area variables from:
#http://www.fao.org/faostat/en/#data
#http://www.statbank.dk/

#Species habitat uses from the SOM of:
#http://www.sciencedirect.com/science/article/pii/S1470160X11000768

#R-INLA for fitting population models from:
#http://www.r-inla.org/


######################################################################

#Environmental variables models

######################################################################


inla1<-inla(log(Count) ~ avWinter.temp + prev.Maize.area+#fixed effects
             f(Year.index, model="ar1", replicate=Species.idx, constr=T)+#ar1 terms
             f(Species.int, model="iid", constr=T)+#species random intercept
             f(Species.winter.id, avWinter.temp, model="iid",constr=T)+#random
slope
             f(Species.maize.id, prev.Maize.area, model="iid",constr=T),#random
slope
             data = inla_df, family = "gaussian")
```

```
######################################################################
#Species attribute models
######################################################################
#constant effects
inla1<-inla(log(Count) ~ Year * (Temp.pref + Habitat.breadth
             + log.Arable.use + log.Meadow.use + Migration)+#fixed effects
             f(Year.index, model="ar1", replicate=Species.id,constr=T)+#ar1 term
             f(Species.int, model="iid", constr=T),#species random intercept
             data = inla_df, family = "gaussian")

#time-varying effects
inla1<-inla(log(Count) ~ Temp.pref + Habitat.breadth +
             log.Arable.use + log.Meadow.use + Migration+#fixed effects
             Year * Migration2 +#long-term effect of migration
             f(Year.index, model="ar1", replicate=Species.idx, constr=T)+#ar1 term
             f(Species.int, model="iid", constr=T)+#species random intercept
             f(Year.hb, Habitat.breadth, model="rw1")+#time-varying habitat breadth
             f(Year.tp, Temp.pref, model="rw1")+#time-varying temp pref
             f(Year.m, log.Meadow.use, model="rw1")+#time-varying meadow use
             f(Year.a, log.Arable.use, model="rw1"),#time-varying arable use
             data = inla_df, family = "gaussian")


######################################################################
#Environment X Species attribute models
######################################################################
inla1<-inla(log(Count) ~ Temp.pref * avWinter.temp +
             Habitat.breadth * prev.Maize.area+
             log.Meadow.use * prev.Maize.area +
             Migration * prevSpring.temp+#fixed effects
             Year * Migration +#long-term effect of migration
             f(Year.index, model="ar1", replicate=Species.idx, constr=T)+#ar1 term
             f(Species.int, model="iid", constr=T)+#species random intercept
             data=inla_df,family="gaussian")
######################################################################
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Table S1 Summary of long-term trends in the environmental variables, as tested in linear regression models with each as the response and year as the predictor.

ENVIRONMENTAL VARIABLE	TREND	SE	LOWER	UPPER	TYPE
MAIZE AREA	6155.16	435.067	5265.35	7044.97	Agricultural area
WINTER WHEAT AREA	14880.39	1608.31	11591.03	18169.75	Agricultural area
SPRING BARLEY AREA	-22820.30	2979.24	-28913.52	-16727.07	Agricultural area
GRASSLAND AREA	-1629.19	1176.58	-4035.56	777.18	Agricultural area
CEREAL YIELD	496.18	98.23	295.30	697.07	Agricultural yield
BARLEY YIELD	310.43	100.15	105.59	515.27	Agricultural yield
WHEAT YIELD	257.15	100.16	52.30	462.00	Agricultural yield
SUMMER PRECIP	0.93	0.30	0.31	1.55	Climatic
(2-YEAR AVERAGE) SUMMER PRECIP	0.59	0.21	0.16	1.01	Climatic
(PREVIOUS) SUMMER PRECIP	0.24	0.35	-0.48	0.97	Climatic
(PREVIOUS) WINTER TEMP	0.08	0.04	-0.001	0.16	Climatic
(PREVIOUS) SUMMER TEMP	0.06	0.02	0.02	0.10	Climatic
WINTER TEMP	0.06	0.04	-0.03	0.14	Climatic
(2-YEAR AVERAGE) SUMMER TEMP	0.05	0.013	0.03	0.08	Climatic
(3-YEAR AVERAGE WINTER TEMP)	0.05	0.02	0.002	0.10	Climatic
(PREVIOUS) SPRING TEMP	0.05	0.02	0.003	0.09	Climatic
SUMMER TEMP	0.05	0.02	0.006	0.09	Climatic

(2-YEAR AVERAGE) SPRING TEMP	0.05	0.02	0.015	0.08	Climatic
SPRING TEMP	0.05	0.02	0.002	0.09	Climatic
WINTER PRECIP	0.04	0.34	-0.65	0.74	Climatic
(2-YEAR AVERAGE) WINTER TEMP	0.04	0.03	-0.03	0.11	Climatic
(PREVIOUS) WINTER PRECIP	0.02	0.34	-0.67	0.71	Climatic
(CURRENT) WINTER TEMP	0.02	0.04	-0.06	0.10	Climatic
SPRING PRECIP	-0.24	0.21	-0.67	0.20	Climatic
(2-YEAR AVERAGE) SPRING PRECIP	-0.17	0.17	-0.52	0.18	Climatic
(PREVIOUS) SPRING PRECIP	-0.11	0.23	-0.58	0.36	Climatic
(CURRENT) WINTER PRECIP	-0.08	0.34	-0.77	0.60	Climatic
(2-YEAR AVERAGE) WINTER PRECIP	-0.02	0.21	-0.45	0.41	Climatic
(3-YEAR AVERAGE) WINTER PRECIP	-0.005	0.15	-0.32	0.31	Climatic

Table S2 Effects (mean effect size ± 95% confidence intervals) of all environmental variables tested on the log of species' population abundance indices. All variables were tested separately on the community data in simple regression models, with species included as random terms (intercept and slopes).

ENVIRON VARIABLE	MEAN	SD	LOWER CI	UPPER CI	TYPE
GRASSLAND AREA	0.00004	0.00000	0.00026	-0.00019	Agricultural area
MAIZE AREA	-0.00868	0.00000	-0.01016	-0.00721	Agricultural area
WINTER WHEAT AREA	-0.00498	0.00000	-0.00643	-0.00353	Agricultural area
SPRING BARLEY AREA	-0.00367	0.00000	-0.00224	-0.00509	Agricultural area
CEREAL YIELD	-0.00173	0.00000	-0.00265	-0.00082	Agricultural yield
BARLEY YIELD	-0.00084	0.00000	-0.00140	-0.00027	Agricultural yield
WHEAT YIELD	-0.00031	0.00000	-0.00079	0.00016	Agricultural yield
(PREVIOUS) WINTER TEMP	0.00000	0.00247	-0.00039	0.00039	Climatic
(3-YEAR AVERAGE) WINTER TEMP	0.00055	0.00479	0.00005	0.00105	Climatic
(2-YEAR AVERAGE) WINTER TEMP	0.00039	0.00383	0.00009	0.00069	Climatic
SPRING TEMP	0.00033	0.00475	-0.00009	0.00075	Climatic
WINTER TEMP	0.00024	0.00247	-0.00004	0.00051	Climatic
(2-YEAR AVERAGE) SPRING TEMP	0.00019	0.00642	-0.00038	0.00077	Climatic
SUMMER TEMP	0.00013	0.00471	-0.00030	0.00056	Climatic

(CURRENT) WINTER TEMP	0.00010	0.00261	-0.00001	0.00021	Climatic
WINTER PRECIP	0.00000	0.00025	-0.00002	0.00003	Climatic
(PREVIOUS) SUMMER TEMP	-0.00066	0.00465	-0.00123	-0.00010	Climatic
(2-YEAR AVERAGE) SUMMER TEMP	-0.00044	0.00662	-0.00114	0.00027	Climatic
(2-YEAR AVERAGE) SUMMER PRECIP	-0.00041	0.00048	-0.00097	0.00015	Climatic
SUMMER PRECIP	-0.00036	0.00029	-0.00090	0.00017	Climatic
SPRING PRECIP	-0.00026	0.00040	-0.00007	-0.00044	Climatic
(2-YEAR AVERAGE) SPRING PRECIP	-0.00018	0.00049	-0.00001	-0.00034	Climatic
(PREVIOUS) SPRING TEMP	-0.00013	0.00470	-0.00056	0.00030	Climatic
(2-YEAR AVERAGE) WINTER PRECIP	-0.00001	0.00050	0.00001	-0.00002	Climatic
(PREVIOUS) SPRING PRECIP	-0.00001	0.00037	0.00006	-0.00009	Climatic
(CURRENT WINTER PRECIP	-0.00001	0.00025	0.00004	-0.00005	Climatic
(PREVIOUS) SUMMER PRECIP	-0.00001	0.00029	-0.00014	0.00013	Climatic
(3-YEAR AVERAGE) WINTER PRECIP	-0.00000	0.00055	0.00000	-0.00001	Climatic
(PREVIOUS) WINTER PRECIP	-0.00000	0.00025	-0.00001	0.00001	Climatic

Table S3 Effects of the species attributes on species' long-term population trends.

SPECIES ATTRIBUTE	EFFECT SIZE	SD	T-VALUE	LOWER CI	UPPER CI
MIGRATION	0.01179	0.00272	4.3346	0.00643	0.01713
TEMPERATURE PREFERENCE	0.00613	0.00132	4.6440	0.00355	0.00872
HABITAT BREADTH	0.00511	0.00131	3.9008	0.00254	0.00768
ARABLE LAND-USE	0.00267	0.00141	1.8936	-0.00010	0.00543
MEADOW USE	-0.00375	0.00153	-2.4510	-0.00675	-0.00076

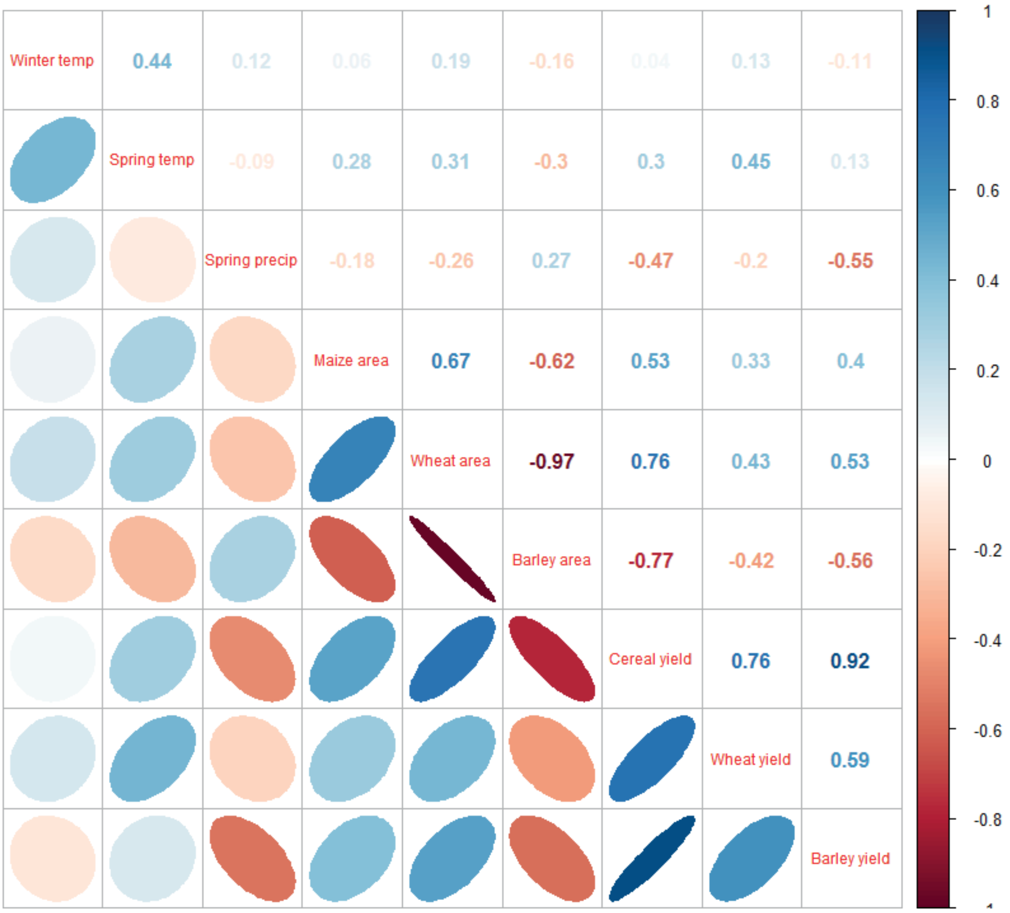

Fig. S1: Correlations among environmental variables. Blue shading refers to positive correlations and red shading refers to negative correlations.

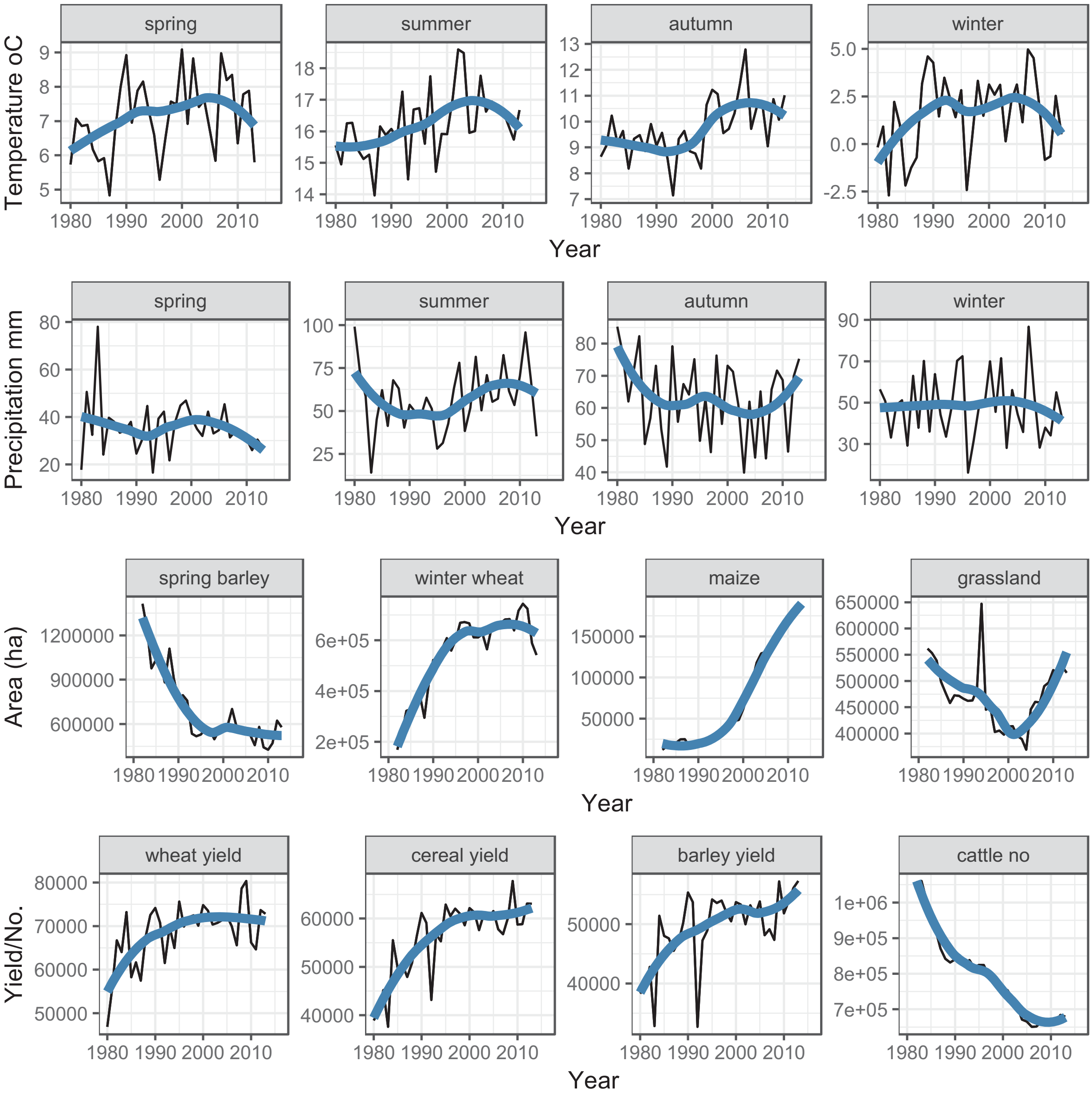

Fig. S2: Time series of annual temperatures, precipitations, agricultural areas and yields for Denmark since 1980. The blue line is a loess smoother to highlight the trend.

