

## Master's thesis

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# Fluctuations in populations of common Danish breeding birds - Using ringing data from the Danish Constant Effort Sites.



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Front cover photo: Reed Warbler (*Acrocephalus scirpaceus*), Christiansø, May 2014. The  
most abundant species in Danish CE-sites from 2006-2012.  
Photo: Vicky Knudsen

H. CHR. C. MORTENSEN  
1856 ORNITHOLOGEN 1921

HANS VID OG SINDRIGHED BAR FRUGT,  
HVAROM DER GAAR I VERDEN RY.  
HAN FULGTE FUGLEN PAA DENNS FLUGT;  
SELV BLEV HAN I DEN STILLE BY

In English: "H. Chr. C. Mortensen, 1856 The Ornithologist 1921, The fruit of his ingenuity and knowledge made him reputed in the world. The birds he followed on their journey; but in the quiet town he stayed himself".

*Cited from Preuss 2001*



# Preface

Throughout the past year, this Master's thesis was conducted at the Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark at the University of Copenhagen, where I spent my internship at the Bird Section of the Zoological Museum. Associate Professor Anders P. Tøttrup and associate Professor Kasper Thorup, from the above-mentioned center, have supervised the project.

Half of this year I spent preparing and sorting out data collected at Constant Effort Sites in Denmark during the period of 2004-2012, since this is the first adaption of the complete data set. For just over a week in May, I was lucky to get some insight in ringing birds, when I volunteered as a field assistant on Christiansø, helping with the collection of blood samples from over 100 passerine birds for the West Nile Virus project run by The Danish Veterinary Institute. Throughout the 18 years that I have been watching birds, this was my first experience with aging birds in hand by physical characteristics; furthermore, it was a good way to acquire knowledge about how ringers are working in the field, collecting data on Constant Effort Sites.

This thesis consists of two parts. The first part is a synopsis highlighting the background and importance of ringing and a detailed description of Constant Effort Sites monitoring including an introduction to the Danish sites. Furthermore, is a short introduction to the data set and the species used for analyses. The second part consists of a paper with the most important results gained during this thesis and some future perspectives.

Vicky Knudsen,  
5<sup>th</sup> of January 2015

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Thanks to Dr. Robert A. Robinson from the British Trust for Ornithology and Dr. Christian Kampichler from Sovon Dutch Centre of Field Ornithology for providing me with their special designed scripts to analyze CES data in the program R. I ended up using only one of the scripts, but you have both been so patient and kind, helping a new beginner in statistical analyzing through statistical programming in the best way. If it was not for you, I would never have been able to analyze the data so thoroughly performing demographic indices and estimates.

Thanks to the whole Bird Section at the Zoological Museum for letting me be a part of the joyful environment throughout a year, I could not imagine a better place to write my thesis. Thanks to Jesper J. Madsen and Kjeld T. Pedersen for helping me with extracting and sorting out CES data. I would never have find the end and the beginning of the data set without your support.

Thanks to my officemates Marta Lomas Vega, Mathilde Lerche Jørgensen and Mikkel Willemoes Kristensen for always being supportive and helpful. Especially thanks to Mikkel for the many questions, I have thrown at you. You have really helped me with understanding many issues within my project. Thanks to Jens Mikkel Lausten for letting me assist with ringing at Christiansø in May and Peter Lyngs for being a fantastic host at the ringing station. It was amazing for a bird geek like me to get this experience and insight in capturing and ringing birds. Also thanks to the rest of the people on the section: Andrew, Monika, Jan, Jens and Jon for loads of good times especially in coffee and lunch breaks with interesting stories and good humor.

Thanks to the best family, friends and colleagues at Birdlife Denmark one could imagine. You have been my solid rock and support throughout a year where I often needed some cheerful words. Especially thanks to Heather Williams and Chantal Werleman for proofreading.

At last, I want to send a huge thanks to all the volunteer ringers at Danish CE-sites. If it were not for you and your many hours of collecting data year after year, this project would never have been realistic. Furthermore thanks to Morten Jenrich-Hansen, Henning Ettrup, Hans Rytter, Henning Heldbjerg, Tage Leegard, Jan Drachmann, Søren Hjort Andersen, Henrik Vang Christensen and Michael Anker for answering numerous e-mails with questions to their CE-sites. I also want to thank Henning Heldbjerg for help to extract data on Common Bird Census and answering questions whenever I asked and Lennart Karlsson from Falsterbo Ringing Station for quick and kind help providing me data on catches from Falsterbo.

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# Summary

Biodiversity has globally suffered a rampant loss due to anthropogenic factors, causing declines and extinctions of species. In Europe, populations of common breeding birds have been declining drastically throughout the last decades with trans-Saharan migratory birds declining most. Obligations to reverse these tendencies with conservation and management plans are most appropriate, if we can find the underlying mechanism causing declines. This is seldom straightforward. Environmental changes and poor condition areas can affect populations negatively both at breeding and non-breeding grounds. Furthermore, these negative impacts are often linked, increasing the risk of declines.

Constant Effort Sites (CES) ringing of breeding birds provide invaluable data on demography in form of abundance, productivity and survival. Data, which is hard to obtain from other monitoring methods and which has the prerequisite to determine causes of fluctuations on breeding grounds can give us links to the causes of declines at non-breeding grounds.

This thesis is the first analysis of Danish CES data. I test demographic data of 14 abundant species divided into three groups, depending on their migratory strategy; short-, medium- and long-distance migrants. The groups are tested with linear regressions to see if demographic data follows other national and Scandinavian monitoring tendencies. Furthermore, I perform linear regressions to look at population trends for the seven-year period, key factors determining population size and how precipitation affects productivity.

The main findings of this thesis are that the demographic data show overall expected results of correlations. Interesting, long-distance migratory birds seem to be increasing on CE-Sites compared to the national trend, which might be due to habitat-specific species being better monitored on CE-Sites or simply because some species are doing better locally than nationally due to habitat-preferences.

The results of this thesis establish a foundation for further analyses, with importance for conservation matters both on a national and European plan. Links between breeding and non-breeding grounds, habitat analyses and focus on individual species and their biometric measures are some of the most important objects for further research. When the data set from Denmark increases in form of more sites and years, future studies will be stronger and more reliable. This will also make analyses of more species possible, which is not achievable yet due to lack of data, here among species with high conservation concern due to the European Birds Directive.

# Resumé

Biodiversitet har globalt lidt et voldsomt tab på grund af menneskeskabte faktorer der medfører tilbagegang og uddøen af arter. I Europe er antallet af almindelige ynglefugle faldet drastisk igennem de seneste årtier, med trækfugle der krydser Sahara i størst tilbagegang. Forpligtelser til at vende denne tendens med bevarings- og forvaltningsstrategier, er mest hensigtsmæssige, hvis vi finder de underliggende årsager til tilbagegangen. Dette er sjældent lige til. Miljømæssige forandringer kan påvirke populationer negativt både på og uden for ynglepladserne. Tilmed, er disse negative påvirkninger ofte koblet og forøger risikoen for tilbagegang.

Constant Effort Sites (CES) ringmærkning af ynglefugle skaffer os uvurderlig data vedrørende demografi i form af forekomst, produktivitet og overlevelse. Data, som er svært at opnå med andre moniteringsmetoder, og som har forudsætninger for at bestemme årsagerne til fluktuationer på ynglepladser og koble dem til årsagerne uden for ynglepladserne.

Denne afhandling er den første analyse af det danske CES data. Jeg tester demografisk data for 14 almindelige arter delt op i tre grupper afhængigt af deres trækstrategi; kort-, mellem- og langdistance trækfugle. Grupperne testes med lineære regressioner for at se om CES data følger andre nationale og Skandinaviske moniteringstendenser. Derudover, udfører jeg lineære regressioner for at se på trends for den syvårige periode, hvilke nøglefaktorer der bestemmer bestandsstørrelse og nedbørs effekt på produktivitet.