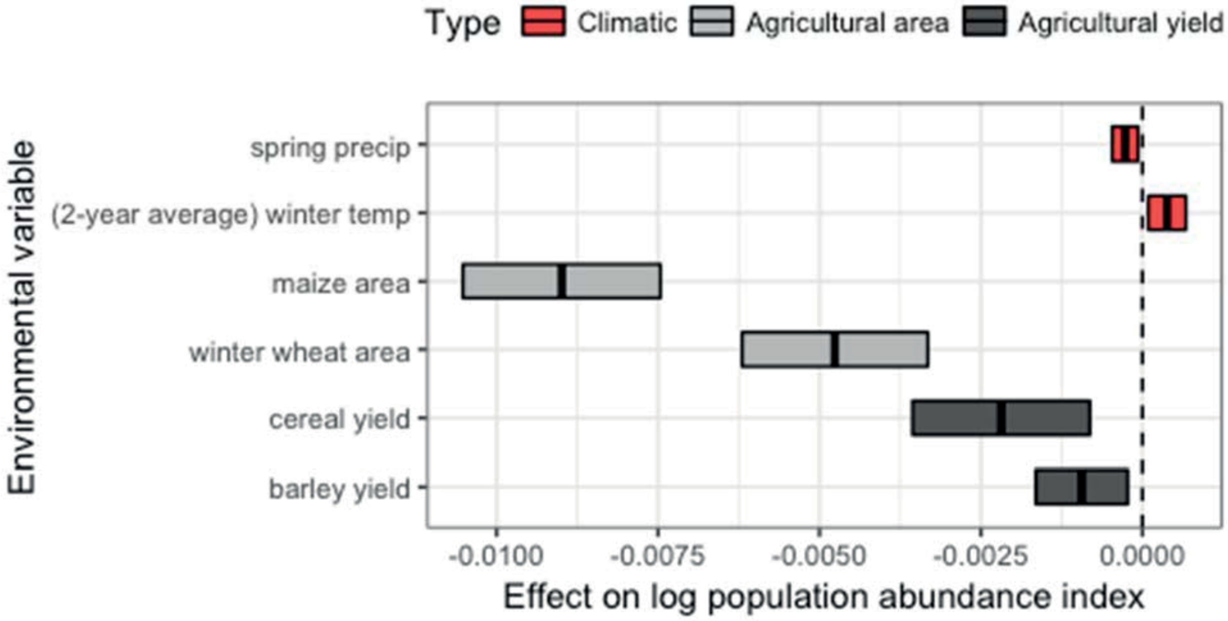

Fig. S3: Effects (mean effect size ± 95% confidence intervals) of environmental variables on the log of species' population abundance indices. All variables were tested separately on the community data in simple regression models, with species included as random terms (intercept and slopes). Unlike Fig. 3, these effect sizes were standardized by the trends in each environmental variable. The same pattern is found as in Fig. 3 regarding the absolute magnitude of climatic versus agricultural variables. One small difference here is that the effect size of spring precipitation is now negative because spring precipitation had a small negative trend.

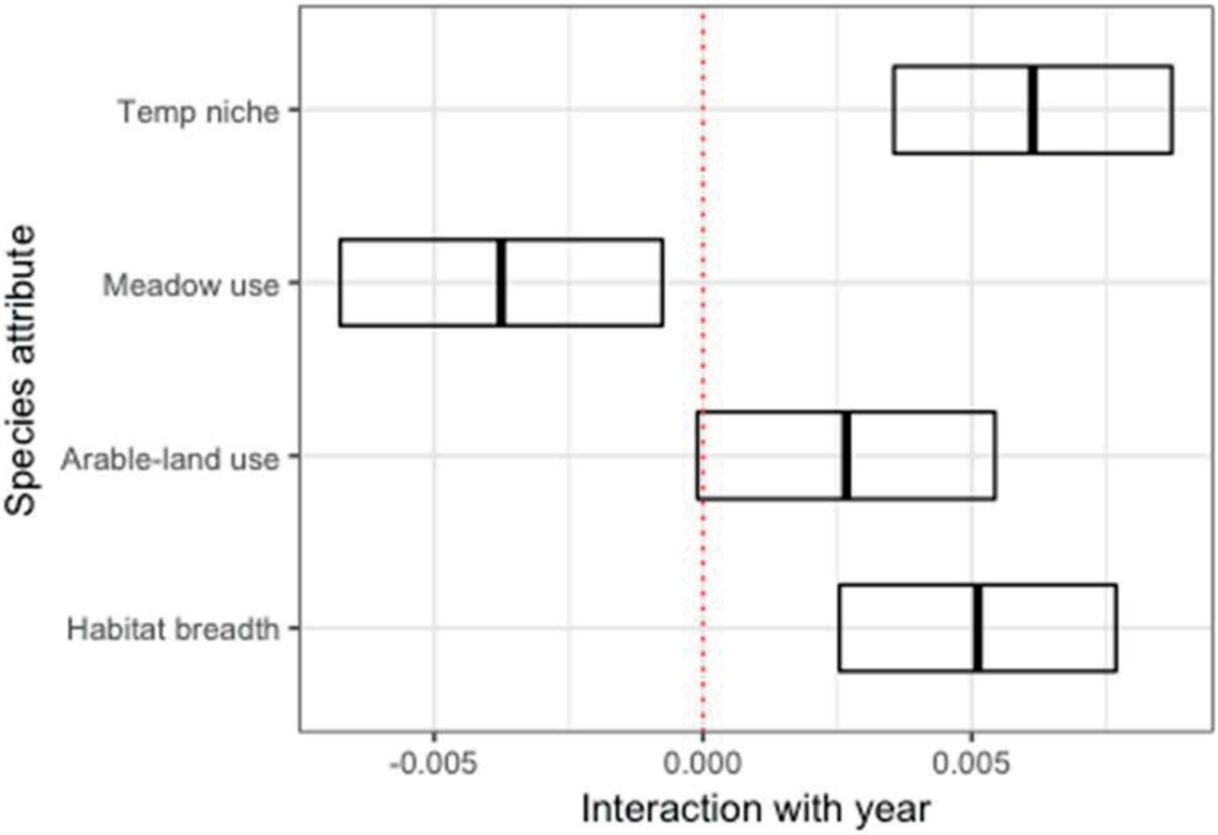

Fig. S4: Effect of species attributes on their long-term population trends (determined by the effect of “year” on their log abundance). Cross bars are mean ± 95% confidence interval.

PAPER 8

UNSTRUCTURED CITIZEN SCIENCE DATA FAIL TO DETECT LONG-TERM POPULATION DECLINES OF COMMON BIRDS IN DENMARK

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BIODIVERSITY RESEARCH

Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark

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ABSTRACT

Aim Long-term monitoring of biodiversity is necessary to identify population declines and to develop conservation management. Because long-term monitoring is labour-intensive, resources to implement robust monitoring programmes are lacking in many countries. The increasing availability of citizen science data in online public databases can potentially fill gaps in structured monitoring programmes, but only if trends estimated from unstructured citizen science data match those estimated from structured monitoring programmes. We therefore aimed to assess the correlation between trends estimated from structured and unstructured data.

Location Denmark.

Methods We compared population trends for 103 bird species estimated over 28 years from a structured monitoring programme and from unstructured citizen science data to assess whether trends estimated from the two data sources were correlated.

Results Trends estimated from the two data sources were generally positively correlated, but less than half the population declines identified from the structured monitoring data were recovered from the unstructured citizen science data. The mismatch persisted when we reduced the structured monitoring data from count data to occurrence data to mimic the information content of unstructured citizen science data and when we filtered the unstructured data to reduce the number of incomplete lists reported. Mismatching trends were especially prevalent for the most common species. Worryingly, more than half the species showing significant declines in the structured monitoring showed significant positive trends in the citizen science data.

Main conclusions We caution that unstructured citizen science databases cannot replace structured monitoring data because the former are less sensitive to population changes. Thus, unstructured data may not fulfil one of the most critical functions of structured monitoring programmes, namely to act as an early warning system that detects population declines.

Keywords

citizen science, common bird monitoring, JAGS, occupancy model, population trend, volunteer.

INTRODUCTION

Monitoring changes in species' populations is an essential element of biodiversity conservation. Objective quantification of population change allows problems to be identified and conservation responses to be developed. The performance of subsequent management can then be evaluated from continued monitoring. Dedicated population monitoring schemes for biodiversity have been running for decades in many countries, particularly in Europe and North America

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(Greenwood, 2003; Schmeller *et al.*, 2012). However, these structured schemes require considerable investment and organization, and usually rely on a large number of dedicated volunteers who are able and willing to apply standardized methods over large areas and long time periods (Schmeller *et al.*, 2009). Many biodiversity-rich countries, however, lack the resources for such schemes, necessitating the identification of other sources of data and methods to monitor biodiversity.

Casual observations collected without following a structured protocol by members of the public may potentially contribute to research and conservation, and a growing number of unstructured 'citizen science' databases have become available in recent years (Devictor *et al.*, 2010; Sullivan *et al.*, 2014; Theobald *et al.*, 2015). However, several sources of bias in unstructured data are well known and the information content of unstructured data can be highly variable (Dickinson *et al.*, 2010; Hochachka *et al.*, 2012; Isaac & Pocock, 2015). Field observations collected in an unstructured manner usually do not represent random samples and exhibit considerable spatial bias towards more densely populated regions (Boakes *et al.*, 2010; Lin *et al.*, 2015), protected areas, and areas rich in biodiversity and threatened species (Tulloch *et al.*, 2013a). Observation effort is not standardized as in structured monitoring schemes (Dickinson *et al.*, 2010), and there might be considerable reporting bias, as many observers tend to report only unusual or rare species (van Strien *et al.*, 2013). These characteristics of unstructured data make it difficult to assess how reliable they can be for biodiversity monitoring.

Several approaches have been developed to account for some of the bias inherent in unstructured data and extract more reliable information (van Strien *et al.*, 2010; Hochachka *et al.*, 2012; Isaac *et al.*, 2014). Correcting for varying observation effort in unstructured data has been achieved using the number of species reported per visit ('list length'; Szabo *et al.*, 2010) or, where recorded, the time spent per field visit (Kindberg *et al.*, 2009). A more significant challenge, the problem that an unknown proportion of those species that are present will not be detected during a given visit, has been addressed using site-occupancy models that account for imperfect detection and may simultaneously correct for reporting bias (Kéry *et al.*, 2010a,b; van Strien *et al.*, 2013). However, a robust validation of such approaches is necessary before unstructured data can be used with confidence for biodiversity monitoring (Isaac *et al.*, 2014).

The value of unstructured monitoring data can be assessed by comparing population trends derived from unstructured citizen science data against the best available independent, structured monitoring schemes. Previous comparisons have detected correlations between reporting rates from weakly structured atlas data and data from a standardized random-sampled survey that range from strong (Szabo *et al.*, 2012) to weak and inconsistent (Snäll *et al.*, 2011). Accounting for imperfect detection using occupancy models based on comprehensive species lists matched the trends of a robust monitoring scheme better than presence-only data (van Strien *et al.*, 2010), and strong trends in structured monitoring data may be recovered from unstructured data when analysed with occupancy models (van Strien *et al.*, 2013; Isaac *et al.*, 2014). The usefulness of unstructured data therefore clearly depends on how they are processed and analysed.

One major difference between many long-term structured monitoring programmes and unstructured citizen science data is that the former often provide counts or indices of abundance, whereas unstructured citizen science data often only provide detection/non-detection data because of highly varying recording intensity in space and over time (Isaac *et al.*, 2014). However, if unstructured data are to fulfil the role of structured monitoring programmes, then they need to be able to identify approximately the same population trends as structured monitoring despite this inherent difference in data quality. Because even simple detection/non-detection data can allow inference about the abundance of a population (Royle & Nichols, 2003), population trends should be detectable with unstructured citizen science data (van Strien *et al.*, 2013; Isaac *et al.*, 2014), but may be less reliable than trends derived from structured monitoring data with higher information content (Johnston *et al.*, 2015). The potential for unstructured data to recover trends could therefore possibly be improved using only records with higher information content (Roy *et al.*, 2012). A typical deficiency of many online public databases is the lack of differentiation between complete species lists (which allow inference about the non-detection of species) and incidental records of a subset of the species actually observed (Kéry *et al.*, 2010b; van Strien *et al.*, 2013; Tulloch *et al.*, 2013b). Using data sets with higher information content that allow the statistical modelling of detection probability can yield improved trend estimates (Kéry *et al.*, 2010a; Isaac & Pocock, 2015), but whether such filtering can overcome other deficiencies of unstructured citizen science data is unclear.

Here, we assess whether unstructured observation records can recover population trends derived with confidence from structured surveys, despite having data with inherently lower information content. We use unstructured bird monitoring data from a country-wide public online database containing more than 12 million records collected over 28 years in Denmark. We first estimated population trends of 103 bird species from unstructured data using occupancy models. We then correlated these trends with population trends estimated over the same period by a structured, standardized common bird monitoring programme in the same country. Finally, we compared trend estimates from both data sources and assessed whether mismatches in these estimates were a consequence of fundamentally different information content by: (1) reducing the information content of structured monitoring data from count to detection/non-detection data, and (2) applying multiple filtering criteria to retain only records in the unstructured data with increasing information content. Our study thus provides a thorough examination of the potential of unstructured citizen science data to detect population trends and identifies factors that may affect the correspondence between structured and unstructured data sources for biodiversity monitoring.

MATERIALS AND METHODS

Structured monitoring and unstructured observation data

The Common Bird Monitoring (CBM) scheme in Denmark was established in 1975 (Heldbjerg *et al.*, 2014) following standard guidelines for structured bird monitoring programmes (Gregory *et al.*, 2004). Birds were monitored once during the breeding season (1 May to 15 June) on observer-chosen (non-randomly placed) routes, with each route containing 10–20 points which were spaced at least 300 m apart and were visited each year by the same observer. At each point, all birds seen or heard within a 5-min interval were counted. This forms the key difference to unstructured observation data, which are generally obtained from random surveys of highly variable duration yielding only detection/non-detection information. Although no *a priori* stratification of routes was applied, the survey routes covered all main habitat types in Denmark and were distributed relatively evenly across the country with no obvious concentrations in urban areas. We used data from 1986 to 2013, during which the number of routes remained relatively stable at between 300 and 400 (Fig. 1; Heldbjerg *et al.*, 2014).

We used unstructured observation data from the online database ‘DOFbasen’ (http://www.dofbasen.dk, Nyegaard *et al.*, 2012), developed by the Dansk Ornitologisk Forening (DOF). DOFbasen was launched in 2002, and most observations have been entered since then (Fig. S1 in Supporting Information). However, many observers have entered data retrospectively, and DOFbasen now holds sufficient historical data to compare trends with structured monitoring data from 1986 to 2013. All records include key fields such as species, date and location. As with many public online databases, DOFbasen did not differentiate until 2012 between complete bird lists (lists of all the species observed on each visit) and incidental records of a subset of the species observed (Kéry *et al.*, 2010b; van Strien *et al.*, 2013; Tulloch *et al.*, 2013b).

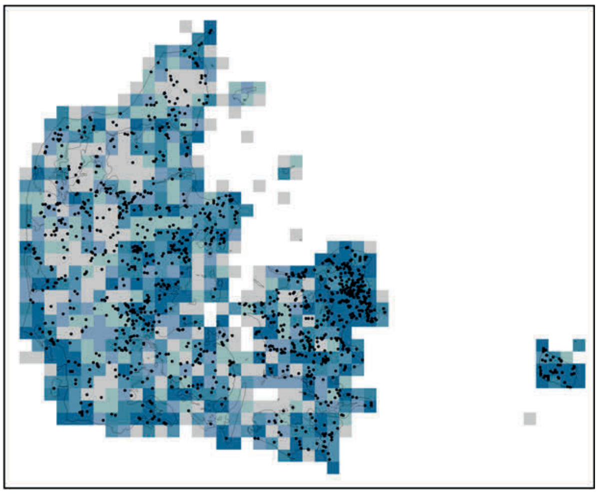

Figure 1 Map of Denmark showing the distribution of common bird monitoring census points used between 1986 and 2013 (black dots) and the distribution of records available from the online database ‘DOFbasen’ until 2013 aggregated over a grid of 10 × 10 km squares. Darker shading indicates higher density of records. The quantity of data from each data source per grid cell was positively correlated ($r_S = 0.78$).

Observations recorded in DOFbasen were not distributed randomly across Denmark (Fig. 1). However, records covered all parts of the country and areas with a larger number of structured monitoring survey routes from the common bird monitoring overlapped with areas of high DOFbasen data density (Spearman’s rank correlation between the number of contributed DOFbasen records and the number of common bird monitoring counts per 100 km^2 area, $r_S = 0.78$; Fig. 1). It is therefore reasonable to assume that trends derived from these unstructured data were as representative of a well-covered country such as Denmark as the structured monitoring data.

Population trend estimation

We compared population trends estimated from a standardized population monitoring scheme (CBM) and from unstructured observation data (DOFbasen) to assess the extent to which trends estimated from the two data sources matched. We estimated population trends for 103 species breeding in Denmark (Table S1) over a 28-year period (1986–2013) for which data were available from both data sources. However, because the citizen science database was launched only in 2002, we also estimated trends for a shorter 11-year period (2002–2013) corresponding to the period after the launch of the database when observers could enter contemporary records.

From the structured monitoring data, we estimated a population trend for each species using a generalized linear mixed model with a Poisson error distribution and a random ‘route’ effect to account for spatial and habitat differences at the route level. This approach is the standard analytical procedure for estimating trends from bird count data when no ancillary data (e.g. distance to detected birds, continuous covariates affecting detectability) or repeat visits are available to account for imperfect detection (Kéry & Schaub, 2012; Inger *et al.*, 2014). We implemented the GLMM in R package ‘lme4’ for each species with the generic formula glmer (Number ~ Year + (Year|Route_ID), family = ‘poisson’). ‘Year’ was fitted as a continuous covariate.

From the unstructured citizen science data, we first extracted only breeding season records (May and June), corresponding to the recording period of the structured monitoring scheme. Every record in DOFbasen includes a location identifier, which served as our definition of a 'site' at which observations of species were recorded, but these sites are not of a defined size, which makes any abundance information difficult to interpret. Every visit to a site that was entered into the online database was treated as a 'list' of species, and species that were not recorded on the list were assigned a value of 0 (not observed or not reported). To estimate population trends from the unstructured data, we used a multi-year occupancy modelling framework to account for imperfect detection or recording (van Strien *et al.*, 2013; Isaac *et al.*, 2014). We used the detection/non-detection information contained in contributed species lists and considered that two covariates influenced the probability of detection: we included 'month' (May or June) as a covariate because for some birds, the probability of detection can vary over the course of the breeding season, and we included the number of species recorded during that visit at that site, as an indication of observer effort and quality (Franklin, 1999; Roberts *et al.*, 2007; Szabo *et al.*, 2010).

We fitted occupancy models using Markov Chain Monte Carlo (MCMC) methods in a Bayesian framework following the approach described by Isaac *et al.* (2014), including a random site effect to account for spatial differences. The trend model component of the multi-year occupancy model was therefore structurally similar to the trend GLMM used for the structured monitoring data described above. For each species, we ran three Markov chains each with 5000 iterations and discarded the first 2500 iterations as burn-in. From the remaining iterations we only used every second iteration for inference. Convergence was tested using the Gelman-Rubin diagnostic (Brooks & Gelman, 1998), and trend estimates were retained only if this diagnostic indicated convergence (R-hat < 1.02). We fitted all occupancy models in JAGS 3.3 (Plummer, 2012) via the R2JAGS package (Su & Yajima, 2012) called from R 3.1.1 (R Development Core Team, 2013).

Comparison of trends derived from structured and unstructured data

We used Spearman's rank correlation coefficient to assess whether population trends derived from the unstructured and the structured data across the 103 species were correlated using a significance threshold of $\alpha = 0.05$, and we performed separate correlations for the long (1986–2013) and the short (2002–2013) time series. Because the correlation does not account for the uncertainty in trend estimates, we also compared the direction of trend estimates between the two data sources taking uncertainty into account. We first classified trend direction as either increasing or decreasing if the 95% confidence interval of the estimated population growth rate was > 0 or < 0. Species for which the 95% confidence interval of the estimated population growth rate spanned 0 were considered to have stable or inconclusive trends. We then cross-tabulated the trend directions from both data sources and calculated the proportion of species that had matching and non-matching trend directions for the period 1986–2013 and 2002–2013.

Examining causes for mismatches in trend direction

Because the structured monitoring data have a higher information content than the unstructured data (abundance vs. detection/non-detection), and because the value of unstructured monitoring data may vary among species (van Strien *et al.*, 2013), we expected some discrepancies among trend estimates and examined whether these were due to the information content of the data or could be explained by species-specific traits such as abundance and migratory strategy.

To examine the information content of data, we first reduced the structured monitoring data to simple detection/non-detection data and estimated trends using a similar GLMM as described above but with a binomial rather than a Poisson error structure, which is analogous to the trend model used for the unstructured data. In a second step, we aimed to increase the quality of the unstructured data by retaining only selected records with high information content. We applied three hierarchical data filters to the unstructured data, discarded all records that did not meet these filtering criteria and estimated trends from the data remaining after each iteration.

The first filter was applied to the number of species recorded during a site visit to increase the likelihood that a list was complete and that the species missing from that list could therefore be considered as not observed in data analysis. We discarded all records that reported only a single species during a visit to one site on one day, and considered the remaining lists 'complete' if the number of species recorded exceeded a threshold that was scaled to the total number of species recorded at a given site to avoid bias due to spatial effects of species richness (Kéry *et al.*, 2010a). We explored three different thresholds, considering lists as 'complete' if the number of recorded species exceeded 5%, 10% or 25% of the cumulative total number of all species ever recorded at a particular site. We explored higher thresholds, but because the number of records that reported > 25% of all known species at a site was very small, it was rarely possible to estimate trends when a higher threshold was chosen.

The second data filtering step considered the number of reported visits to a given site during May and June in one year. Repeat visits during a period of demographic closure are necessary to account for imperfect detection in an occupancy modelling framework. The probability of observing a species increases with the number of visits to a site, and we therefore used thresholds of 3, 5 and 10 visits during the breeding season to include sites in the estimation of occupancy. We eliminated sites that had less than the various thresholds of site visits on the subset of 'complete' lists based on the criteria described in the first filtering step above. The third and final data filtering step considered the number of years during which sites were covered with a sufficient number of visits meeting the criteria for 'complete' lists (Roy *et al.*, 2012; Isaac *et al.*, 2014). Trend estimation is generally more reliable if the same sites are monitored over a longer period of time. We therefore eliminated sites if they had visits with 'complete' lists for < 3, < 5 or < 10 years. These different data filtering rules resulted in a total of 27 combinations (3 thresholds for list length, 3 thresholds for number of visits and 3 thresholds for number of years) of selected data for estimating annual occupancy and population trend for all our target species. For the estimation of trends from 2002 to 2013, we omitted the data filtering step that mandated sites with at least 10 years of monitoring data, because the monitoring interval included only 11 years and very few sites matched this criterion.

Besides the information content of the data, we also examined species-specific biological traits that explained statistical variation in the mismatches between population trend estimates derived from structured and unstructured data. We used the cross-tabulation of matching and non-matching trend estimates over the period 1986–2013 described above and linked this response (match/mismatch) to five explanatory variables: male body mass (as a proxy for body size), national population size in Denmark, breeding system (colonial, semi-colonial and territorial), habitat preference (marine, coastal, inland wetland, boreal and temperate forests, farmland and grassland, habitat generalists) and migration strategy (resident, partial migrant, migrant within Europe, short-distance migrant to North Africa or the Middle East, long-distance migrant to sub-Saharan Africa or Asia). We extracted body mass data, migration strategy and habitat preferences from standard references (Glutz von Blotzheim, 1985–1998; Tucker & Evans, 1997; Snow & Perrins, 1998). Population size was calculated as the geometric mean of the minimum and maximum population estimates for Denmark (BirdLife International, 2004).

We used a machine-learning algorithm based on ensembles of regression trees (RandomForest) to evaluate which of these five variables explained the most variation in mismatching trend estimates (Cutler *et al.*, 2007; Hochachka *et al.*, 2007).We used a random forest procedure with unbiased classification trees based on a conditional inference framework (package 'party' in R 3.1.1; Hothorn *et al.*, 2006) that allows to account for bias in variable importance measures among categorical variables with different numbers of levels (Strobl *et al.*, 2007; Boulesteix *et al.*, 2012). We constructed 1500 classification trees and used a random subset of 64% of the data without replacement to build single trees. We report the relative variable importance as the decrease in model accuracy after permutation scaled to 100% for the most important variable. The accuracy of the random forest model was assessed with a simple confusion matrix of the predicted and actual trend estimate matches.

RESULTS

Based on the structured monitoring for the full 28 years, 60 species showed significant long-term declines in abundance, 26 species increased significantly and the remaining 17 species showed either stable or fluctuating populations without a significantly positive or negative trend (Table 1). For the shorter time period (2002–2013), 48 species declined significantly, 25 species increased significantly and 30 were stable or the trend estimate was too imprecise to assign the trend as increasing or decreasing (Table S2). By contrast, the unstructured data identified only 20 species as declining over 28 years (19 species over 11 years), 49 species as increasing (48 over 11 years) and 34 species (35 over 11 years) that were either stable or where the trend estimate was too imprecise (Tables 1 & S2).

There was a general positive correlation between population trends estimated from structured and unstructured data sources (Table 2, Fig. 2). However, despite the positive correlation between trends derived from structured and unstructured data, the direction of trend estimates matched for < 50% of species when taking the uncertainty in trend estimates into account (Table 1). The majority of species that were in decline based on the structured monitoring were estimated to have a stable or increasing population trend in the unstructured data (Table 1). Conversely, population declines estimated from unstructured data were largely confirmed by the structured monitoring (Table 1).

Reducing the information content of the structured monitoring data to estimate trends in occupancy rather than abundance did not increase the strength of the trend correlation (Table 2, Fig. 2) or the proportion of matching trend directions between structured and unstructured data (Tables 1 & S2 for 2002–2013). Similarly, filtering the unstructured data to retain only data with higher information content did not improve the strength of the correlation; increasingly strict filters led to poorer correlations (Table 2). By contrast, trends in occupancy and abundance derived from the structured monitoring data were strongly correlated ($r_S = 0.87$, Fig. S2), and the trend direction matched for 82.5% of all species (Table S3).

The three most important variables explaining the mismatch of trend estimates between the structured monitoring and unstructured citizen science data were population size, body size and habitat preference (classification success of random forest model = 84.2%). Trend estimates did not match at all for very abundant species (blackbird *Turdus merula*, chaffinch *Fringilla coelebs* and skylark *Alauda arvensis*, all with population sizes > 1 million birds) and matched poorly for relatively small birds, especially in forest and inland wetland habitats (Fig. 3). When the structured monitoring data were reduced to detection/non-detection data, mismatches in trend direction were almost exclusively explained by male body size (classification success = 80.3%), with birds below 500 g body size having generally poorly matching trends, while trend estimates matched well for birds > 500 g. In both analyses, migration strategy and breeding system had no influence on the extent to which trends from the two data sources matched (both < 5% relative variable importance).

Table 1 Number of species with matching and non-matching population trend directions for 103 bird species between 1986 and 2013 in Denmark derived from an unstructured observation database and a structured monitoring scheme using either original abundance data or simple detection/non-detection data (occupancy)

			Unstructured data		
			Decreasing	Stable/inconclusive	Increasing
Structured monitoring	Abundance	Decreasing	16	23	21
		Stable/inconclusive	4	7	6
		Increasing	0	4	22
	Occupancy	Decreasing	18	25	24
		Stable/inconclusive	2	4	1
		Increasing	0	5	24

Trends were considered increasing or decreasing if the 95% confidence interval of the population growth rate estimate was > 0 or < 0, respectively, and stable or inconclusive if the interval spanned 0.

DISCUSSION

Population trends estimated from structured and unstructured data were generally positively correlated, but there was substantial variation among species, and the declines of many common species were not detected with unstructured citizen science data. This pattern was evident regardless of whether we used the abundance information in the structured monitoring data or reduced these data to simple detection/non-detection data. We therefore conclude that structured monitoring programmes are more powerful to detect population declines than unstructured citizen science data.

Many common European bird species are declining (Sanderson *et al.*, 2006; Inger *et al.*, 2014), and range retractions are also common (Balmer *et al.*, 2014). However, more than half of the species that showed significant long-term population declines in both abundance and occupancy based on our structured monitoring data were classified as either stable or even increasing by the unstructured data (Table 1). This discrepancy indicates that caution is needed when using unstructured data for estimating population trends, and that unstructured citizen science data cannot generally replace standardized monitoring schemes. While this mismatch may be explained by factors such as the reporting of complete lists which may not apply to all online databases, we caution that unstructured citizen science data may not fulfil one of the most critical functions of structured monitoring programmes, namely to act as an early warning system that detects population declines, especially of common and widespread species (Inger *et al.*, 2014).

The structured monitoring data yielded similar numbers of species declining, increasing or with stable or inconclusive trend regardless of whether we used abundance data or reduced the information content to use just detection/non-detection data. The mismatching trends derived from structured monitoring data and unstructured citizen science data are therefore not due to the inherently lower information content of unstructured data. Furthermore, our filtering to extract only records with the highest information content from the unstructured citizen science data did not improve the correlation between trend estimates. Stricter filter criteria led to a rapid decline in the amount of data that passed the filter, and trend estimates resulting from these smaller data sets were generally less reliable. Appropriate modelling of the various sources of bias in citizen science data may therefore be the best strategy to derive the most reliable trend information (van Strien *et al.*, 2013; Isaac *et al.*, 2014), but this information is nonetheless inferior to the power of standardized monitoring programmes in detecting species declines.

In situations where structured monitoring is not feasible or too costly, online databases might constitute the only data sources available. While such data can be informative, their value for trend monitoring could be improved by informing contributors about deficiencies (Sullivan *et al.*, 2014). For example, in our data set, the number of visits to sites every year was highly skewed, with some sites receiving > 500 visits per year, and others only single visits. Encouraging recorders to repeatedly contribute data from rarely visited areas might increase the suitability of data for trend analyses using recommended methods that account for imperfect detection (van Strien *et al.*, 2013; Isaac *et al.*, 2014; Isaac & Pocock, 2015). The skewed distribution of visits is likely a result of casual observers frequenting easily accessible, well-known and ‘interesting’ sites (e.g. sites with high diversity or rare species, Tulloch & Szabo, 2012; Tulloch *et al.*, 2013a). One solution to this problem could be to survey regions and habitats that are neglected by casual observers with professional observers (Tulloch *et al.*, 2013a), an approach used during fieldwork of the recent UK breeding bird atlas (Balmer *et al.*, 2014). There are many other approaches for enticing ‘citizen scientists’ to provide data that are of higher information content, but the effort required to do this may be better spent on designing a structured monitoring scheme and recruiting observers to participate in this scheme (Isaac & Pocock, 2015). After all, the structured monitoring data we analysed here were also collected by volunteer ‘citizen scientists’, who follow a certain set of standard protocols which renders trend estimation and inference more reliable.

Table 2 Correlation (Spearman's rank correlation coefficient r_S) between population trend estimates for 103 bird species derived from a structured monitoring scheme and an unstructured observation database filtered by certain criteria over a 28-year period (1986–2013) and an 11-year period (2002–2013) in Denmark

			Abundance		Occupancy	
Proportional list length	*n* visits	*n* years	r_S (28 years)	r_S (11 years)	r_S (28 years)	r_S (11 years)
Unfiltered data			**0.600**	**0.491**	**0.625**	**0.501**
0.25	10	10	0.147		0.175	
		5	0.327	0.184	0.376	0.199
		3	0.355	0.185	0.412	0.202
	5	10	0.353		0.346	
		5	0.314	0.197	0.374	0.121
		3	0.358	0.179	0.432	0.212
	3	10	0.363		0.350	
		5	0.402	0.246	0.459	0.259
		3	0.408	0.357	0.467	0.374
0.1	10	10	0.475		0.484	
		5	0.357	0.191	0.405	0.171
		3	0.388	0.222	0.444	0.211
	5	10	0.413		0.463	
		5	0.424	0.416	0.515	0.353
		3	0.437	0.438	0.510	0.394
	3	10	0.464		0.541	
		5	0.485	0.479	0.550	0.463
		3	0.501	0.491	0.574	0.482
0.05	10	10	0.384		0.444	
		5	0.390	0.348	0.469	0.336
		3	0.409	0.359	0.479	0.355
	5	10	0.470		0.545	
		5	0.485	0.435	0.537	0.419
		3	0.469	0.426	0.528	0.426
	3	10	0.517		0.570	
		5	0.503	0.465	0.567	0.434
		3	0.498	0.453	0.548	0.438

Data from the structured monitoring were either used as counts (*abundance*) or reduced to detection/non-detection (*occupancy*). Filters were applied in a hierarchical fashion based on the number of species recorded during each visit (as proportion of the total species number ever recorded at a given site, *prop. list length*), the number of visits with 'complete' lists in a given year, and the number of years with sufficient visits with 'complete' lists. Strongest correlations are highlighted in bold.

The most important biological variables explaining mismatching population trend estimates were population size for the abundance data and body mass for occupancy. Abundance trends estimated for extremely common and widespread species matched very poorly between the structured and unstructured data, which may be a consequence of the unstructured data yielding only information about occurrence: very common species may experience declines in abundance before completely disappearing from certain areas, and the unstructured data may therefore not be ideal to detect the declines of common species which are currently occurring across Europe (Inger *et al.*, 2014). When we reduced the structured monitoring data to occurrence data, the mismatches persisted but were better explained by male body size, indicating that trends of mostly small birds are very poorly captured by the unstructured citizen science data.