De vigtigste resultater for denne afhandling er, at det demografiske data overordnet viser forventede resultater. Interessant nok, virker langdistance trækfugle til at forøges på CE-Sites i forhold til den nationale tendens, hvilket kan skyldes habitat-specialiserede arter som er bedre moniteret på CE-sites eller måske fordi at nogle arter klarer sig bedre lokalt i forhold til nationalt på grund af habitat præferencer.

Resultaterne i denne afhandling etablerer et fundament for flere analyser med stor betydning for bevaring både nationalt og på Europæisk plan. Sammenhænge mellem yngle- og ikke yngleområder, habitats analyser og fokus på individuelle arters fysiske mål er nogle af de vigtigste objekter i kommende analyser. Når datasættet forøges i form af flere sites og år med CE-ringmærkning, vil fremtidige studier styrkes og være mere pålidelige. Det vil også gøre analyse af flere arter mulige, som endnu ikke er muligt på grund af mangelfuld data, heriblandt arter som har høj bevaringsstatus under det Europæiske Fuglebeskyttelsesdirektiv.

# Synopsis

## Introduction

Anthropogenic factors and climate change is today the main reason for changes in population dynamics, leading to species declining and being in risk of extinction (Lande 1998). Loss of species is happening at a speed 100 to 1000 times faster than would naturally occur and since humans are the main cause of this loss of biodiversity, we have a responsibility to conserve ecological important species and their habitats, to change the declining tendency (EC/European Commission 2011). In order to do this proper, we need to understand the underlying mechanisms that influence population dynamics and lead to species declines (Lande 1998).

Birds ability to move over long distances have always intrigued man (Woodbury et al. 1956, Newton 2008), but it also make them a difficult organism to study in detail. Population size can be affected on breeding grounds, during migration and in wintering areas (Norris and Taylor 2006, Newton 2008). Therefore, we need to obtain knowledge about how events throughout the annual cycle affect individuals and hence population dynamics negatively, in order to develop suitable conservation efforts (Norris and Taylor 2006).

Especially in the last three decades, bird species in Europe have gone through a massive decline (Inger et al. 2015). The decline seems to be most drastic for long-distance migrants (Sanderson et al. 2006, Fox and Heldbjerg 2008, Vickery et al. 2013), which is thought to be caused by factors working mainly on wintering-grounds, affecting populations both immediately and as carry-over effects (Inger et al. 2010, Vickery et al. 2013, Finch et al. 2014). However, this does not mean that conservation should be focused on long-distance migrants alone, since resident species or with shorter migratory strategies are also declining (Fox and Heldbjerg 2008). Conservation and management efforts should be focused on our breeding birds in general to optimize overall population dynamics in the future.

One of the oldest used, but still one of the most vital tools, in acquiring knowledge about bird populations and their migration routes, is to put a simple ring around their leg (Baillie et al. 2009). This have in recent years been more standardized, especially during the breeding season, making it possible to get fairly accurate rates of demography in form of abundance, productivity

and survival (Robinson et al. 2009), which can provide us with valuable information of population dynamics on breeding grounds.

## Ringing of birds

With the development of marking animals, there was suddenly a way of identifying individuals and tracking their distribution and movements. One of the most amazing movement-patterns was obtained when we gained knowledge about birds migrating from breeding ground to non-breeding grounds (Woodbury et al. 1956). Bird migration between summer and winter grounds has intrigued and fascinated man for thousands of years and is even mentioned in the Old Testament and by the ancient Greeks (Woodbury et al. 1956). However, the well-known scientific marking of birds with rings was first invented in 1899 by the Danish teacher H. C. C. Mortensen (Preuss 2001, Baillie et al. 2009), who put a thin aluminum ring on a Starling (*Sturnus vulgaris*) to find out where it was going outside the breeding season. After this, the USA followed in 1902 with their first scientific ringing and the experiments continued to spread to other countries (Woodbury et al. 1956) with ringing centers in most of Europe, North America, India, Australia, New Zealand and some African and South American countries already in the 1930's (Preuss 2001).

Since the ringing of birds started to be scientifically relevant, the purpose has been to understand more about population dynamics and fluctuations due to the movement of the birds, which gives us information about trends in numbers, longevity, growth rates, age and sex ratios (Woodbury et al. 1956, Bønløkke et al. 2006). Today, in Europe alone, around four million birds are ringed every year (EURING 2007). EURING (The European Union for Bird Ringing) is the umbrella organization for all ringing centers in Europe and the Pan-European database consists of 10 million records of ringing recovery for 552 different species from more than 100 years of recording ([www.euring.org](http://www.euring.org)).

Catching birds in thin mist-nets and providing them with a lightweight rustproof metal ring containing information about the ringing center and a unique code, is the most commonly used tool for ringing birds, but this method is most suitable for capturing birds of smaller size (Bønløkke et al. 2006). Birds can also be captured e.g. by hand or with traps and other marking methods are seen in form of colored rings for neck and legs, plastic tags for wings and beak tags. These methods of marking are often used on birds of a certain size making it possible to read the marks or combination of colors without recapturing the birds (Bønløkke et al. 2006). Technology is also

improving constantly within bird marking. Especially bird migration have revealed new information after the invention of geolocators, satellite transmitters and GPS devices (Bridge et al. 2011), giving us precise information of movement patterns. This technology will continue to develop at a high speed but is costly and so far can only be used on a few individuals at the time (Bridge et al. 2011). Furthermore, these methods should not be used as an alternative to ringing, but as a tool box for addressing specific questions (Baillie et al. 2009)

However, if we want to link population dynamics in bird species with environmental factors directly, it is not enough to have information about migratory patterns, fluctuation and size; we need to have information about demography in terms of productivity and survival (Baillie 1990). The best way of accessing this demographic information is with standardized and constant data collecting efforts in an area over a long-term period.

## Constant Effort Sites

By repeatedly capturing and recapturing breeding birds in an area, it is possible to estimate the survival and reproduction of the ringed birds along with abundance (Peach et al. 1996). One year of standardized ringing will only have a real value when the ringing has been repeated for a longer and constant period of years (Drachmann 2004). Already in the 1960's the first efforts of CE ringing was performed in Britain and Ireland to obtain this data, which was followed up by a pilot scheme during 1981-1986 (Robinson et al. 2009). This pilot scheme and its results were reported to the British Trust for Ornithology (BTO) in 1986 (Baillie et al. 1986) and the same year it became a part of BTO's Integrated Population Monitoring Programme (Peach et al. 1996). This scheme has more or less been adopted by nearly 20 countries spread over two continents; Europe and North America (Robinson et al. 2009). Denmark follows this scheme strictly, both in collecting data and when analyzing the data. In 1999 European countries contributing with data to CES schemes agreed to develop the CES scheme further on a Pan-European scale, which could help with more effective monitoring of birds on a European scale, leading to better conservation and ecological research (Balmer et al. 2004).

## **Guidelines**

EURING has a webpage constituting of methods, guidelines and other information about CE-ringing in Europe ([www.euring.org/research/ces\\_in\\_europe/](http://www.euring.org/research/ces_in_europe/)), which the Danish Ringing Central has used to make guidelines for ringers in Denmark.

CE-sites should preferably comprise different but specified habitats; reeds, shrubs and deciduous forests, since these habitats are lacking in other monitoring schemes and contain many different species of passerine birds, which can tell us something about the population dynamic across and within habitats (Baillie et al. 1986). Most habitats go through a certain amount of succession across years and it is preferable that some sort of management takes places if succession is high, to avoid interference affecting interpretation of results. In addition, habitats that will go through major changes due to human interference should be avoided. Besides these recommendations for habitats, ringers are free to choose their own site.