Another potential explanation for differences in trend estimates could be that the different analytical approaches used for both data sources account for variable amounts of uncertainty. In particular, imperfect detection is a well-known problem for the monitoring of wild animals (Royle & Nichols, 2003; Kéry *et al.*, 2009). We used occupancy modelling to correct for varying detection probability in the unstructured data, but we could not apply this method to the structured monitoring data as neither repeated visits nor ancillary data were available from our CBM programme, as is the case for a large number of standardized monitoring programmes (Schmeller *et al.*, 2012). While our method of trend estimation incorporates some uncertainty associated with spatial heterogeneity, the inability to account for imperfect detection may introduce bias into the structured monitoring data if detection probability changes systematically over time (Kéry *et al.*, 2010b).

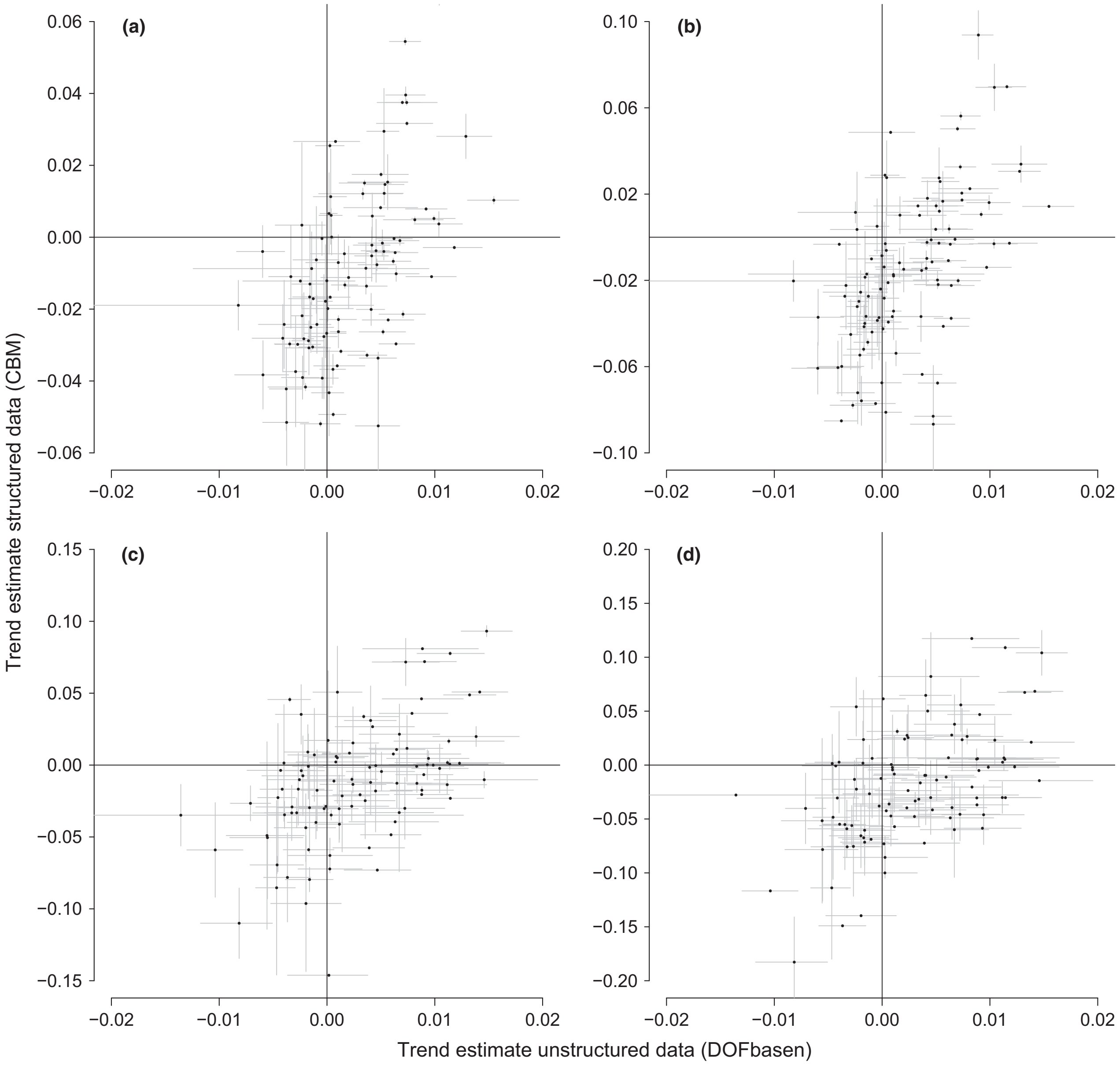

Figure 2 Correlation between population trend estimates (± 95% confidence interval) derived from structured monitoring data (CBM) and from unstructured observation records (DOFbasen) for 103 bird species in Denmark in 1986–2013 (a and b) or 2002–2013 (c and d); trends from structured monitoring data were either based on abundance data (a and c) or reduced to detection/non-detection data (b and d). Note that the scale of axes differs among plots for better clarity.

Non-matching trends from the two data sources could arise either because the unstructured data were inadequate for trend estimation, or the structured monitoring was inadequate for certain species that prefer habitats that are poorly covered by the routes used for the structured monitoring. Structured monitoring schemes are generally designed to cover a large number of common, widespread and territorial species (Newson *et al.*, 2005). Such schemes are therefore often unsuitable for species with localized breeding distributions such as some waterbird species, which may explain the poorly matching trends estimated for species preferring inland wetlands (Fig. 3). Non-matching trends for such species highlight the potential value of unstructured online databases even in countries where structured monitoring schemes exist: casual observations for some species may provide a better basis for population trend estimation than structured monitoring routes that are suboptimal for certain species. However, trends derived from unstructured data would have to be validated with relevant monitoring schemes such as specific wetland bird counts (Zbinden *et al.*, 2014). Identifying the species that are poorly covered by structured monitoring schemes and communicating this knowledge gap to casual observers may enhance the value of data contributed to online databases.

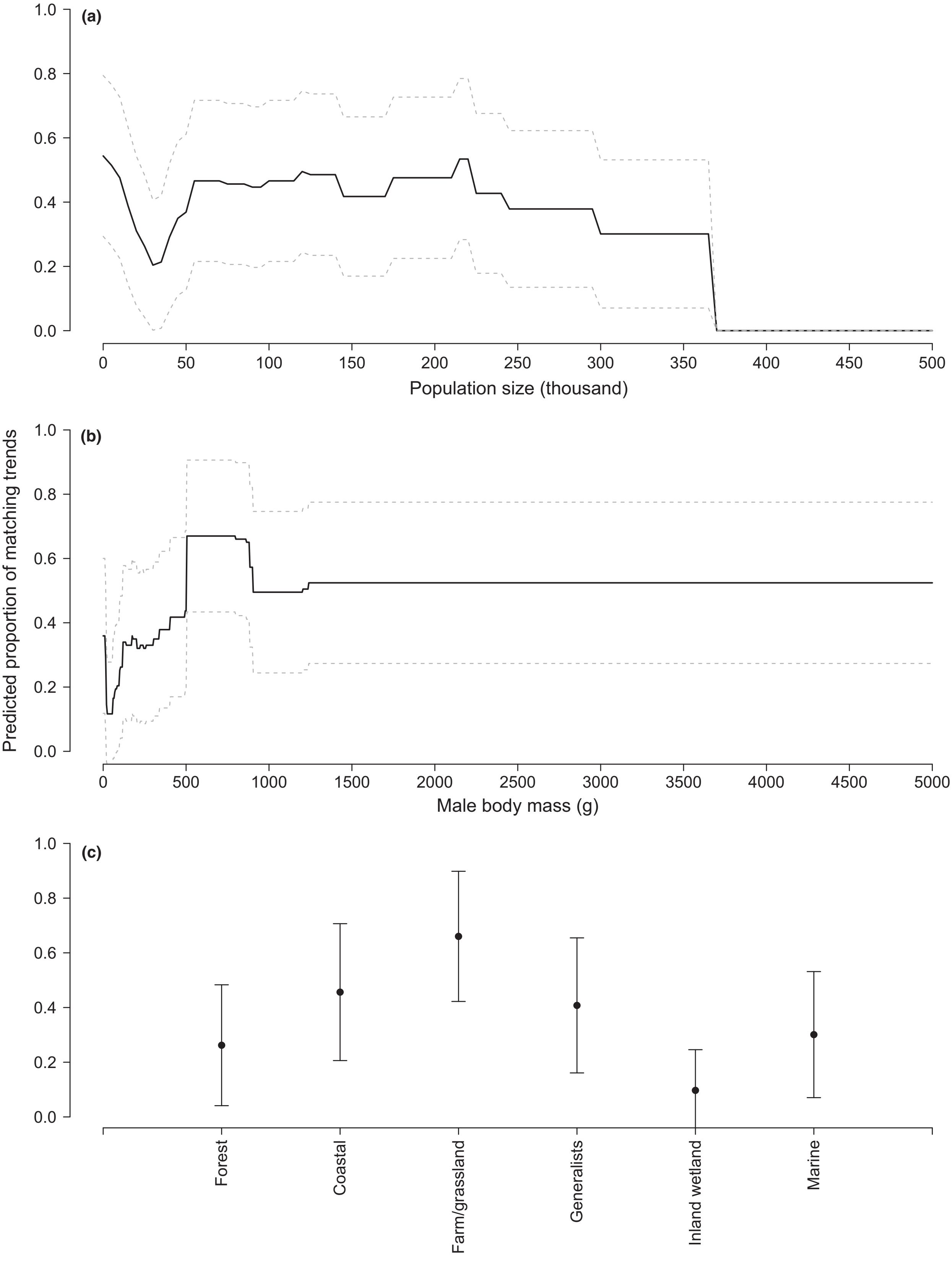

Figure 3 Predicted proportion of matching population trend estimates (± 1 standard deviation) derived from structured monitoring data and from unstructured citizen science data for 103 bird species depending on (a) their total population size in Denmark, (b) their body size measured as male body mass (in g) and (c) their preferred habitat. Predictions are based on a conditional random forest model classifying trend matches.

Further important causes of non-matching trends between structured and unstructured data are changes in reporting behaviour or the observer community over time (Snäll *et al.*, 2011). We found positive trends for several common species in the unstructured data, which declined according to the structured monitoring data. There are two potential explanations for this pattern: (1) the initial contributors to an online reporting scheme are likely to be experienced birdwatchers, who may tend to record mostly those species they consider 'interesting' (Isaac & Pocock, 2015). As a scheme becomes more publicized and widely known, an increasing number of citizens might join who may record also more common and widespread birds (Fig. S1). Our finding that trends did not match for the most common and smallest species is consistent with such an interpretation. (2) In addition to the change in the reporting community, declines of species revealed by structured monitoring schemes might be publicized and lead to a higher awareness among birdwatchers, resulting in changes in reporting behaviour and more contributed records of formerly common and underreported species (Snäll *et al.*, 2011). Examples in our data that are consistent with such explanations include the House Sparrow (*Passer domesticus*; widespread, heavily publicized declines of a familiar urban bird, Hole *et al.*, 2002; De Laet & Summers-Smith, 2007) and the Willow Warbler (*Phylloscopus trochilus*; flagship species for a suite of declining long-distance migrants, Morrison *et al.*, 2010). The best solution to tackle reporting bias is to offer recorders the possibility to submit 'complete' checklists, that is lists that contain all species recorded and allow inference about species that were not detected (Sullivan *et al.*, 2009; Kéry *et al.*, 2010a; van Strien *et al.*, 2013). This feature, which was absent from the Danish online database when we conducted our analysis, has in the meantime been launched in Denmark and other online databases and is considered a standard solution to address some of the biases inherent in citizen science data (Isaac & Pocock, 2015).

CONCLUSIONS

Our analyses suggest that citizen science data collected using unstructured methods may be useful for biodiversity monitoring for species or in areas where dedicated, structured survey data are not available, but that various sources of bias need to be considered in the interpretation of population trend estimates. We recommend retaining all data for analysis and encouraging database managers to distinguish between the reporting of complete and incomplete lists. We suggest that in countries currently without dedicated monitoring systems, encouraging observers to submit records to online databases could make a useful contribution to the monitoring of biodiversity. In countries where structured monitoring data are available, unstructured databases may play a useful role in public education and monitoring of areas or species that cannot be covered with a structured approach. However, our results warn against abandoning existing structured monitoring schemes in the hope that unstructured data contributed by volunteers would be able to fulfil the same purpose with the same power and precision.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Number of records in DOFbasen from 1986 to 2013.

Figure S2 Correlation between population trends from occupancy and abundance data.

Table S1 List of all species and trend estimates derived from structured and unstructured monitoring data.

Table S2 Number of species with matching population trends between 2002 and 2013.

Table S3 Number of species with matching population trends derived from structured occupancy and abundance data.

BIOSKETCH

Johannes Kamp, **Steffen Oppel** and **Paul Donald** are conservation scientists at the University of Münster and the RSPB Centre for Conservation Science. Their work focuses on monitoring populations of threatened species, identifying causes for decline and developing conservation solutions.

Henning Heldbjerg and **Timme Nyegaard** are conservation scientists coordinating citizen science based monitoring of bird populations as well as identifying and communicating causes for population changes.

Author contributions: J.K. and P.D. conceived the idea and coordinated the project. H.H. and T.N. coordinated surveys and accumulated and managed the data. S.O. analysed the data. J.K. and S.O. wrote the manuscript, and all authors contributed to the text.

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SUPPORTING ONLINE INFORMATION

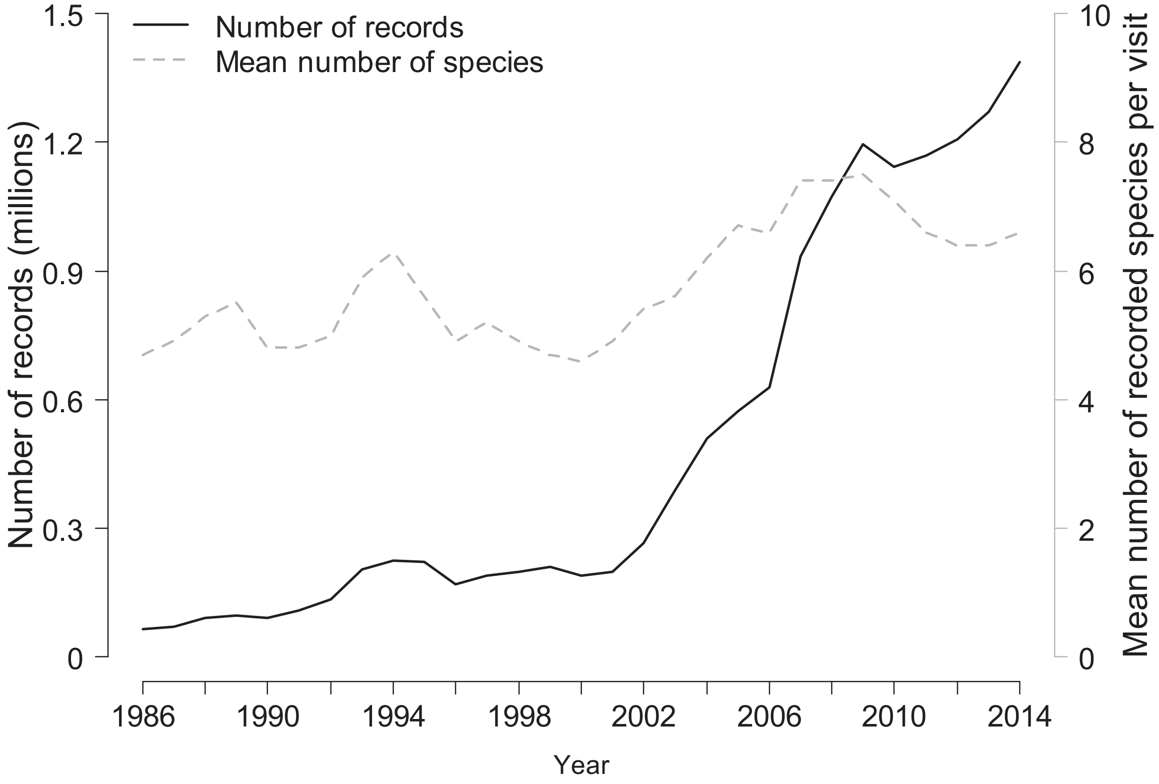

Figure S1: Number of records per year in DOFbasen and the mean number of recorded species per visit in 1986 – 2013.