Between May-August, there is 12 specified periods of ten days where ringers should aim to mist-net one time during each period with at least six days in between two visits, to avoid birds getting used to the nets. The quantity and positioning of nets should remain as constant as possible during all years. It is preferable to have ten nets of nine meters each, but extra nets and some difference in lengths are allowed (between 6-12 nets of 9, 10 or 12 meters). CES ringers aim is to ring for six consecutive hours, starting half an hour before sunrise. Of most importance is that ringers follow the same routine at each visit, to keep the data standardized. Unforeseen events, like rain, can cause changes to the routine, and if less than half the anointed time is used, ringers are called upon to finish the data collection at another visit within the same period (in Denmark, follow-up visits has been carried out the following day). CE-sites can be run in either a stable or a flexible manner. Stable sites avoid any kind of ringing at least a month before starting CE-ringing; any capturing is also avoided within 400 meters of the sites during all 12 periods. The amount of nest-boxes in an area must remain stable since the start of CES. On stable sites, no extra visits or supplementary nets are allowed. Flexible sites allows extra visits and nets but are rarely used by ringers during the CE-periods. Data collected at CES should be reported electronically and must contain specific information for each bird: capture/recapture, ringing central, ring number, species, sex, age, and date. Furthermore, information can contain weight, wing length, muscle score, fat score, incubation patch score, position of net and if it is a subspecies. Data must also contain name of location and ringer in charge. Because of the chance of succession in an area, it is important to

collect information about habitat in general and preferable changes from the previous years, so it is possible to take this into consideration, when analyzing the data.

## Danish sites

Between the years of 2004-2012, there have been eight active sites with mist-netting for use in CES schemes (Figure 1). Dybendal was the first site to start up in 2004, and it was the only site running that year and in 2005. In 2006, three more sites (Brabrand, Ravnstrup and Vestamager) followed. In 2008, Tarup came into the program and Ovesø in 2009. Unfortunately, Dybendal had to give up ringing after 2009 due to discrepancies with landowners. In 2011 Hanvejle followed and in 2012 Skagen. Unfortunately, data collected on these sites could not be used in analyses in this thesis, because at least four years of ringing are required for reliable analyses (Baillie et al. 1986).

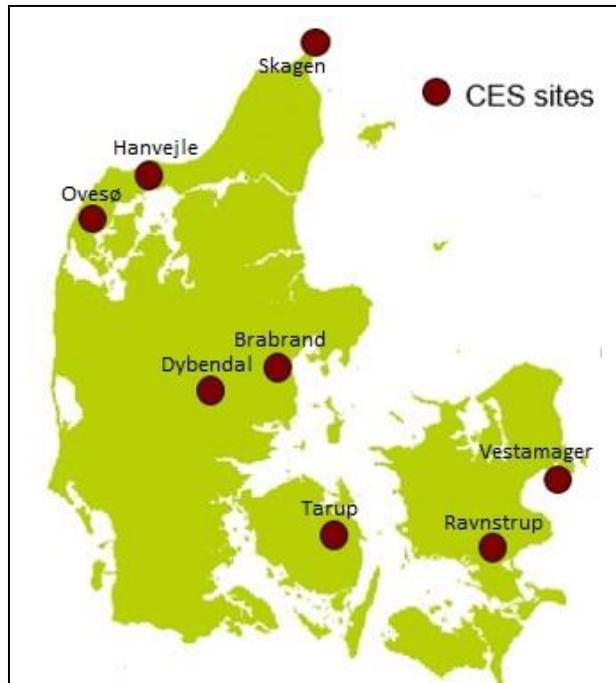


Figure 1: Danish Constant Effort Sites running during 2004-2012.

Here follows a brief introduction of the six sites used for analyses. Information about each site has kindly been e-mailed by the responsible ringer at the location and further information was gained from the Danish Ringing Society's homepage ([www.ringmaerkning.dk](http://www.ringmaerkning.dk)).

### *Dybendal*

Dybendal is an open woodland area situated in the Middle part of Jutland, in the Salten Langsø forest area (56.03.50.04N-009.27.09.71E). Dybendal consist mainly of moor areas with spread vegetation of pine and rowan trees. This vegetation type is fairly stable over time, which makes it suitable for standardized ringing efforts, which has been conducted in the tree areas, classifying the habitat as woodland in analyses. During 2004-2012 Dybendal contributed with 1189 captures of 35 species and 417 recaptures of 24 species caught in 72 meters of mist-net.

### ***Brabrand***

Brabrand Lake is a subglacial wet area formed under the last Ice Age close to the city of Århus in Eastern Jutland (56.08.38.18N-010.07.12.79E). The Lake is surrounded by reed beds and wet scrub consistent of mainly birch, willow and alder. There has been used a total of 100 meters of mist nets placed in 60% reed beds and the remaining 40% in wet scrub. Habitat code used in analyses is reed bed, since only one habitat is selectable. The area is managed by cutting down reeds in some winters and scrub trees are removed in other years. Due to the management of the reed bed, the ringers were forced to move the position of three nets in 2007. During 2006-2012 Brabrand contributed with 2457 captures of 35 species and 606 recaptures of 15 species.

### ***Vestamager***

The site at Vestamager is placed in a huge protected Nature area just outside of Copenhagen in Eastern Zealand (55.37.640N-12.33.200E). The area mainly consist of both short-grassed and untouched meadows, dry and wet scrub areas with willow, birch and alder and furthermore wet areas with reed beds. Mist-netting has been conducted in wet scrub areas, which is the habitat code used in analyses. During 2006-2012 Vestamager contributed with 2376 captures of 38 species and 766 recaptures of 18 species caught in 164\* meters of mist-net.

### ***Ravnstrup***

Ravnstrup is a lake area protected as a bird sanctuary by the owner Fugleværnsfonden. It is situated in Mid-Zealand surrounded by farmland (55.19.04.07N-011.43.24.28E). Like Brabrand, it is a subglacial area made during the last Ice Age. Besides the lake, the area consists of old deciduous forest, scrub areas, reed beds and meadows. The CES ringing has been conducted in the wet scrub area, which is the habitat code used in analyses. Two nets had to be moved to new positions in 2006 due to one to far from the others and one because of low catches of birds. During 2006-2012 Ravnstrup contributed with 2774 captures of 42 species and 1007 recaptures of 28 species caught in 110 meters of mist-net.

### ***Tarup***

This area was previously farmland, but after it was turned in to a gravel pit, the area is now a restored nature reserve with lakes of ground water, surrounded by high vegetation of willow, birch and alder. The site lies on Fyn in the Mid-Eastern part (55.19.40.69N-010.31.36.60E). This area also has some blackberry scrubs and reed beds, but because of the main habitat consisting of higher tree vegetation, the habitat code is woodland in analyses. This also means that the area has not been

\*This might be 146 meters, since this is reported in a yearly report from Vestamager. Nevertheless, 164 meters has been used for further analyses, since that was the netlength reported when ringers were asked to inform about this.

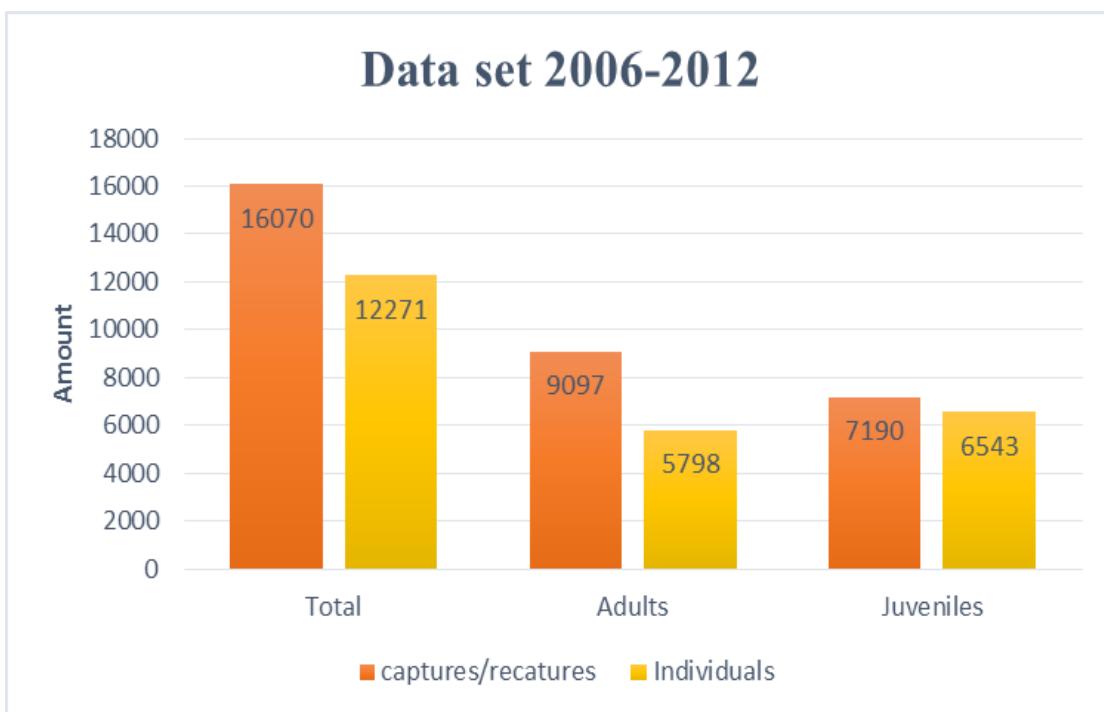
affected by succession since the trees from the start was near maximum height. One net was moved in 2010 because of a disagreement between the landowners. During 2007-2012 Tarup has contributed with 1668 captures of 41 species and 409 recaptures of 28 species caught in 96 meters of mist-nets.

### ***Ovesø***

*Ovesø* is a three and a half square-kilometers big lake in Mid-Jutland (56.51.33.95N-008.25.01.92E). The lake is narrow and the deepest parts of the lake is two and a half meter. The area is a protected Natura 2000 area and consists mainly of reed bed, which is also the habitat code in analyses. In the starting year, there was 102 meters of mist-net used, this was extended to 152 meters from 2010-2012. During 2009-2012 *Ovesø* contributed with captures of 2090 individuals of 41 species and recaptures of 679 individuals of 13 species.

## **Data set**

Since Dybendal was the only active site in 2004-2005, it resulted in sparse and unstable data not suitable for analyses and those two years were excluded. It is preferred that sites contributes with at least 200 new captures and recaptures within a year (Baillie et al. 1986). Dybendal did not manage to in 2006. However, data from this year maintained in the data set, since it was just below 200 (193 new captures/recaptures) and hence not expected to have any negative influence on analyses. Finally, analyses were made on data from 2006-2012 where at least four sites had run per year and with a maximum of six sites in 2009. Together the six sites contributed with 16070 captures and recaptures of 12271 individuals divided on 69 species. Here among, 9097 captures/recaptures were adults of 5798 individuals divided on 63 species and 7190 captures/recaptures were juveniles of 6543 individuals divided on 62 species (for a summary capture/recapture and individuals, see Figure 2). Numbers indicate a higher recapture rate of adults compared to juveniles due to the lower amount of individuals compared to amount of captures/recaptures. This could be due to a higher mortality among young birds compared to adults. In the case, with CE-sites, it in all likelihood indicates the frequency for which much young birds disperse into new areas both after fledging and in subsequent years (Baillie et al. 1986, Du Feu and McMeeking 1991) and this cannot be distinguished from mortality (Robinson et al. 2009).



*Figure 2. Amount of captured/recaptured birds and amount of individuals divided into juveniles and adults and a total of both. Data from Danish CE-sites used for further analyses between 2006-2012.*

## Species for further analyses

Of the 69 species caught on CE-sites in Denmark during 2006-2012, 14 species (all passerines) were collected for further analyses of data. The species belongs to three groups of migratory strategy. All 14 species are found across Denmark and will not show any regional-preference disturbance in analyses. They were divided into short-, medium-, and long-distance migrants following *The Danish Bird Migration Atlas* (Bønløkke et al. 2006) which is based on recoveries of Danish ringed birds in the years 1899-2002.

Short-distance birds are mainly resident but few can, especially in winters, migrate south of Denmark and as far as South-Southwest Europe. Medium-distance migrants mainly winter in Southwest Europe and no further than North Africa. Some even stay in Denmark, especially in mild winters. Long-distance migrants winter south of the Sahara mainly in West Africa.

Birds can travel far out of their normal breeding- and wintering area especially due to weather factors. Furthermore, some species can be both resident and migratory depending on especially harsh winters making them move south. The category of strategy a species is selected for

is therefore based on their preferable migratory strategy based on numbers of recoveries in the winter period. Hereby follows a short introduction of the 14 species comprising the Danish population and their migratory strategies based on *The Danish Bird Migration Atlas*. Including a population size and population tendency for 1999-2011, based on the Danish contributions from Birdlife Denmark and from the University of Aarhus to the Birdlife Internationals project, *Birds in Europe III* ([www.dofbasen.dk/ART](http://www.dofbasen.dk/ART)). Species in each group are listed after their EURING 2000 European exchange code, which follows taxonomic order (Robinson 2013).

## **Short-distance migrants**

### ***Wren (Troglodytes troglodytes)***

Wrens can be found in many different habitat types from woodland to gardens where it needs some denser trees and bushes to build its round nest, where it raises one or two broods. Can also breed in nest-boxes. Feeds on beetles, other insects and spiders. Harsh winters can take out a very big part of the population in an area and might trigger some of the mainly resident birds to migrate to South-Southwest Europe. Very few recoveries in total (51) leaves open questions about their migratory strategy. Population tendency: Decline. Population size (2011): 130.000.

### ***Blackbird (Turdus Merula)***

One of the most common breeding birds in Denmark. Blackbirds have changed breeding strategy during the last 100-200 years, where it has gone from mainly breeding in woodland to mainly breeding in cities, building its open nest in both trees, bushes, hedgerows and on human constructions. They can raise up to two or three broods per year. Feed on earthworms, insects and snails on the ground and supply their diet with berries and fruits, especially outside the breeding season. The Danish population is mainly resident but some migrate especially west and southwest to the British Isles and France. Population tendency: Decline. Population size (2011): 1.700.000.

### ***Blue tit***

The Blue tit is common in all of Denmark but with the highest concentrations on all islands and Eastern Jutland. It breeds in deciduous forest, parks and gardens and is a hole-nester gladly using nest-boxes, raising one brood per year. Feeds on insects in summer and seeds in winter. The Danish Blue tits are highly resident birds and recoveries show that 88% of adults and 75% of juveniles are recovered within one kilometer from the nesting site. Population tendency: Stable. Population size (2011): 235.000.

### ***Great tit***

The most common tit species in Denmark. Breeds in all kinds of woods, scrubs, parks and gardens and is, like Blue tit, a hole-nester. Also very gladly using nest-boxes, raising one or two broods per year. Feeds on insects and seeds. Most of the population are resident birds with few migrating west in winter. Population tendency: Stable. Population size (2011): 700.000.

### ***Yellowhammer***

Very common bird in Denmark, breeding in open areas with hedgerows and smaller scrubs, where it builds open nest and raises two broods. Feeds mainly on insects in breeding season and outside the breeding season it feeds on different kinds of seeds and corns. Seems to be highly resident with 80% recovered at the same site they were ringed even with years in between. Population tendency: Decline. Population size (2011): 310.000.

## **Medium-distance migrants**

### ***Dunnock***

Breeds in deciduous forests, farmland edges, parks and gardens where it builds an open nest raising two broods. Feeds on insects in summer and berries and seeds supply during winter. The migration route goes strictly south-southwest through Germany, Belgium and France sometimes as far as Spain, but some Dunnocks tend to stay in Denmark during winters. It seems like the migratory birds mainly leave Denmark in September-October and return in April. Population tendency: Decline. Population size (2011): 50.000.