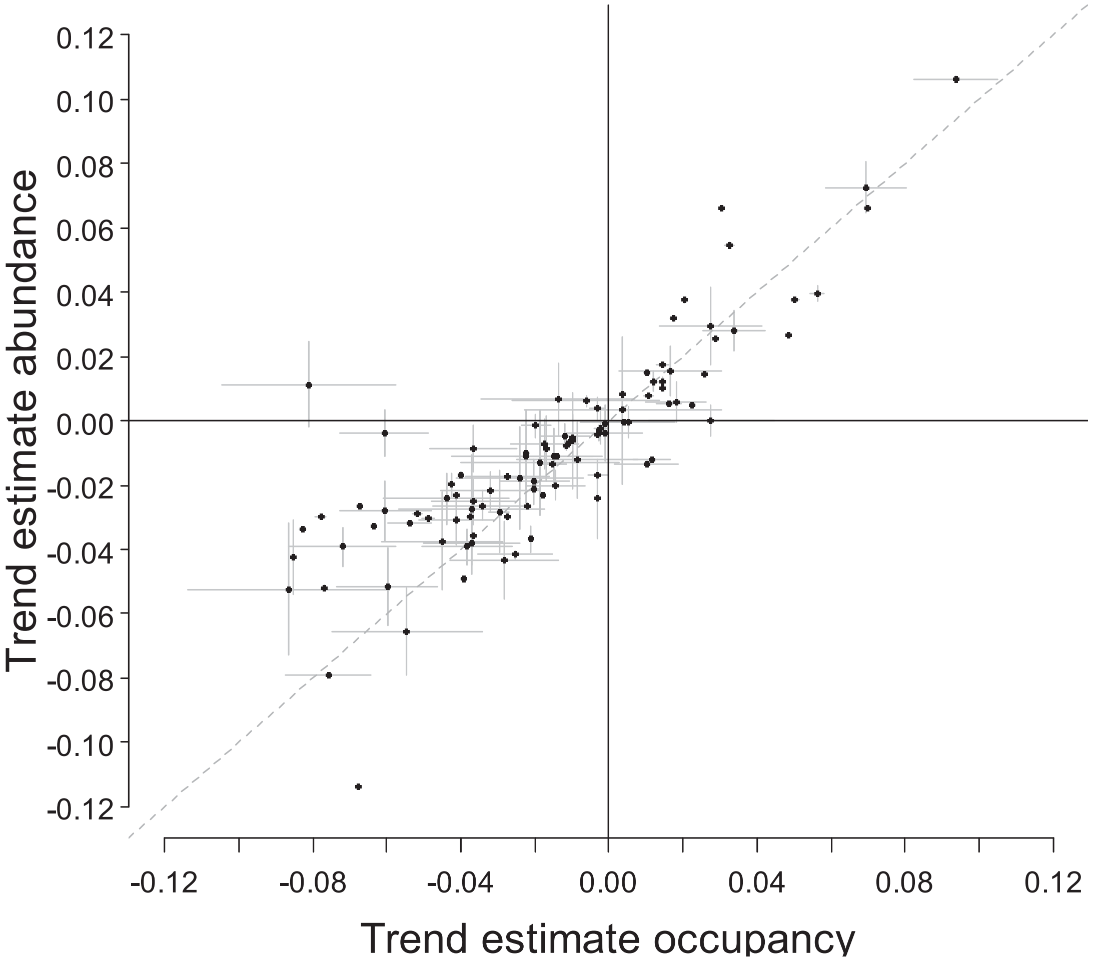

Fig. S2 Correlation between population trend estimates (± 95% confidence interval) derived from structured monitoring data (CBM) in their original form (abundance) and when the data were reduced to detection/non-detection data (occupancy) for 103 bird species in 1986–2013 in Denmark.

Table S1: List of species included in the analyses, and population trends in Denmark from 1986 – 2013 as estimated from unstructured public data (DOFbasen) and from structured monitoring data (Common Bird Monitoring). Note that due to analytical differences uncertainty is reported as 95% credible interval from a Bayesian occupancy model for the unstructured data, and as 95% confidence interval from a GLMM for the structured monitoring data.

Species	Scientific name	unstructured data				structured monitoring data			
		mean	lower 95% CrI	upper 95% CrI	trend	mean	lower 95% CI	upper 95% CI	trend
Barn Swallow	*Hirundo rustica*	0.0099	0.0078	0.0119	increase	0.0052	0.0045	0.0059	increase
Black Redstart	*Phoenicurus ochruros*	-0.0016	-0.0033	-0.0003	decline	-0.0130	-0.0295	0.0034	stable
Black Woodpecker	*Dryocopus martius*	-0.0001	-0.0009	0.0005	stable	-0.0178	-0.0336	-0.0021	decline
Blackbird	*Turdus merula*	0.0062	0.0045	0.0079	increase	-0.0004	-0.0004	-0.0003	decline
Blackcap	*Sylvia atricapilla*	0.0070	0.0054	0.0086	increase	0.0375	0.0370	0.0380	increase
Black-headed Gull	*Larus ridibundus*	0.0051	0.0033	0.0069	increase	-0.1140	-0.1145	-0.1136	decline
Blue Tit	*Parus caeruleus*	0.0035	0.0011	0.0060	increase	0.0151	0.0143	0.0159	increase
Bullfinch	*Pyrrhula pyrrhula*	0.0041	0.0026	0.0057	increase	-0.0052	-0.0123	0.0019	stable
Buzzard	*Buteo buteo*	0.0053	0.0034	0.0071	increase	0.0122	0.0090	0.0154	increase
Carrion Crow	*Corvus corone*	0.0155	0.0130	0.0178	increase	0.0103	0.0092	0.0114	increase
Chaffinch	*Fringilla coelebs*	0.0061	0.0047	0.0078	increase	-0.0067	-0.0076	-0.0058	decline
Chiffchaff	*Phylloscopus collybita*	0.0116	0.0099	0.0133	increase	0.0661	0.0659	0.0664	increase
Coal Tit	*Parus ater*	0.0000	-0.0022	0.0018	stable	-0.0267	-0.0275	-0.0259	decline
Collared Dove	*Streptopelia decaocto*	0.0016	-0.0015	0.0039	stable	-0.0046	-0.0085	-0.0007	decline
Coot	*Fulica atra*	-0.0013	-0.0026	-0.0001	decline	-0.0306	-0.0312	-0.0299	decline
Great Cormorant	*Phalacrocorax carbo*	0.0073	0.0058	0.0087	increase	0.0545	0.0535	0.0554	increase
Corn Bunting	*Miliaria calandra*	0.0004	-0.0016	0.0022	stable	0.0000	-0.0049	0.0050	stable
Crested Tit	*Parus cristatus*	-0.0041	-0.0069	-0.0020	decline	-0.0281	-0.0375	-0.0187	decline
Red Crossbill	*Loxia curvirostra*	-0.0004	-0.0023	0.0011	stable	-0.0392	-0.0449	-0.0335	decline
Cuckoo	*Cuculus canorus*	0.0063	0.0040	0.0084	increase	-0.0043	-0.0044	-0.0042	decline

Curlew	*Numenius arquata*	0.0003	-0.0013	0.0018	stable	0.0113	-0.0020	0.0245	stable
Dunnock	*Dryocopus martius*	0.0001	-0.0024	0.0024	stable	-0.0199	-0.0234	-0.0163	decline
Eider	*Somateria mollissima*	0.0004	-0.0007	0.0014	stable	0.0061	0.0042	0.0080	increase
Fieldfare	*Turdus pilaris*	-0.0060	-0.0084	-0.0039	decline	-0.0040	-0.0112	0.0033	stable
Garden Warbler	*Sylvia borin*	0.0052	0.0030	0.0073	increase	-0.0263	-0.0271	-0.0256	decline
Goldcrest	*Regulus regulus*	-0.0027	-0.0048	-0.0006	decline	-0.0298	-0.0300	-0.0296	decline
Goldfinch	*Carduelis carduelis*	0.0129	0.0102	0.0153	increase	0.0281	0.0219	0.0342	increase
Grasshopper Warbler	*Locustella naevia*	-0.0003	-0.0018	0.0010	stable	-0.0276	-0.0449	-0.0104	decline
Great Black-backed Gull	*Larus marinus*	0.0056	0.0019	0.0075	increase	0.0153	0.0077	0.0230	increase
Great Crested Grebe	*Podiceps cristatus*	0.0011	0.0003	0.0018	increase	-0.0263	-0.0308	-0.0218	decline
Great Spotted Woodpecker	*Dendrocopos major*	0.0053	0.0036	0.0068	increase	-0.0040	-0.0063	-0.0016	decline
Great Tit	*Parus major*	0.0068	0.0048	0.0085	increase	-0.0010	-0.0022	0.0003	stable
Green Woodpecker	*Picus viridis*	-0.0029	-0.0041	-0.0019	decline	-0.0374	-0.0528	-0.0220	decline
Greenfinch	*Carduelis chloris*	0.0081	0.0052	0.0108	increase	0.0049	0.0041	0.0057	increase
Grey Heron	*Ardea cinerea*	0.0046	0.0029	0.0064	increase	-0.0077	-0.0093	-0.0060	decline
Grey Partridge	*Perdix perdix*	-0.0059	-0.0086	-0.0036	decline	-0.0383	-0.0478	-0.0288	decline
Greylag Goose	*Anser anser*	0.0089	0.0074	0.0103	increase	0.1062	0.1051	0.1073	increase
Hawfinch	*Coccothraustes coccothraustes*	-0.0013	-0.0036	0.0004	stable	-0.0171	-0.0172	-0.0170	decline
Herring Gull	*Larus argentatus*	0.0128	0.0108	0.0147	increase	0.0661	0.0657	0.0666	increase
House Martin	*Delichon urbicum*	0.0050	0.0023	0.0075	increase	0.0175	0.0168	0.0181	increase
House Sparrow	*Passer domesticus*	0.0013	-0.0014	0.0035	stable	-0.0317	-0.0323	-0.0312	decline
Icterine Warbler	*Hippolais icterina*	0.0071	0.0048	0.0091	increase	-0.0214	-0.0224	-0.0205	decline
Jackdaw	*Corvus monedula*	0.0050	0.0016	0.0084	increase	0.0082	0.0077	0.0088	increase
Jay	*Garrulus glandarius*	0.0051	0.0029	0.0072	increase	-0.0016	-0.0053	0.0020	stable

Kestrel	*Falco tinnunculus*	0.0010	-0.0020	0.0035	stable	-0.0071	-0.0148	0.0007	stable
Northern Lapwing	*Vanellus vanellus*	-0.0035	-0.0049	-0.0021	decline	-0.0297	-0.0306	-0.0288	decline
Lesser Whitethroat	*Sylvia curruca*	0.0104	0.0081	0.0126	increase	0.0037	0.0003	0.0071	increase
Linnet	*Carduelis cannabina*	0.0009	-0.0012	0.0035	stable	-0.0358	-0.0359	-0.0356	decline
Little Grebe	*Tachybaptus ruficollis*	-0.0034	-0.0054	-0.0016	decline	-0.0110	-0.0253	0.0034	stable
Long-tailed Tit	*Aegithalos caudatus*	-0.0014	-0.0124	0.0095	stable	-0.0087	-0.0189	0.0015	stable
Magpie	*Pica pica*	0.0118	0.0089	0.0144	increase	-0.0029	-0.0033	-0.0024	decline
Mallard	*Anas platyrhynchos*	0.0003	-0.0011	0.0016	stable	0.0255	0.0248	0.0261	increase
Marsh Harrier	*Circus aeruginosus*	0.0053	0.0037	0.0067	increase	0.0295	0.0175	0.0414	increase
Marsh Tit	*Parus palustris*	0.0036	0.0014	0.0056	increase	-0.0086	-0.0158	-0.0014	decline
Marsh Warbler	*Acrocephalus palustris*	0.0042	0.0024	0.0059	increase	-0.0022	-0.0072	0.0028	stable
Meadow Pipit	*Anthus pratensis*	-0.0015	-0.0038	0.0006	stable	-0.0251	-0.0321	-0.0181	decline
Mew Gull	*Larus canus*	0.0074	0.0046	0.0098	increase	0.0317	0.0311	0.0322	increase
Mistle Thrush	*Turdus viscivorus*	-0.0019	-0.0039	-0.0002	decline	-0.0793	-0.0794	-0.0792	decline
Moorhen	*Gallinula chloropus*	-0.0017	-0.0039	0.0003	stable	-0.0308	-0.0383	-0.0233	decline
Mute Swan	*Cygnus olor*	0.0017	0.0004	0.0028	increase	-0.0133	-0.0142	-0.0124	decline
Thrush Nightingale	*Luscinia luscinia*	0.0006	-0.0008	0.0018	stable	-0.0493	-0.0500	-0.0487	decline
Nuthatch	*Sitta europaea*	0.0042	0.0029	0.0053	increase	0.0059	-0.0005	0.0123	stable
Oystercatcher	*Haematopus ostralegus*	0.0006	-0.0007	0.0017	stable	-0.0368	-0.0409	-0.0326	decline
Pheasant	*Phasianus colchicus*	0.0097	0.0073	0.0120	increase	-0.0110	-0.0110	-0.0109	decline
Pied Flycatcher	*Ficedula hypoleuca*	-0.0037	-0.0060	-0.0017	decline	-0.0515	-0.0635	-0.0396	decline
Pochard	*Aythya ferina*	-0.0021	-0.0032	-0.0012	decline	-0.0283	-0.0411	-0.0154	decline
Raven	*Corvus corax*	0.0104	0.0087	0.0120	increase	0.0726	0.0646	0.0806	increase
Red-backed Shrike	*Lanius collurio*	0.0002	-0.0014	0.0016	stable	-0.0433	-0.0552	-0.0313	decline
Red-breasted Merganser	*Mergus serrator*	-0.0009	-0.0023	0.0004	stable	-0.0243	-0.0323	-0.0162	decline

Red-necked Grebe	*Podiceps grisegena*	0.0002	-0.0006	0.0010	stable	0.0066	-0.0048	0.0180	stable
Redpoll	*Carduelis flammea*	-0.0082	-0.0228	0.0043	stable	-0.0189	-0.0259	-0.0120	decline
Redshank	*Tringa totanus*	-0.0023	-0.0033	-0.0014	decline	-0.0219	-0.0279	-0.0158	decline
Redstart	*Phoenicurus phoenicurus*	0.0073	0.0054	0.0091	increase	0.0396	0.0373	0.0418	increase
Reed Bunting	*Emberiza schoeniclus*	0.0011	-0.0007	0.0027	stable	-0.0229	-0.0230	-0.0228	decline
Reed Warbler	*Acrocephalus scirpacaeus*	0.0041	0.0027	0.0053	increase	-0.0201	-0.0246	-0.0156	decline
Robin	*Erithacus rubecula*	-0.0006	-0.0025	0.0012	stable	-0.0519	-0.0527	-0.0511	decline
Rook	*Corvus frugilegus*	-0.0025	-0.0078	0.0026	stable	-0.0122	-0.0127	-0.0117	decline
Sand Martin	*Riparia riparia*	-0.0020	-0.0055	0.0005	stable	-0.0417	-0.0427	-0.0407	decline
Sedge Warbler	*Acrocephalus schoenobaenus*	0.0000	-0.0012	0.0010	stable	-0.0121	-0.0239	-0.0003	decline
Shelduck	*Tadorna tadorna*	-0.0017	-0.0033	-0.0003	decline	-0.0288	-0.0289	-0.0287	decline
Siskin	*Carduelis spinus*	-0.0040	-0.0064	-0.0020	decline	-0.0243	-0.0365	-0.0120	decline
Skylark	*Alauda arvensis*	0.0037	0.0019	0.0056	increase	-0.0328	-0.0335	-0.0322	decline
Snipe	*Gallinago gallinago*	-0.0038	-0.0054	-0.0023	decline	-0.0422	-0.0538	-0.0306	decline
Song Thrush	*Turdus philomelos*	0.0003	-0.0016	0.0022	stable	-0.0167	-0.0169	-0.0164	decline
Sparrowhawk	*Accipiter nisus*	-0.0010	-0.0032	0.0011	stable	-0.0063	-0.0212	0.0086	stable
Spotted Flycatcher	*Muscicapa striata*	0.0020	-0.0006	0.0042	stable	-0.0112	-0.0200	-0.0025	decline
Starling	*Sturnus vulgaris*	0.0057	0.0033	0.0080	increase	-0.0230	-0.0234	-0.0226	decline
Stock Dove	*Columba oenas*	0.0008	-0.0031	0.0030	stable	0.0266	0.0266	0.0267	increase
Swift	*Apus apus*	0.0064	0.0041	0.0085	increase	-0.0102	-0.0123	-0.0080	decline
Tawny Owl	*Strix aluco*	-0.0023	-0.0048	-0.0001	decline	0.0034	-0.0196	0.0263	stable
Tree Pipit	*Anthus trivialis*	-0.0016	-0.0032	-0.0002	decline	-0.0166	-0.0174	-0.0158	decline
Tree Sparrow	*Passer montanus*	0.0033	-0.0008	0.0070	stable	0.0121	0.0106	0.0137	increase
Treecreeper	*Certhia familiaris*	0.0046	0.0032	0.0058	increase	-0.0038	-0.0125	0.0050	stable