### ***Robin***

Mainly breeds in forest but also in parks and gardens where it builds an open nest, but can also breed in special nest-boxes. Two broods per year. Feeds on insects and spiders on the ground. Most of the population seems to follow a migratory route southwest going through the Netherlands, Western Germany, Belgium and France to Southern Spain and Portugal. Robins tend to leave the breeding-sites no later than mid-October and return in April. Population tendency: Stable. Population size (2011): 160.000.

### ***Song thrush***

A timid bird that breeds in forests where it builds an open nest and raises two broods. Feeds on both snails, worms, insects and berries. The majority of birds leave Denmark in September and follow a

south-western migratory route to South-Western France, Spain, Portugal and even Italy and North Africa. Most of the breeding birds return in April. Population tendency: Stable. Population size (2011): 220.000.

### ***Reed bunting***

Reed bunting breeds in wet areas with reeds where they build their open nest near the water surface. Two broods per year. Feeds on seeds all year and supplies it with insects in breeding season. The migratory route is also southwestern and goes through Germany, the Netherlands, Southern England, France and Belgium with most recoveries from France (57 %). The majority of breeding birds leaves in October and return by the end of April. Population tendency: Stable. Population size (2011): 36.000.

## **Long-distance migrants**

### ***Sedge warbler***

Breeds in dry reed beds with high herbs, grasses and scrub trees where it builds its open nest and raises one or two broods. The migratory route goes south-southwest to West Africa. Feeds on insects and spiders. Aphids are an important food source when building up fat reserves before departing to wintering grounds. Sedge warblers are capable of taking the long trip to Africa without stop-overs. They depart from Denmark no later than October and return the second half of April. Population tendency: Decline. Population size (2011): 2000.

### ***Reed warbler***

The Reed warbler lives up to its name and is found in reed beds where it builds its open nest. Feeds on insects and spiders. Breeding birds arrive from late April and migration to winter grounds in West Africa mainly goes on in August-September. Compared to Sedge warbler it has several stop-overs on the migratory route. Birds from the Eastern population have a more west-going migratory route than birds from the more Western populations in Denmark and their migratory routes seem to converge along the Iberian Peninsula. Population tendency: Decline. Population size (2011): 34.000.

### ***Whitethroat***

Common in open areas with shrubs where it builds its open nest. One or two broods per year. Feeds on insect, spiders and berries. Whitethroat also follows a southwestern migratory route along the Iberian Peninsula mainly to West Africa. It returns to Denmark from wintering grounds during May

and leaves again in August-September. Population tendency: Stable. Population size (2011): 320.000.

#### ***Garden warbler***

Prefers to breed and build its open nest in shrub and forest areas with open space. Garden warblers show a tendency to become more common the more east it breeds in Denmark and on the most eastern island in Denmark, Bornholm, it seems to be the most common breeding bird among the warblers. It feeds on insects and spiders during breeding season and berries outside the breeding season. Birds arrive in May and leave in August-September. It follows a south-southwestern migratory route to wintering-areas in Central and West Africa. Population tendency: Stable. Population size (2011): 130.000.

#### ***Willow warbler***

Breeds in deciduous forest preferring birch and willow, where it builds its open nest and raises one brood per year. Feeds on insects and spiders. The population arrives in mid-April and departs in August-September. The Danish population belongs to a population that follows a southwest migration route via the Iberian Peninsula and Northwest Africa to West Africa. Population tendency: Decline. Population size (2011): 260.000.

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# Fluctuations in populations of common Danish breeding birds – Using ringing data from the Danish Constant Effort Sites.

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## Abstract

*Constant Effort Sites (CES) provide information about productivity indices and survival estimates in bird populations, which, together with abundance potentially link these demographic rates and observed population changes with environmental factors, both on breeding and non-breeding grounds. Most other monitoring schemes provide information on abundance only. Between the years of 2006-2012, six sites provided enough data to perform analyses on population demography in Denmark. Here, I investigate these demographic rates for 14 common passerine species according to their migratory strategies, dividing them into three groups of migrants: Short-distance (resident/Europe), medium-distance (SW Europe/North Africa) and long-distance (Africa, trans-Saharan) migrants. I test how well the CES data of each group and in total correlates in four different ways for the seven years period. First, I test how abundance and productivity tendencies follows tendencies from other monitoring schemes, both on a national and Scandinavian plan. Secondly, I look at population trends for the seven-year period on CES and compare it with trends for Common Bird Census (CBC) in the same period. Third, I look at key factors determining population size. Fourth, I look at to what degree productivity is explained by environmental factors based on precipitation in the months between May-August. The correlations were performed with simple linear regression and a confidence interval test was performed to test significance of the linear regressions. Results overall show expected patterns. Most importantly, survival show best correlation with adult abundance and immense the importance of linking factors affecting species both at breeding and non-breeding grounds to determine main causes of population fluctuations. Interestingly, long-distance migrants seems to increase over the period compared to short- and medium distance migrants, which is not the trend obtained in CBC. This could indicate that some species are better monitored at CES compared to other methods, or that some species due to habitat-preferences do better locally than nationally. This paper presents the first analyses of CES data in Denmark, and is a foundation for further analyses in the future. Such analyses can provide information about habitat management and proper conservation of species in order to reverse the massive population decline that many European bird species have gone through during the last decades.*

**Key words:** Constant Effort Sites, demography, abundance, productivity, survival, population dynamics, breeding and non-breeding grounds, habitat-preferences

## **Introduction**

Fluctuations in populations and distribution of bird species have for a long time puzzled ecologist, birdwatchers and conservationist (DeSante et al. 1995). National avian monitoring schemes have, for several years, been conducted on large- and long-term scales in both Europe and North America, giving us knowledge about declines and increases in certain bird species (DeSante et al. 1995). Those long-term monitoring programs provides us with information on how bird populations fluctuate over the years. However, no information is provided on demographic parameters, such as productivity and survival, which is necessary when studying bird populations (Baillie et al. 1986), if we want to find the underlying mechanism determining population fluctuations (DeSante et al. 1999, Robinson et al. 2009).

In the beginning of the 1980's a new form of bird monitoring, Constant Effort Sites (CES) ringing, started in Britain (Baillie et al. 1986, Robinson et al. 2009). CES should provide the missing information on productivity and survival with standardized mist netting each year, during specific periods in the breeding season from May-August (Baillie et al. 1986). The standardization on a CE-sites leads to a high recovery of previously ringed birds and a good estimate of post-fledging productivity (ration of juveniles to adults) (Baillie et al. 1986). Demography data collected at CES therefore has the ability to compliment other monitoring schemes (Peach et al. 1996, Robinson et al. 2009).

Biodiversity is faltering and species are declining across the globe (Lande 1998), and a new study by Inger et al. (2015) confirms the worrying decline for birds in Europe. It shows a total avian decrease of 421 million individuals from 1980-2009. Most of this decline is due to common species disappearing and not the rarer species that tend to draw attention from conservation. This underlines the need for monitoring schemes that can provide us with the necessary information on why our common breeding birds are declining. When collecting data on abundance, productivity and survival, information is also gained on what environmental factors are causing the decline in breeding birds (DeSante et al. 1995). There have been several studies showing that long-distance trans-Saharan migrants are declining more rapidly when compared to species with shorter migration routes to non-breeding grounds (Sanderson et al. 2006, Heldbjerg and Fox 2008, Vickery et al. 2013). When links between breeding and non-breeding grounds are found to be causing the root of population declines, information on how to conserve local

populations of species and how to manage key habitats is gained (DeSante et al. 1995, Robinson et al. 2009).

Both the Danish CES, which began monitoring in 2004 (Drachmann 2004), as well as almost all other European countries (Robinson et al. 2009) and the North American MAPS (Monitoring Avian Productivity and Survivorship) (DeSante et al. 1995) is modelled after the British Constant Effort Sites Scheme. Besides demographic information, CES can give specific information about the value of a habitat compared to other monitoring methods, since every site is situated in a specific habitat. It is preferred that habitats on CES are either scrubs, reeds or deciduous forests (Baillie et al. 1986), which is the case for all sites in Denmark so far. These habitats are preferred as they are generally less covered by other monitoring schemes and contain a high amount of species (Baillie et al. 1986).

In this paper, CES data for 14 common and highly abundant passerine species on Danish CE-sites are investigated further, to see how reliable the method is after seven years of ringing. To do this, I test and analyze CES data by correlating the data both individually and against other parameters with importance for population changes.

CES monitoring is a Pan-European project with the aim of monitoring population changes at both a national and European level (Balmer et al. 2004). Therefore, I aim to test if there is consistency between CES indices of abundance and productivity with both Common Bird Census (CBC) of Danish breeding birds and ringing data from Falsterbo Ringing Station in Southern Sweden, to see if different monitoring schemes shows the same tendencies. The exact population of birds in an area both local and on greater scales is impossible to measure precisely. This can cause doubts about the reliability of the methods for counting birds, but if more methods show consistency, it will make the results more reliable (Baillie et al. 1986). However, inconsistency does not mean that one of the methods is unreliable; it could mean that there is differences in species distribution between habitats (Baillie et al. 1986). I will also look at population trends over the seven years for both CES and CBC, to see if they show the same results for the seven-year period.

Another aim is to investigate which demographic key factors are controlling population size. First, I will see if there is positive correlation between juvenile and adult abundance, as would be expected due to higher productivity. If this is the case, it is interesting to see if adult abundance is most dependent on survival or productivity from the previous year, to find out which of these factors is the most important for the number of adults in a breeding season and hence population size.

At last, I aim to find out if environmental factors on breeding grounds have an effect on productivity. I use an easily measured factor in form of precipitation, which is known to affect productivity negatively (Harrison et al. 2000, CES news 2013).

This paper will not try to gain new evidence or close a gaping void within CES, since it is the first of its kind in Denmark and because data is still scarce compared to other countries (Robinson et al. 2009). Instead, it will make some important overall analyses and evaluate whether or not the few years with CES ringing in Denmark already show some interesting and expected tendencies and results. If the results are substantial, there is justification for further analyses in the near future, detailing specific species, habitats and possible reasons for population changes.

## Methods

### Data collection

#### CES data

Between 2004-2012 there have been eight active CE-sites in Denmark. Two sites had only data from one year and were excluded for further analyses; because at least four years is required to make data standardized enough (Baillie et al. 1986). During 2004-2005 only one site was running, these years also had to be excluded because data was too scarce and unreliable for analyses. Therefore all data and material used in this paper is based on six sites with data from 2006-2012.

Denmark follows the BTO Guidelines for Pan-European CES-ringing (Balmer et al. 2004), which have been thoroughly described elsewhere (Baillie et al. 1986, Peach et al. 1996, Miles et al. 2007). In short terms, ringers perform standardized mist-net captures of breeding birds in 12 specified periods of ten days between 1<sup>st</sup> May and 28<sup>th</sup> August. If ringers cannot make the 12 visits, data is accepted in the Danish Ringing database if they at least make the six first visits (Baillie et al. 1986). This is because most adults are captured in these six periods (Peach et al. 1996). If analysis of data is to be undertaken, at least four of these six visits must be completed in both the first half and second half of the period (Peach et al. 1996, Miles et al. 2007, Robinson 2013). In Denmark, all sites managed to ring at least ten times within a year. In fact, only four out of 404 expected visits were missed corresponding to less than 1%. This follows the trend for other CES countries where very few visits are missed (Peach et al. 1998, Robinson et al. 2009) and the missed visits effect on calculations of indices seems to be very small in general (Miles et al. 2007).

## **Other data collected**

Data for comparison with the CES data were collected by the Danish Common Bird Census (CBC) (Heldbjerg et al. 2014), where annual index-values for each of the species were extracted during the period 2006-2012 ([www.dof.dk/fakta-om-fugle/punkttaellingsprojektet/indeks-og-tendenser](http://www.dof.dk/fakta-om-fugle/punkttaellingsprojektet/indeks-og-tendenser)). CBC are conducted once a year in the breeding period between 1<sup>th</sup> of May – 15<sup>th</sup> of June by volunteers that follows the same route every year with 10-20 stop-overs, where they note down all species they see or hear. There are around 400 routes spread across Denmark. These lay in nine different main habitat-types (Larsen et al. 2011). Lennart Karlsson from Falsterbo Ringing Station kindly provided annual autumn total numbers of juvenile and adult catches for the selected species caught in the period 21<sup>th</sup> of July – 30<sup>th</sup> of September during the years 2006-2012. Falsterbo mainly captures migratory species compared to both CES and CBC. Monthly total precipitation across Denmark measured in millimeters for each of the months May, June, July and August was extracted ([www.dmi.dk/vejr/arkiver/maanedsaesonar](http://www.dmi.dk/vejr/arkiver/maanedsaesonar)) for each of the years 2006-2012. Furthermore, annual mean precipitation for all four months was calculated.

## **Calculating indices of abundance and productivity and estimates of survival**

Tools are needed to analyze raw CES data, to provide us with information about adult and juvenile abundance, productivity and survival rates. Professor Robert A. Robinson has developed such a tool in form of a package called cesr to use in the statistical program R ([www.r-project.org/](http://www.r-project.org/)). R is a software programming language widely used for statistical computing programming performing data analyses and graphics. R can be specialized for certain purposes by user-produced packages and scripts. Before analysis, the data must be set up in a certain form containing information about country-ID, site-ID, coordinates, habitat, visit-number, day, month, year, netlegth, scheme identifier, ring number, species, sex and age. For detailed information on the cesr see manual (Robinson 2013).

Abundance indices and yearly index-values for juveniles and adults were extracted and the function corrected for missing visits using the standard BTO method (Peach et. al. 1996). Productivity indices and yearly index-values were calculated as the ratio of juvenile to adult birds from the first year where both adults and juveniles were caught. This was also set to be the reference year (index=1) for both adults and juveniles (Figure 1).