Tufted Duck	*Aythya fuligula*	-0.0005	-0.0016	0.0006	stable	-0.0004	-0.0050	0.0043	stable
Northern Wheatear	*Oenanthe oenanthe*	0.0048	0.0026	0.0067	increase	-0.0525	-0.0730	-0.0319	decline
White Wagtail	*Motacilla alba*	0.0074	0.0046	0.0102	increase	0.0375	0.0367	0.0383	increase
Whitethroat	*Sylvia communis*	0.0092	0.0073	0.0111	increase	0.0079	0.0078	0.0079	increase
Willow Warbler	*Phylloscopus trochilus*	0.0047	0.0030	0.0064	increase	-0.0336	-0.0343	-0.0330	decline
Winter Wren	*Troglodytes troglodytes*	0.0037	0.0017	0.0056	increase	-0.0136	-0.0141	-0.0131	decline
Wood Pigeon	*Columba palumbus*	0.0054	0.0037	0.0071	increase	0.0147	0.0146	0.0147	increase
Wood Warbler	*Phylloscopus sibilatrix*	-0.0023	-0.0042	-0.0007	decline	-0.0390	-0.0451	-0.0330	decline
Yellow Wagtail	*Motacilla flava*	-0.0021	-0.0036	-0.0006	decline	-0.0657	-0.0793	-0.0521	decline
Yellowhammer	*Emberiza citrinella*	0.0064	0.0048	0.0081	increase	-0.0297	-0.0302	-0.0292	decline

Table S2: Number of species with matching and non-matching population trend directions for 103 bird species between 2002 and 2013 in Denmark derived from an unstructured observation database and a structured monitoring scheme using either original abundance data or when data were reduced to simple detection/non-detection (occupancy). Trends were considered increasing or decreasing if the 95% confidence interval of the population growth rate estimate was >0 or <0, respectively, and stable or inconclusive if the interval spanned 0.

			unstructured data		
			decreasing	stable / inconclusive	increasing
structured monitoring	abundance	decreasing	11	22	15
		stable / inconclusive	6	9	15
		increasing	2	5	18
	occupancy	decreasing	12	22	23
		stable / inconclusive	6	7	7
		increasing	1	6	18

Table S3: Number of species with matching and non-matching population trend directions for 103 bird species between 1986 and 2013, and between 2002 and 2013 in Denmark derived from a structured monitoring scheme using either original abundance data or when data were reduced to simple detection/non-detection (occupancy). Trends were considered increasing or decreasing if the 95% confidence interval of the population growth rate estimate was >0 or <0, respectively, and stable or inconclusive if the interval spanned 0.

			structured abundance data		
			decreasing	stable / inconclusive	increasing
structured data reduced to occupancy	1986 - 2013	decreasing	56	10	1
		stable / inconclusive	1	5	1
		increasing	3	2	24
	2002 - 2013	decreasing	43	10	4
		stable / inconclusive	3	13	4
		increasing	2	6	17

PAPER 9

INVASIVE ALIEN BIRDS IN DENMARK

Anthony D. Fox, Henning Heldbjerg and Timme Nyegaard

Dansk Orn. Foren. Tidsskr. 109 (2015): 193-205

Photo: Albert Steen-Hansen

Invasive alien birds in Denmark

ANTHONY D. FOX, HENNING HELDBJERG AND TIMME NYEGAARD

(Med et dansk resumé: Invasive fuglearter i Danmark)

Abstract Avian Introduced Alien Species (IAS) constitute a threat to the integrity of native biodiversity, the economy and human health, so here we briefly review some of the problems posed by such species around the world in relation to such bird species in Denmark. A new European Union Regulation on Invasive Alien Species implemented in January 2015 establishes a framework for actions to combat alien species, which requires Member States to prevent the spread of alien species, provide early warning and rapid responses to their presence and management of established alien species where they occur. We show the importance of mechanisms such as DOF's (Dansk Ornitologisk Forening, BirdLife Denmark) Atlas project, Common Bird Census (breeding and wintering species) and DOFbasen to contribute data on the current geographical and numerical distribution of the few serious alien avian species already present in Denmark. We review the status, abundance and distribution of seven critical IAS that do, or have, occurred in Denmark in the last 10 years and conclude that none of these pose a major threat as things stand at the present, although breeding Egyptian Geese *Alopochen aegyptiaca* and Canada Geese *Branta canadensis* potentially give cause for future concern. We underline the need for continued surveillance of all avian IAS through data collection via DOF's monitoring programmes and Aarhus University's mid-winter waterbird census, hunting bag and wing surveys. These programmes are essential if we are to continue to effectively monitor the extent and nature of the problems constituted by IAS in support of the Danish Nature Agency in their direct management of alien species problems in this country.

Introduction

Humans have been introducing plant and animal species to areas across the globe outside of their natural native ranges for thousands of years, some deliberately and others accidently. Many such modifications to distributional range have been to feed us, for instance, the Greylag Goose *Anser anser* was one of the first bird species known to be domesticated some 5000 years ago (Sossinka 1982), and the species has since been introduced around the world. In more recent times, human colonisers have taken examples of the European avifauna around the world to remind themselves of home (e.g. Thomson 1922, Lever 2010). In the case of a very wide range of wildfowl (members of the Anatidae; Fox 2009) and parrot species (from the order Psittaciformes; Cassey *et al.* 2004), substantial numbers have been introduced to Europe since the 1700s as a source of curiosity, entertainment and ornamental decoration. The introduction of such alien species outside their native range as a result of human action is usually benign, because the vast majority of such organisms fail to survive in often unsuitable environments (Blackburn *et al.* 2014). However, we see some alien species adapting to new conditions and establishing viable, self-sustaining populations in the wild where they can also cause significant ecological, economic and human health impacts, although these are not always easily foreseeable (Blackburn *et al.* 2014). These impacts can be many and varied (see for example some case studies provided in Tab. 1), but because these cannot easily be predicted in advance, it is far better to

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Tab. 1. Some example case studies of the effects of alien introduced species on native fauna.
Eksempler på effekter af invasive arters forekomst på den hjemmehørende natur.

Effect	**Description and examples of effects**	**Source references**
Predation	Introduced predators such as feral cats *Felis catus,* American mink *Mustela vison* and even house mice *Mus musculus* radically effect ground nesting seabirds never previously exposed to such threats.	Craik 1997, Holdaway 1999, Keitt *et al.* 2002, Croll *et al.* 2005, Wanless *et al.* 2007, Kurle *et al.* 2008
Hybridisation	Hybridisation of alien and native forms can lead to the dilution of the native genotype, e.g. North American Ruddy Duck *Oxyura jamaicensis* with White-headed Duck *Oxyura leucocephala* in Spain.	Kershaw & Hughes 2002, Hughes *et al.* 2006, Muñoz-Fuentes *et al.* 2007
Demographic ascendancy	Despite similar survival rate, the greater breeding success of the alien introduced Mallard *Anas platyrhynchos* compared to the native and closely related Grey Duck *Anas superciliosa* in New Zealand, makes it numerically abundant over the native species.	Williams & Basse 2006
Disruption to ecosystem function	Danish lakes stocked with reared Mallards had higher phosphorus level than those not stocked, with acidic, nutrient-poor waterbodies being more sensitive to change as a result of relatively modest elevations in phosphorus concentrations. Rearing of Common Pheasants *Phasianus colchicus* creates conflict with birds of prey such as Northern Goshawk *Accipiter gentilis* which are then persecuted.	Paludan 1967, Noer *et al.* 2008
Diseases and parasites	Some Hawaiian birds are now restricted to high altitudes to escape diseases and parasites brought by introduced avian species that thrive in the lowlands. Duck Viral Enteritis is almost confined to captive reared or non-migratory waterfowl in Europe, Asia and North America, and outbreaks in wild waterbirds often follow contact with captive or released individuals.	Burgess *et al.* 1979, Burgess & Yuill 1982, Gough 1984, Brand 1988, Brand & Docherty 1988, Gough & Alexander 1990, Bibby 2000, LaPointe *et al.* 2005
Damage to agriculture	Escaped free-flying Rose-ringed Parakeets *Psittacula krameri* have bred in SE England for 40 years, where they create damage to fruits, vineyards and market gardens.	Pithon & Dytham 1999, Butler 2003, FERA 2009
Urban conflicts	Alien avian species in urban environments may have fewer predators and (at least initially) a supportive human population. However, introduced Canada Geese *Branta canadensis* in Europe and North America have caused damage to crops, disruption to golf courses, problems with droppings, have attacked humans and collided with vehicles or aircraft and created many other problems.	Conover & Chasko 1985, Watola *et al.* 1996, Owen *et al.* 2006, Dolbeer 2009
Damage, degrade or modify habitats	Introduced Canada Geese have destroyed wild rice stands in eastern North America. Mute Swan *Cygnus olor* in Maryland remove submerged aquatic vegetation (e.g. widgeon grass *Ruppia maritima* and eelgrass *Zostera marina*) affecting sediment patterns, submerged plant, invertebrate and fish communities.	Perry *et al.* 2004, Allin & Husband 2004, Naylor 2004, Tatu *et al.* 2007, Nichols 2014
Health and safety	Waterfowl can be natural reservoirs for zoonotic pathogens, e.g. abundant introduced resident Canada Geese in urban and suburban North American can potentially transmit *Campylobacter* and Avian Influenza through human contact with faecal deposits and contaminated water.	Rutledge *et al.* 2013
Competition for nest sites	In Australia, the introduced Common Myna *Acridotheres tristis* and European Starling *Sturnus vulgaris* compete with native species for nest holes, potentially affecting the breeding success of the Red-rumped Parrot *Psephotus haematonotus*, Crimson *Platycercus elegans* and Eastern Rosella *Platycercus eximius*.	Pell & Tidemann 1997
Competition for food	Native garden birds showed reduced feeding rates and increased vigilance in response to Rose-ringed Parakeet compared to Great Spotted Woodpeckers *Dendrocopos major*.	Peck *et al.* 2014

attempt to stop the arrival and colonisation of all new invasive species rather than attempt to manage a major problem once such species have become established and creating challenges. Such species spread by human agency outside their natural range are known as Invasive Alien Species (IAS) and they increasingly pose problems to global biodiversity, where they are considered to be one of the greatest current threats to natural systems and species diversity (Sala *et al.* 2000). As a result of the threats such aggressive species pose to biodiversity, the economy and human health, it is estimated that IAS have cost the European Union (EU) €12 billion (89 billion Danish kroner) per year over the last 20 years and that figure is increasing annually (Sundseth 2014). For that reason, the EU has implemented a new Regulation on Invasive Alien Species that came into effect on 1 January 2015 (European Commission 2014). This was a major objective of the EUs Biodiversity Strategy Target 5 for 2020 to coordinate EU-wide actions to prevent, minimise and mitigate the adverse impacts of IAS on biodiversity and ecosystem services, the economy and public health. The Regulation seeks to establish three types of measures, namely (i) prevention, (ii) early warning and rapid response and (iii) management of already established IAS.

But how does this affect DOF and Danish birds? Denmark has been highlighted as supporting particularly high densities of IAS compared to countries like Spain and France, even if the number of IAS is not that different (Sundseth 2014), so we have good reasons to be vigilant. Furthermore, as we hope to establish here, DOF and the volunteers contributing to the various existing recording schemes have a major role to play now and increasingly in the future in monitoring the distribution and abundance of avian IAS throughout Denmark.

In this analysis, we first assess the status of avian IAS in Denmark (which constitute problems elsewhere in Europe) based on knowledge from existing monitoring schemes and present an overview of all IAS species so far recorded here (excluding the Common Pheasant *Phasianus colchicus*). Then we review why IAS constitute such a problem and consider briefly the mechanisms with which to deal with them. We will also briefly consider how the EUs framework for action under the new Regulation can be implemented in Denmark with regard to avian IAS. Finally, we assess the importance of mechanisms such as DOFs Atlas project, the point counts schemes and DOFbasen data to contribute knowledge and advice to the Danish Nature Agency for the effective management of IAS problems in this country.

Methods

Using existing avian monitoring programmes to track IAS distribution and abundance

DOF maintains a series of different ornithological monitoring projects, all of which provide some basis for monitoring IAS now and in the future. The data on IAS from the Common Bird Census (based on point counts) are often too sparse to provide a useful perspective on such species and the present atlas period (2014-2017) means that although data will be forthcoming in the future, it is too early to use this source in the present review. Despite the unsystematic nature of data reported to DOFbasen, the volume of records (c. 16 million) entered by a couple of thousand observers from many sites (c. 18 000) throughout Denmark provides an excellent basis for estimating the abundance and distribution of IAS. In our review, we included data from 2005-2014 to assess changes in the abundance and distribution for the selected species. One complication is that contributions to DOFbasen have increased considerably in this period. The number of annual records in DOFbasen have increased 2.4 times from c. 578 000 in 2005 to c. 1.4 million records in 2014, the number of visited sites have increased 1.9 times from c. 7200 in 2005 to 13 600 in 2014 and the number of observers have increased 2.2 times from c. 1000 observers in 2005 to c. 2200 observers in 2014. Hence, relative changes in abundance and distribution must take this increase in effort into account. However, because most IAS are relatively scarce anyway, rather than weight the observations in DOFbasen for overall annual increases in observers and observations, we here first imposed a 10 × 10 km grid layer across Denmark and generated annual maximum counts from all sites within each square. Whilst such an approach may generally underestimate the true numbers present, it is a very useful indicator of presence and relative change in abundance for such species. Sites were assigned to grid squares based on the central coordinate of each site. We used changes in the annual sum of all grid square maximum counts generated in this way per year as an annual index to evaluate abundance trends for each species. The present abundance status of each species was calculated as a mean from the years 2011-2014 to incorporate fluctuations from year to year. Linear regression models were fitted to trends in abundance (annual sums of grid square maximum counts) and distribution (number of occupied grid squares) for all species over the period 2005-2014. In order to normalise the residual variance, the regression models were performed on natural logarithm transformed annual indices (results are given for the most numerous IAS in Tab. 2).

Selecting species for particular attention

Under the European Commission's Sixth Framework Programme, the Delivering Alien Invasive Species In Europe project (DAISIE 2014) was established to (i) create an inventory of European invasive species, (ii) provide the basis for prevention and control of biological invasions, (iii) assess the risks and impacts of the most widespread and/or noxious invasive species, and (iv) provide distribution data and experiences from Member States as a framework for considering indicators for early warning and action against IAS. This process includes profiling of the "100 of the worst" a database of the most aggressive, noxious or problematic of IAS

Tab. 2. Fitted trends for the four most abundant invasive alien species using simple linear regression models based on records in DOFbasen from 2005 to 2014 inclusive. Information on abundance was based on the annual sum of maximum counts from sites amalgamated in 10 × 10 km grid squares distributed across Denmark and for distribution on the annual numbers of occupied grid squares (see text for details). Regression coefficient, r^2, F-value and P value are shown for all fitted models.
Tendenser for udviklingen for de fire mest almindelige invasive fuglearter i Danmark 2005-14 baseret på data fra DOFbasen. Både tendensen i antal og i udbredelse er vist. For Canadagås er kun rastende og ynglende fugle fra månederne maj-juli inkluderet. For de øvrige arter er alle fugle fra hele året inkluderet.

Species	**Included period**	**Trend abundance**				**Trend distribution**			
		Coefficient	r^2	*F*	*P*	*Coefficient*	r^2	*F*	*P*
Black Swan *Cygnus atratus*	All year	-0.248	0.760	25.3	0.001	-0.201	0.6976	18.4	0.003
Canada Goose *Branta canadensis*	May-July	0.209	0.828	38.5	<0.001	0.126	0.919	91.1	<0.001
Egyptian Goose *Alopochen aegyptiaca*	All year	0.053	0.610	12.5	0.008	0.026	0.384	5.0	0.06
Ruddy Shelduck *Tadorna ferruginea*	All year	0.051	0.204	2.0	0.190	0.063	0.400	5.3	0.05

(DAISIE 2014), which includes only four species of birds that are present in Denmark or have been reported here, the Canada Goose *Branta canadensis*, North American Ruddy Duck *Oxyura jamaicensis*, Sacred Ibis *Threskiornis aethiopicus* and Rose-ringed Parakeet *Psittacula krameri*.

DOFbasen data on these species have been analysed and presented in the annual reports *Fugleåret* (Lange 2014), but here we present a more detailed analysis. For most of the species, we base our analysis on numbers gathered throughout the entire year, but in the case of the Canada Goose we are interested in separating the modest but potentially problematic breeding population from the much larger numbers present during the migration and winter periods.

Results

Canada Goose

The Canada Goose is a regular winter visitor to Denmark but a scarce breeder. Although introduced to this country as an ornamental waterbird in the late 1930s (Løppenthin 1967), the breeding population has not increased dramatically over the last 40 years. This is something that needs maintained vigilance and monitoring, however, since we show that the number of birds in Denmark during summer is now increasing more rapidly (see below and Fig. 3). Large established breeding populations exist in Sweden, southern Norway and southern Finland, and it is thought that considerable numbers of mainly Swedish breeding Canada Geese are those that winter in Denmark (Bønløkke *et al.* 2006), especially in the south-eastern part of the country, but aggregations also occur in Thy and at Tøndermarsken. Usually the species occurs in small flocks of up to a few hundred, often with swans and other geese, but more than 1000 birds are regularly recorded, for example, on Basnæs Nor near Skælskør and Nyord near Møn. Management of the population occurs through hunting, as the species is legally huntable in Denmark and is a popular quarry species. Numbers killed are monitored via the Danish Hunting Bag and Wing Surveys, according to which less than 100 were shot per annum in the 1960s, this rose to 1000-1500 in the 1990s (Bregnballe *et al.* 2003) and to between 5100 (2009/10) and 10 000 (2013/14) per annum in the last six years (Asferg 2011, 2014). The recent levels of exploitation seem until now to have been compatible with holding the population at a similar level in mid-winter in recent years, as both the DOF winter point counts and the Aarhus University midwinter goose counts show that the population is relatively stable and slightly below the peak since 2000 (Fig. 1). This suggests for the avian IAS which is the most numerically threatening to Denmark, the situation is at least not currently getting any worse. This also seems to match with trends in the population breeding in Sweden (Ottvall *et al.* 2009) which also winter there, where mid-winter counts peaked at over 70 000 in January of 2009 and 2010, but since numbers have declined there as well (Nilsson 2014). Such a 'holding pattern' for this IAS is important, since although this species is considered the most damaging avian IAS in Europe (Kumschick & Nentwig 2010) it would be extremely complex and

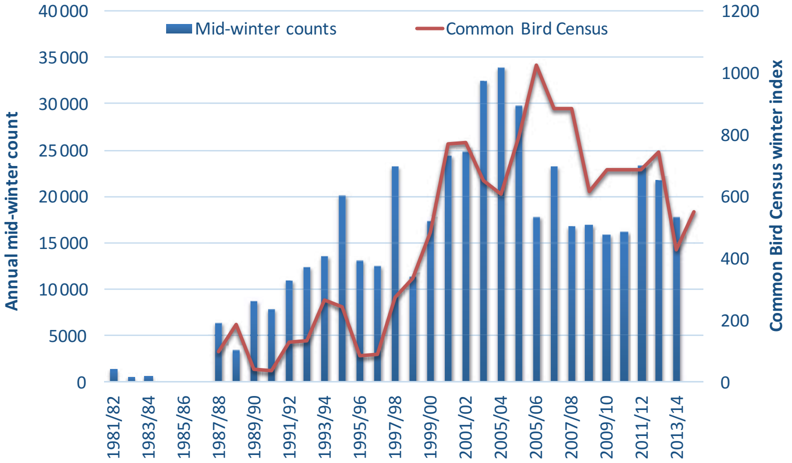

Fig. 1. Changes in the Danish winter population of Canada Goose based on changes in relative annual abundance, shown by annual winter point count indices for the Canada Goose in Denmark 1987/88-2014/15 (red line; Nyegaard *et al.* 2015, updated 2015) with 1987/88 set to a value of 100 and annual mid-winter counts of the Canada Goose in Denmark 1981-2013 (blue histograms, Danish Centre for Environment and Energy, Aarhus University).
Udviklingen i den danske vinterbestand af Canadagås baseret på henholdsvis punkttællingsdata i perioden 1987/88-2014/15 (kurve) og data fra midvintertællingerne fra januar i årene 1981-2013 (søjler).

costly to agree, coordinate and mount an international programme to eradicate the species from Europe at the present time. Thus, this is likely to be a species that is maintained at acceptable levels for the current time.

In contrast, we see a significant 21% increase in the number of birds reported and a 13% increase in the number of occupied 10 × 10 km grid squares in the breeding period during 2005-2014 (Tab. 2 and Fig. 2). In summer, the geese are spread over most of coastal Denmark (Fig. 3). The population was estimated at c. 20 breeding pairs in the first Atlas in 1971-1974 (Dybbro 1976) and at 25-50 breeding pairs during the second Atlas project in 1993-1996. The range, defined as breeding in 5 × 5 km squares, increased from the first to the second Atlas by more than 180% (Grell 1998). Also now there are several confirmed breeding pairs in the southern and eastern parts of the country, as well as signs of increase on Bornholm, albeit still in low numbers, suggesting the potential for further expansion of a breeding population in Denmark. The increase in range does not seem to have continued, but this and the current size of the breeding population will become clearer after the third Atlas period in 2014-2017. So far, all recoveries of juveniles ringed in Denmark are local which indicates that there is as yet no major migration by the Danish population (Bønløkke *et al.* 2006). It remains important that contributions to DOFbasen and the present Atlas track the changing status of this species as a breeding bird now and in the future.

North American Ruddy Duck

The North America Ruddy Duck escaped from captivity in England in the mid twentieth century, and established a feral breeding population of 6000 individuals by 2000 (Kershaw & Hughes 2002, Hughes *et al.* 2006). Although there were no apparent competitive or other adverse interactions with the native avifauna (Hughes 1992), increasing immigrants to Spain from the core concentration in Britain threatened the successful conservation efforts to restore the Spanish population of White-headed Duck *Oxyura leucocephala* from the brink of extinction. Hybrids between the two *Oxyura* species rapidly appeared, threatening to create a hybrid swarm of *Oxyura* ducks of mixed genotype with the eventual disappearance of the White-headed Duck as the genetic entity we recognise today (Muñoz-Fuentes *et al.* 2007). Conservation plans for the White-headed Duck highlighted the need for action to save the species (Anstey 1989, Green & Hughes 1996, Li & Mundkur 2002, Hughes *et al.* 2006). This led to the development of a strategy to eradicate the Ruddy Duck from throughout the Western Palearctic, because the species was increasingly dispersing from Britain and breeding elsewhere in Europe (see Henderson 2009). By the winter of 2014/15, this eradication strategy was close to success, largely due to the concentrated campaign in the United Kingdom (Robertson *et al.* 2015). Recent estimates of the cost of the Ruddy Duck eradication there have been in the order of £3.6 to £5.4 million (36-54 million DKK), a very substantial amount of money in relation to other conservation budgets. However, it is perhaps instructive to compare the relative costs of control of a species like the Ruddy Duck with those of nine invasive plant species that cause serious economic consequences, amounting to an expenditure of £300 million (3 billion DKK) per annum in the United Kingdom, and the adverse costs of native weed plant species which cost well over twice that amount without resolution (Williamson 2002).

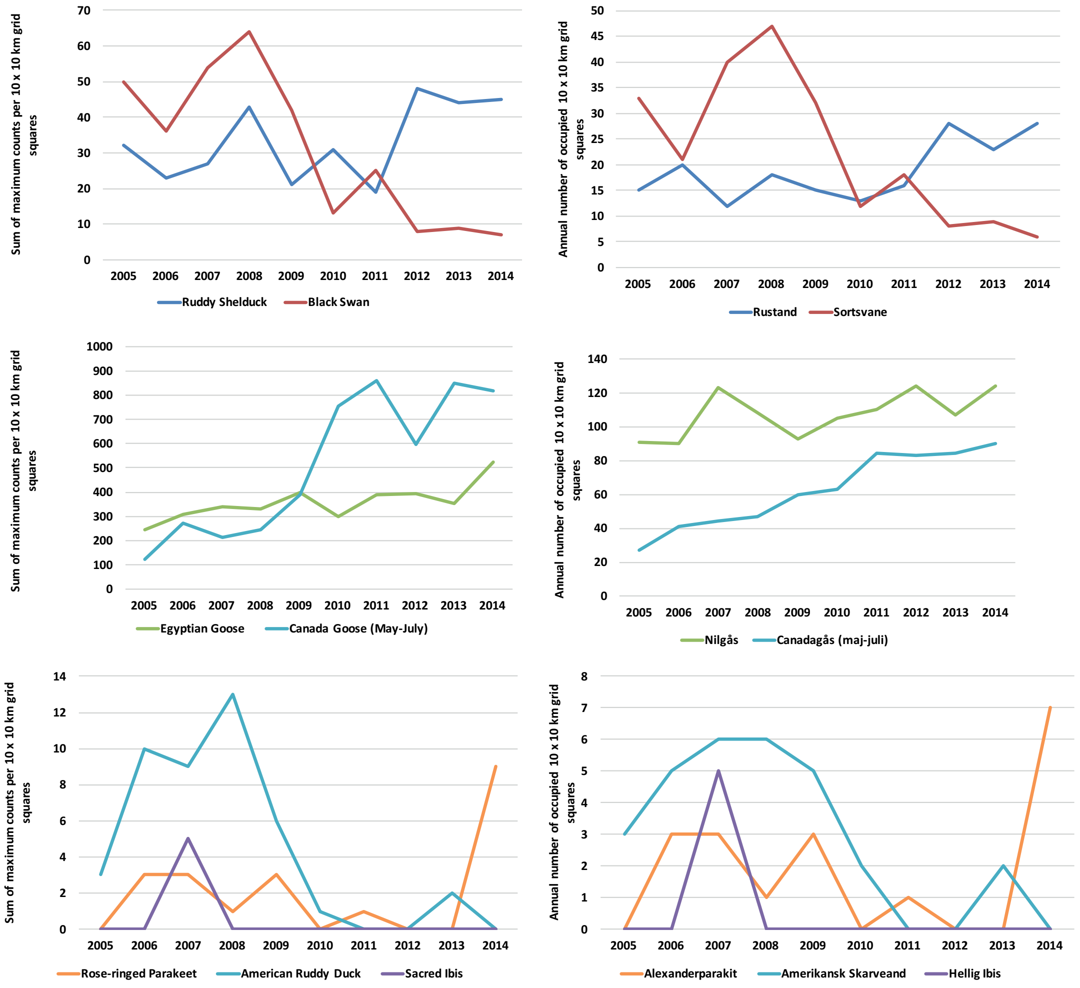

Fig. 2. The trends in abundance (left) and distribution (right) for seven invasive alien avian species in Denmark in 2005-2014 based on records in DOFbasen. See text for full explanation of the methods used and Tab. 2 for associated statistics and explanations.
Udviklingen i hyppighed (venstre) og udbredelse (højre) for syv invasive fuglearter i perioden 2005-14 baseret på data i DOFbasen.

The first North American Ruddy Duck in Denmark was seen in 1985 (Olsen 1988). Numbers peaked in 2007 (Fig. 2), culminating in the only confirmed breeding by the species in Denmark at Maribo Nørresø in 2006, 2007 and 2008 (DOFbasen). Luckily, the species did not consolidate as a breeding species, and numbers have since fallen, almost certainly as a result of the highly successful eradication programme in the United Kingdom, where it is thought the majority of Danish birds originated. As of early 2015, it is thought that the population in Britain is less than 15 females, down from a population there of over 6000 individuals at its peak in 2000. The abundance and the distribution of North American Ruddy Ducks reported in Denmark are both significantly declining during the last decade, confirming the trend from Britain (Figs 2 and 3). The species is listed as huntable in Denmark, and 20-30 birds are estimated to have been shot here over the last 30 years (T. Asferg pers. comm.). Clearly, Denmark needs to remain vigilant to this species given its capacity to breed here, but given the loss of the source population and the apparent lack of any observations in three out of the last four years, it would appear the species does not constitute the threat it once did in the mid-2000s.

Sacred Ibis

The African Sacred Ibis seems an unlikely threat to the European avifauna, but it has been introduced to

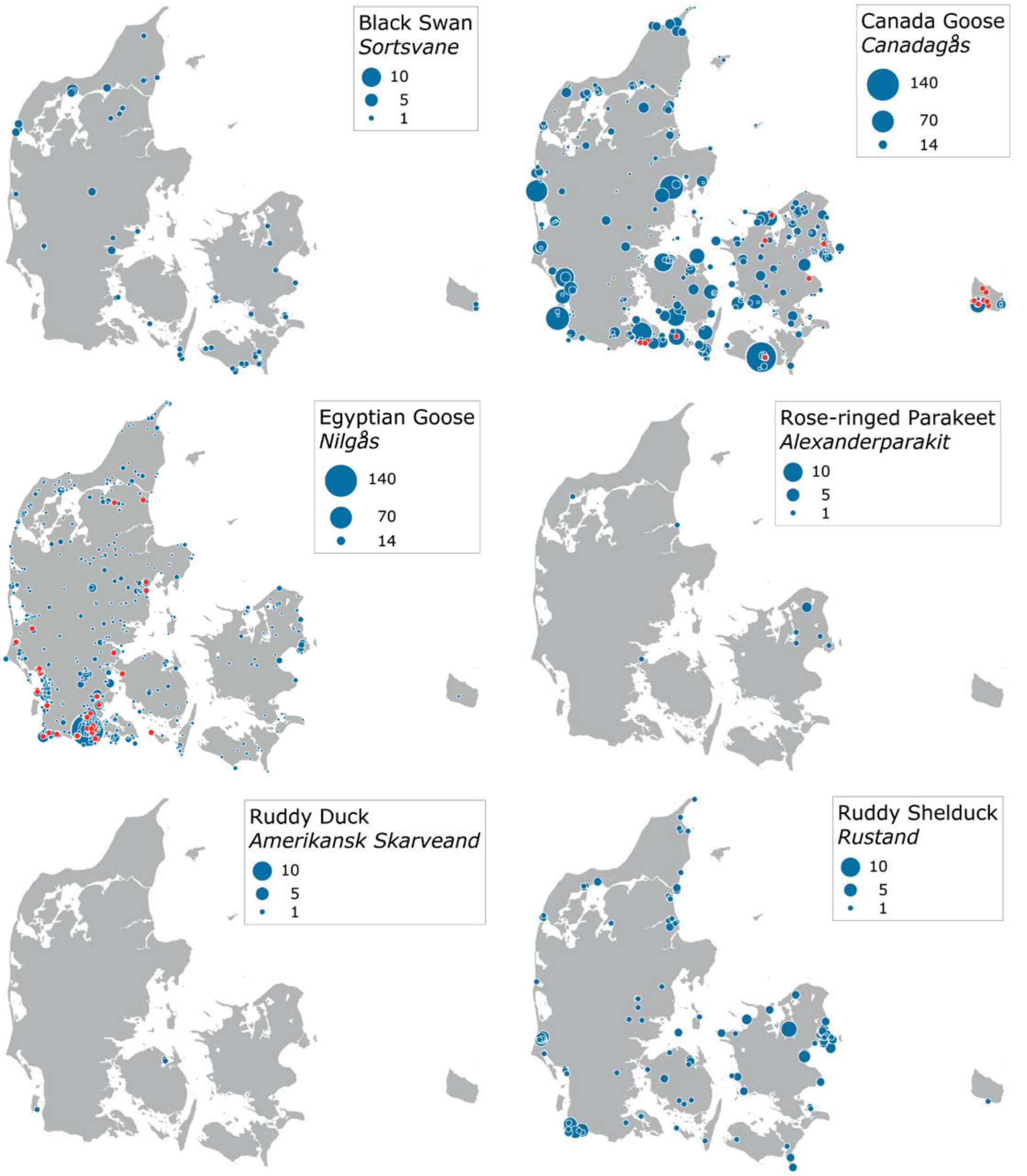

Fig. 3. Maximum counts (individuals) in DOFbasen of six invasive alien bird species in Denmark in 2011-2014. Red circles indicate breeding records. For Canada Goose, only staging birds during May-July and breeding birds are included. All other species maps include all records (regardless of season) in these years.
Maksimumantal i DOFbasen for seks invasive fuglearter i Danmark i årene 2011-14. Røde cirkler indikerer yngleforekomster. For Canadagås er kun rastende fugle fra månederne maj-juli og ynglefugle inkluderet. For de øvrige arter er alle fugle fra hele året inkluderet.

France, Italy and Spain where rapidly growing populations in southern Europe are seen as a major problem, because of their devastating effects on breeding colonies of species such as terns, as well as their successful competition with native Cattle *Bubulcus ibis* and Little Egrets *Egretta garzetta* for nest sites (Clergeau & Yésou 2006). Their adaptability to forage on rubbish tips has enabled them to survive harsh winters in temperate regions, so it is not beyond the bounds of possibility that the species could colonise Denmark. To date there have

Tab. 3. Status of seven invasive alien species based on records in DOFbasen. The status assessment is based on annual data from 2011-2014. Values indicate the mean number of records, the mean summed maximum number recorded per 10 × 10 km grid square per year (abundance) and the number of these squares occupied (distribution). [1]indicates a pair of Black Swans seen with cygnets in 2007 where it was not known for sure whether the breeding was in a park or on a natural breeding site.
Status for syv invasive fuglearter i Danmark baseret på forekomsten i 2011-14 og på data fra DOFbasen.