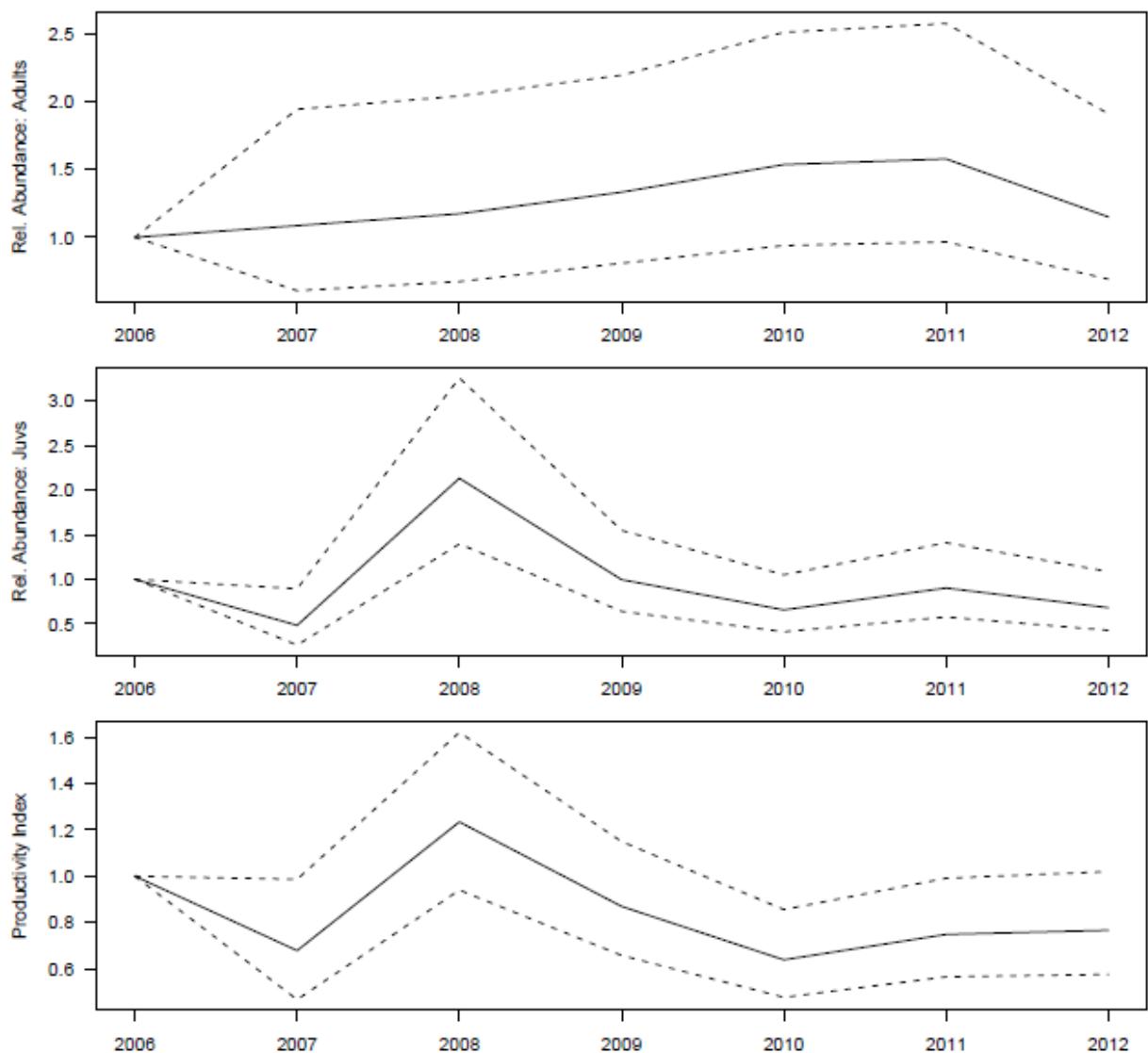


Figure 1. Example of indices on adult abundance (top), juvenile abundance (middle) and productivity (bottom) extracted for Reed warbler (*Acrocephalus scirpaceus*) in the statistical program R using a specified package for CES analysis (cesr). The figure show annual index-values for the years 2006-2012 with upper and lower confidence limits (dashed lines).

Survival estimates between years were found by running the program MARK (White and Burnham 1999) through the RMark library to fit the Cormack-Jolly-Seber model which is commonly used in CES (DeSante et. al, 1995, Pradel et al. 1997), modified to account for transient birds (Pradel et al. 1997). Yearly estimate-values for survival (being the same across sites) were extracted for each year (survival from 2006 → 2007 etc.) (Figure 2).

During 2006-2012, the six sites used in data analyses captured and recaptured 16070 birds of 69 species. Of these 69 species, it was only possible to calculate both abundance and

productivity index-values for 33 species, since the last species had insufficient numbers of either juveniles, adults or both between years (e.g. 26 species had less than 20 captures/recaptures of both juveniles and adults for all seven years). Of the 33 species, 14 species were chosen for further analyses. The 14 species were the most abundant within three different migratory strategies (short-, medium- and long-distance). Only four medium-distance migrants were captured on CE-sites and as a result, this group consists of one less species

than the others do. Short-distance migrants are either resident species or species wintering in Europe, medium-distance migrants wintering in Southwestern Europe or North Africa and long-distance migrants wintering in Africa south of the Saharan Desert (Tøttrup et al. 2006, Bønløkke et al. 2006). The 14 species, including data on captures of juveniles and adults plus total amount of captures is found in Appendix 1. Two very common species at the CE-sites, Chiffchaff (*Phylloscopus collybita*) and Blackcap (*Sylvia atricapilla*), were excluded, in spite of high capture rates. Their numbers are increasing substantially across Europe, possibly due to populations having different migratory strategies, wintering both in sub-Saharan Africa and in Europe (Peach et al. 1998, Bønløkke et al. 2006, CES News 2013). Therefore, they could not be included in a specific migratory group.

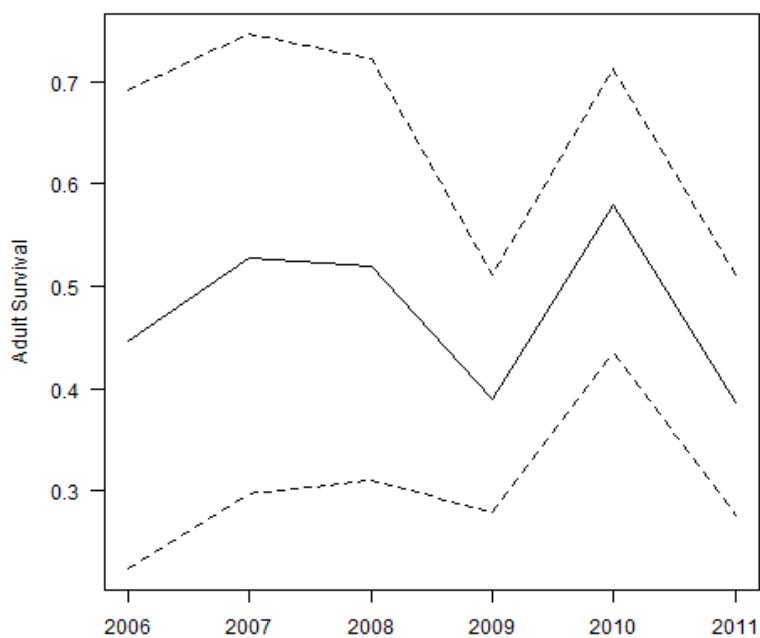


Figure 2. Example of survival estimates between years extracted for Reed warbler (*Acrocephalus scirpaceus*) in the statistical program R using a specified package for CES analysis (cesr). The figure show annual estimates of survival for the years 2006-2012 with upper and lower confidence limits (dashed lines). 2006 corresponds with survival from 2006 → 2007 etc.

## **Linear regression analyses.**

Linear regression was conducted between each of the below listed comparisons. Each regression was performed for all of the 14 species in the three migratory groups annually between 2006-2012 to see whether there was of positive or negative correlation.

### **Correlation between different monitoring schemes**

*Common Bird Census vs. adult abundance.* Is expected to show a positive correlation if local and national trends follow the same tendencies.

*Falsterbo no. of adults vs. adult abundance.* Is expected to show a positive correlation if local Danish and Scandinavian trends follow the same tendencies.

*Falsterbo total no. of birds vs. adult abundance.* Because Falsterbo mainly captures juvenile birds, this regression was performed as a support to the regression between Falsterbo adults and adult abundance, in case numbers of adult catches at Falsterbo is inaccurate.

*Falsterbo productivity vs. productivity.* Is expected to show positive correlation, if productivity on Danish breeding grounds have been affected by the same conditions as Scandinavian breeding grounds, causing either low or high productivity rates. Because of the low catches of adults at Falsterbo, productivity was measured as ratio of juveniles to total catches.

### **Correlation for population trends**

*Adults vs. year (2006-2012).* Will show whether the migratory groups and all species in total show increase, decline or remain stable throughout the seven-year period.

*Common Bird Census vs. year (2006-2012).* Will show the same as above on a national level. This will show if local and national populations shows the same changes over the seven years.

### **Correlation for key factors determining population size**

*Juvenile abundance vs. adult abundance.* Is expected to show a positive correlation because a higher number of adults will be expected to equal higher productivity and hence higher number of juveniles.

*Adult abundance vs. productivity and adult abundance vs. survival.* Will show whether adult abundance is best determined by productivity or survival from the previous year. Both factors is expected to affect adult abundance positively, if there is high survival or high productivity, but one of the factors may show bigger importance for abundance and hence population size if abundance of juveniles is positively correlated to adult abundance.