Species	Phenology	Confirmed breeding	Included period	Mean records per year	Mean sum of max per year	Mean 10 ×10 per year
Sacred Ibis *Threskiornis aethiopicus*	Occasional	No	All year	0	0	0
Black Swan *Cygnus atratus*	All year	Yes[1]	All year	33.0	12.3	10.3
Canada Goose *Branta canadensis*	All year Majority at winter	Yes	May-July	412	781	85.3
Egyptian Goose *Alopochen aegyptiaca*	All year	Yes	All year	882	416	116
Ruddy Shelduck *Tadorna ferruginea*	Occasional	No	All year	111	39.0	23.8
North American Ruddy Duck *Oxyura jamaicensis*	Occasional	No	All year	19.5	0.5	0.5
Rose-ringed Parakeet *Psittacula krameri*	Occasional	No	All year	2.5	2.5	2

been two observations of a single bird in 1994 and 36 observations of probably a single bird in 2007 in DOFbasen, although there have been other observations in previous years not formally recorded. However, there is no evidence at present for any long term colonisation of Denmark by this species, for which DOFbasen again should function as an effective early warning system.

Rose-ringed Parakeet

There have been 32 observations of the Rose-ringed Parakeet in nine different years since 1980 in DOFbasen, mostly from the Greater Copenhagen area, but also from Jutland (see Figs 2 and 3). It is thought that these individuals are escaped birds from captivity within Denmark, but they are strong fliers and it cannot be excluded that these are birds coming from areas further south where established breeding populations exist. So far, there are no signs of breeding here, but this remains a high possibility. In 2014, the species is more widespread and numerous than ever before in the last decade and we need continued vigilance via DOFbasen and the Atlas to be convinced as to whether this is part of a trend or is just a coincidence. There have also been three observations of the Monk Parakeet *Myiopsitta monachus* in DOFbasen from 2014, a species which is known to breed in the wild in small numbers for many years at Solrød Strand, Køge Bugt (K. Flensted pers. comm.). Elsewhere in Europe, both of these species are established, where they can be highly aggressive towards, and cause other problems for, native bird species (Strubbe & Matthysen 2009, Hernández-Brito *et al.* 2014), so these constitute species of concern which also require continued surveillance.

Other species of potential concern

All invasive species give cause for concern, but three waterbird species are, to some extent, already present in Denmark and are considered 'pest' species in neighbouring countries, namely the Egyptian Goose *Alopochen aegyptiaca*, Ruddy Shelduck *Tadorna ferruginea* and Black Swan *Cygnus atratus* (Tabs 2 and 3, Figs 2 and 3).

The first observation of Egyptian Goose in Denmark was in 1983 (Netfugl), but the first confirmed breeding record is from 2000 (DOFbasen). The Egyptian Goose is largely confined to the southern and western parts of Denmark (Fig. 3) where it now breeds in small but increasing numbers that give some cause for future concern if these trends continue. The species seems to have originated from the Dutch population, part of an IAS population estimated at over 26000 breeding pairs in 2010 (Gyimesi & Lensink 2012). Numbers in Denmark do seem to be increasing (Tab. 2), with flocks of up to 136 birds reported from Uge, close to the German border in southern Jutland. It is a legal quarry species in Denmark, shot in relatively small numbers (155 in season 2012/13, 128 in 2013/14; Asferg 2014), but should the population show signs of major increase, this offers a potential form of control.

The Ruddy Shelduck is less numerous and usually encountered singly or in very small groups in Denmark (Tab. 3, Fig. 3). The last survey suggested 105-425 breeding pairs in Western Europe, where it is not considered native, mostly in Germany and Switzerland (Banks *et al.* 2008). However this species has been documented to occur in western Europe since the 1800s and in the past has been notable for 'eruption years' when substantial numbers of apparently wild origin birds (probably from further east in Eurasia) occur simultaneously, even reaching Iceland and Greenland, so some birds may still be of truly wild origin. In 1994, as many as 100 birds were reported in Denmark, although a breeding pair reported from Himmerland that year (the only confirmed recent breeding record) is likely to have been the result of escaped individuals. There is a tendency (which closely approximates to statistical significance at $P = 0.0502$) for an increase in the population in Denmark in 2005-2014, with a marked increase since 2011, which may be partially the result of the free-flying young dispersing throughout the Copenhagen area from a pair of wing-clipped Ruddy Shelduck in Tivoli Gardens (Tab. 2).

Black Swans have been introduced from Australia and are thought to number 155-225 breeding pairs in Europe in 2004-2007, mostly in Netherlands, Belgium and the UK (Banks *et al.* 2008). Numbers reported to DOFbasen seem to show relative low levels since 2010 compared to previous years (Fig. 2), and the species has declined significantly in abundance and distribution during 2005-2014 (Tab. 2). There is one observation of a breeding pair with cygnets near Rågø in 2007 in DOFbasen, but there is doubt whether this confirmed breeding stems from local captive birds within a park there or from a natural site. There have also been other accounts of this species breeding in the past (e.g. on Lolland and Fyn; K. Flensted pers. comm.). Black Swan is also listed as huntable during the open season, but has not been reported shot in very recent years. Since Black Swan does not yet seem to have established itself as a breeding bird, this remains another species for which active management does not seem urgent, but monitoring vigilance is required to ensure no sudden expansion in numbers and range.

Discussion

Does Denmark currently have a serious problem with introduced alien species?

The simple answer appears to be "no, not yet". Of Europe's 100 worst avian IAS, only the Canada Goose is numerous enough as a winter visitor to cause concern, but all the monitoring indications are that after a period of increase, the Nordic population of this species is a legal popular quarry species showing relative stable trends and indeed has shown slight declines in recent years. Worryingly, we see an increase in the numbers of Canada Geese in Denmark during the breeding period. This could potentially be the first sign of an establishing Danish population, which is also confirmed by reports of number of breeding pairs in the last few years. The increasing German population was estimated at 3600-5400 breeding pairs in 2005-2009 (Gedeon *et al.* 2014). Of these, the population in Schleswig-Holstein was estimated to have increased from 180 pairs in 1999 (Berndt *et al.* 2002) to 700 pairs in 2005-2009 with the majority near Kieler Fjord c. 50 km away from Denmark across the Baltic Sea (Koop & Bernt 2014). It remains unknown whether the increasing number of summer visitors is the result of the increasing breeding population south of Denmark (as seems likely) rather than being related to the many geese of Swedish origin that winter in Denmark.

Of the species of known concern in neighbouring European countries, the Egyptian Goose is clearly increasing in Denmark and is a species to watch. The Egyptian Goose has arrived in Denmark recently and was not even mentioned in the second Danish Atlas project in 1993-1996 (Grell 1998), which indicates how fast the species has colonised Denmark. The species is also increasing in Germany with an estimated population at 5000-7500 pairs in 2005-2009 (Gedeon *et al.* 2014) of which more than c. 250 pairs are found in Schleswig-Holstein (Koop & Bernt 2014). We recommend that both of these species be made the subject of future and more detailed analysis of changes in their behaviour, distribution and abundance which should consider their effect on other wildlife and potential management options. Other species do not currently appear to constitute a problem at the present time.

How do we best maintain vigilance with regard to introduced alien species?

The short answer is to continue to improve what we are currently doing. Denmark has a system of avian monitoring in place through DOFbasen that provides data on exotic species, including IAS, as these occur. We therefore urge all contributors to the system to continue to enter records of non-native invasive species as well as native species, so that the programme can contribute to our knowledge of the distribution and abundance of such species. Although DOFbasen data requires correction for spatio-temporal variation in observer effort, it provides an early warning system and the basis for developing more sophisticated systematic monitoring of IAS populations, should the need arise. The same is true for the Common Bird Census systems for breeding and wintering birds and Atlas fieldwork, as these are further means of collecting and collating data on the more numerous species that are already present in Denmark but also as a means of tracking new IAS as they occur.

As huntable species, annual reporting of Black Swan, Ruddy Duck and Egyptian Goose by hunters continues to be important in contributing data on the numbers of birds shot. All of these sources of data are essential to supporting the work of DOF to supply the Nature Agency with information on these species, in concert with the mid-winter counts, hunting bag statistics and wing surveys carried out by Aarhus University.

As we have seen earlier, contributing regular monitoring of these species, even at very low levels of abundance, is essential in supporting all the stages of the EU Regulation on IAS. In particular, monitoring provides vital data to the Nature Agency to support (i) prevention of spread of IAS, (ii) early warning and rapid response to IAS where and when they occur and (iii) management of already established IAS. The famous British ornithologist Colin Bibby (2000) once remarked that IAS were 'the only form of pollution which spontaneously self-replicates'! Many birdwatchers consider IAS as a form of pollution, but that does not mean we should not be recording their presence and numbers, given the threats that these species constitute to our own biodiversity, avifauna and economy! The new EU Regulation gives us ample reason to continue this monitoring in the future, and we thank all those that have been diligent in reporting IAS to the present.

How do we deal with the problem once introduced alien species have arrived?

The new EU Regulation on Invasive Alien Species Regulation proposes three distinct types of measures, which follow an internationally agreed hierarchical approach to combatting IAS. Firstly through prevention, by being aware of the IAS that threaten our avifauna and biodiversity and implementing robust measures to prevent new IAS from entering the EU in the first place, either intentionally or unintentionally. Secondly, by having early warning systems in place to enable rapid responses where these are necessary. The Regulation requires that Member States must put in place an early warning system to detect the presence of IAS as early as possible and as we have shown above, DOFbasen makes a very significant contribution to this mechanism, in concert with breeding bird and winter point counts and through coverage of the present and previous breeding Atlas projects. The existence of such vital monitoring mechanisms provide Denmark with an assessment of the numbers and distribution of IAS as they occur and provide the Nature Agency with the spatial and, to some extent, numerical information required to implement rapid response measures when these are required to prevent such species becoming established. Finally, the Regulation requires management of previously established IAS to minimise their spread, abundance and impact, again a task that falls to the Nature Agency to fulfil. Clearly to judge the effectiveness of such measures requires regular monitoring of the status and distribution of IAS whilst subject to such management, so again the Atlas projects but especially DOFbasen and the point count networks can make direct and essential contributions to this process.

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Resumé

Invasive fuglearter i Danmark

Introducerede arter fra andre geografiske områder udgør en potentiel risiko for den hjemmehørende natur. Dette gælder også for fugle. I denne artikel præsenteres status for og udvikling i bestandsstørrelse og udbredelse for syv af disse invasive fuglearter, der har vist sig at udgøre et problem i andre lande. Status er beregnet som et gennemsnit af forekomsten i perioden 2011-14, og bestandsudviklingen dækker perioden 2005-14 med bemærkninger om forekomsten før denne periode.

I starten af januar 2015 implementeredes et nyt EU-regulativ, der har til formål at skabe en platform for, hvordan EU-medlemslandene skal forvalte de forskellige invasive arter og sikre, at de ikke spreder sig. Målet er at sikre et godt kendskab til arternes udbredelse i de enkelte lande, sikre en tidlig varsling og en hurtig respons på deres forekomst og at forvalte bestandene, hvor de allerede har etableret sig.

I denne forbindelse er der udarbejdet en liste over 'de 100 værste arter' (se DAISIE 2014), hvoraf fire af de her inkluderede arter er med: Canadagås *Branta canadensis*, Amerikansk Skarveand *Oxyura jamaicensis*, Hellig Ibis *Threskiornis aethiopicus* og Alexanderparakit *Psittacula krameri*. Da alle invasive arter potentielt udgør et problem, har vi yderligere inkluderet tre arter vandfugle, der i varierende grad har etableret sig i Danmark: Nilgås *Alopochen aegyptiaca*, Rustand *Tadorna ferruginea* og Sortsvane *Cygnus atratus*.

Der er talrige eksempler på, at invasive arter skaber problemer, når de introduceres til områder uden for deres naturlige udbredelse. Der er eksempler på, at de invasive arter påvirker

Ornamental birds have developed into invasive alien species in many parts of the world. Photo: Steen E. Jensen, Black Swans.
Prydfugle har udviklet sig til invasive arter mange steder I verden. Sortsvaner.

andre arter ved fx prædation, hybridisering og konkurrence. De kan også påvirke levesteder ved fx eutroficering og overgræsning af vandplanter. Endelig kan de skabe konflikter med mennesker som følge af spredning af sygdomme og afgrødeskader (se Tab. 1 for eksempler). Da det er svært at forudsige konsekvenserne ved etablering af en invasiv art i et nyt område, er det bedre at forsøge at stoppe og begrænse arten før indvandring og etablering. Omkostningerne ved at bekæmpe invasive arter vurderes at være stigende, og skønnes at have kostet EU 89 milliarder kroner pr. år i de sidste 20 år, dog primært til kontrol af ukrudt. Dette er baggrunden for, at det nye regulativ er trådt i kraft i 2015. Regulativet er en følge af mål 5 i EU's Biodiversitetsstrategi for 2020 om at lave en koordineret indsats på EU-plan for at undgå, minimere og imødegå påvirkningerne af invasive arter.

De forskellige danske fugleovervågningssystemer er gennemgået for at undersøge deres anvendelighed for denne analyse, og DOFbasen viste sig at udgøre den bedste database for en vurdering af de syv arters forekomst i Danmark. Da anvendelsen af DOFbasen er steget markant i den valgte periode (antal observationer med en faktor 2,4; lokaliteter med 1,9; observatører med 2,2) er det nødvendigt at forholde sig til denne ændring. DOFbasens lokaliteter er derfor grupperet inden for et 10 × 10 km netværk, hvortil DOFbasens lokaliteter er grupperet baseret på deres centerkoordinat. For hver art er herefter anvendt det maksimale antal fugle pr. kvadrat pr. år. På baggrund af summen af disse maksima beregnes en tendens for artens bestandsudvikling. Antallet af kvadrater pr. år anvendes tilsvarende til at vurdere, om der er sket en ændring i artens udbredelse. For Canadagås fokuseres på dens forekomst i yngletiden, hvorfor kun rastende fugle fra månederne maj-juli samt ynglende fugle er inkluderet.

Af de nævnte arter vurderes fem at være uproblematiske i øjeblikket, mens bestandsudviklingen for to bør følges nøje. De enkelte arters tendens er vist i Fig. 2 og deres udbredelse i Fig. 3. Et overblik over arternes tendens og status er vist i henholdsvis Tab. 2 og Tab. 3. De to opmærksomhedskrævende arter er Canadagås og Nilgås. Canadagås har sin primære forekomst her i landet i vinterhalvåret, hvor et stort antal svenske ynglefugle (introducerede) kommer hertil for at overvintre. Både midvintertællingerne af vandfugle og vinterpunkttællingerne viser, at denne bestand var i fremgang i 1980erne og 1990erne, toppede omkring årtusindeskiftet og nu er for nedadgående. Det seneste årti ses dog en fremgang i antallet af fugle i yngletiden, hvilket kan være et tegn på, at arten er ved at etablere sig som fast ynglefugl i Danmark. I Tyskland, nær Østersøkysten spreder Canadagåsen sig og har gjort det i de seneste årtier, og spørgsmålet er, om ikke den danske bestand udvikler sig fra denne og er uafhængig af den svenske?

Nilgås er den anden art, som bør følges nøje. Siden første ynglefund i 2000 er der nu kendskab til talrige ynglepar i Jylland med størst koncentration i Sønderjylland, og bestanden er i signifikant fremgang med meget høje antal registreret på lokaliteter nær den dansk-tyske grænse. Spredningen til Danmark kommer givetvis sydfra, idet der er meget store bestande af Nilgås i både Holland og Tyskland.

De øvrige arter vurderes ikke at ville udgøre et problem i den nærmeste fremtid. Sortsvane har været signifikant nedadgående i de seneste 10 år, og Amerikansk Skarveand er næsten helt forsvundet fra den danske natur, ganske givet som følge af en systematisk forfølgelse af arten i Storbritannien, hvor bestanden er bragt ned fra cirka 13 000 i 2000 til blot 15 hunner i 2015.

Rustand har haft en spredt og nogenlunde stabil forekomst i Danmark i perioden. Det er dog værd at bemærke, at der ses en stigning i udbredelse med et højere antal siden 2012, der dog måske kan forklares af, at der netop i 2012 kom unger af et stækket ynglepar fra Tivoli i København, der opholdt sig på mange lokaliteter i hele Storkøbenhavn.

For Alexanderparakit er der kun ganske få observationer om året, og da det er en almindelig burfugl, er det ikke utænkeligt, at det kan skyldes undslupne fugle. Hellig Ibis er registreret med mindst to fugle her i landet, senest i 2007.

DOFbasen har vist sig at være et glimrende værktøj til at følge udviklingen for de invasive arter i Danmark, og det er vigtigt, at der opretholdes et stort netværk af ornitologer til at bidrage til såvel den systematiske overvågning (fx Atlas, punkttællinger og midvintertællinger) som den mindre systematiske overvågning via DOFbasen.

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