## **Correlation for precipitations effect on productivity**

*Productivity vs. precipitation (annual mean May-August), productivity vs. precipitation (May), productivity vs. precipitation (June), productivity vs. precipitation (July) and productivity vs. precipitation (August).* All annual precipitation values is expected to show negative correlation to productivity possible due bad breeding performance and low food availability.

The linear regressions were conducted in a simple data analysis in Excel 2013 in which slopes, r-values,  $r^2$ -values and p-values were calculated with a 95% confidence interval for all species in each of the migratory groups. For each migratory group a mean of r- and  $r^2$ -values was calculated as well as a total mean for all groups. This was repeated for each of the regressions performed.

P-values show whether the linear regression is significant or insignificant at the 95%-confidence interval. P-values are a common way of rejecting null-hypotheses, but in these linear regressions it will not be very important, since p-values are calculated for individual species, and the purpose here is to look at species as either a whole avian group or a specific migratory group. For supplementary material on CES-data, R-analyses and linear regressions\*.

## **Confidence interval tests**

Since the most important thing in these regressions is to see if the trends are positive or negative, the mean of the r-values were tested for significance on a 95% confidence interval test (CI) for the four or five birds in each migratory group and the 14 species in total. This indicates whether they are significantly different from zero on either the positive or the negative side of zero depending on the upper and lower boundaries. It is not possible to test the  $r^2$ -values since they can only be a positive value or zero and hence does not give us an idea if the regressions made are positive or negative. Values of r provide a good estimate for the regression between two tested variables, since they indicate how strong the relationship is between the tested variables. CI test was performed with a simple data-analysis in Excel ([www.office.microsoft.com/en-gb/excel-help/confidence-function](http://www.office.microsoft.com/en-gb/excel-help/confidence-function)-

\* Supplementary material can be extracted from: [www.dropbox.com/home/Supplementary%20material](http://www.dropbox.com/home/Supplementary%20material). This constitutes of (1) All raw CES capture/recapture data for all species collected at the eight active sites during 2004-2012. (2) Graphs of abundance and productivity indices and graphs of survival estimates for the 14 species analyzed in this paper. Notice, that some species contain the years 2004+2005, since these years were excluded after R-analyses was finished. (3) Slopes,  $r^2$ -values and p-values for all performed regressions for the 33 species, which constituted enough data to run abundance and productivity analyses in the program R during 2006-2012. (4) The manual for cesr is also available (Robinson 2013).

HP010335638.aspx). All results for slopes, r-values,  $r^2$ -values and p-values for all 14 species for all linear regression comparisons can be found in the Appendix 2. Significant results found with CI testing is marked with a \*.

## Results

### Monitoring schemes

Results of the linear regressions between national Common Bird Census (CBC) and local adult abundance at CES-sites did not show an overall positive trend. Short-distance migrants show a positive, but insignificant, result ( $r=0.38$ ). Medium-distance migrants show no correlation ( $r=-0.02$ ) and long distance migrants show a slight positive insignificant result ( $r=0.10$ ). The result for all migratory groups in total is positive but also insignificant ( $r=0.17$ ).

Comparing adult abundance with adult and total numbers of caught birds at Falsterbo Ringing Station show similar, but more positive, results compared to CBC. Short-distance migrants show significant positive results, both compared to adult and total catches from Falsterbo ( $r=0.53^*/0.49^*$ ). Medium-distance migrants show a positive but insignificant result both compared to adult and total catches from Falsterbo ( $r=0.32/0.20$ ). The same is the case for long-distance migrants ( $r=0.38/0.20$ ). The result for all groups in total show a significant positive result for both comparison with adults and with total catches from Falsterbo ( $r=0.42^*$  and  $r=0.30^*$  respectively). Productivity at Falsterbo compared with productivity at CES-sites show significant positive results for short-distance migrants ( $r=0.33^*$ ) while medium-distance migrants show a negative insignificant result ( $r=-0.16$ ) and long-distance migrants show a slight positive and insignificant result ( $r=0.10$ ). The total mean for all groups also show a slight positive but insignificant result ( $r=0.11$ ).

See Figure 3 for plotted mean r-values for each of the migratory groups and total mean for all groups.

## Population trends

Looking at the population trend for adults over the seven year study period shows reverse results compared to the overall European and national trend, which show a heavier decline in long-distance migrants compared to short- and medium-distance migrants (Sanderson et al. 2006, Fox and Heldbjerg 2008, Vickery et al. 2013). In the long-term period of seven years, short-distance migrants show a stable trend (mean  $r=-0.03$ ). Medium-distance migrants are in decline over the period and show a more negative but insignificant trend ( $r=-0.28$ ). Long-distance migrants show a positive but insignificant trend (mean  $r=0.37$ ). All groups in total show a stable and insignificant trend ( $r=0.03$ ), which is not surprising with six species increasing and eight declining. For this particular linear regression, it is interesting to look a little further at both the individual species and migratory groups, to see how well the seven-year trend follows the national CBC trend. Table 1 shows the r-values results for both CES and CBC adult abundance over the period 2006-2012. Here we see that short-distance migrants have a similar negative trend for three out of five species. Blue tit (*Cyanistes caeruleus*) and Yellowhammer (*Emberiza citrinella*) show dissimilar results where Blue tit is increasing in CBC but declining in CES and the opposite is the case for Yellowhammer. For this group, CBC also show an insignificant negative trend ( $r=-0.40$ ). For medium-distance migrants, there are also opposing trends for two out of four species. Robin (*Erithacus rubecula*) show an increase in CES and a decline in CBC while Song thrush (*Turdus philomelos*) show the reverse pattern. CBC also show a negative and insignificant trend for this group ( $r=-0.22$ ). Result for long-distance migrants shows similar increase for three species and strongly opposing results for two species. Reed warbler (*Acrocephalus scirpaceus*) increases

Species	CES	CBC
<b>Short-distance migrants</b>		
<i>Wren</i>	-0,40	-0,71
<i>Blackbird</i>	-0,37	-0,76
<i>Blue Tit</i>	-0,19	0,52
<i>Great Tit</i>	-0,12	-0,34
<i>Yellowhammer</i>	0,80	-0,70
Mean	-0,06	-0,40
<b>Medium-distance migrants</b>		
<i>Dunnock</i>	-0,21	-0,60
<i>Robin</i>	0,25	-0,26
<i>Song Thrush</i>	-0,50	0,92
<i>Reed bunting</i>	-0,64	-0,92
Mean	-0,28	-0,22
<b>Long-distance migrants</b>		
<i>Sedge warbler</i>	0,62	0,11
<i>Reed warbler</i>	0,62	-0,80
<i>Whitethroat</i>	0,95	0,87
<i>Garden Warbler</i>	-0,50	-0,37
<i>Willow Warbler</i>	0,16	-0,81
Mean	0,37	-0,20
Mean (all groups)	0,03	-0,28

Table 1: R-values based on linear regressions of respectively adult abundance in Constant Effort Sites (CES) and Danish Common Bird Census (CBC) against the years 2006-2012. With mean values for each migratory group and a total mean for all species.

steeply according to CES and declines markedly according to CBC. Willow warbler (*Phylloscopus trochilus*) likewise increases in CES and declines in CBC. CBC therefore show an insignificant negative trend for this group ( $r=-0.20$ ) compared to CES. The total trend for all groups in CBC is likewise negative and insignificant ( $r=-0.28$ ).

## **Key factors controlling population size**

Juvenile and adult abundance show overall positive correlations. Short-distance migrants are significantly positive ( $r=0.43^*$ ), while medium-distance migrants ( $r=0.19$ ) and long-distance migrants show insignificant results ( $r=0.08$ ). The groups in total show a significant positive result ( $r=0.23^*$ ).

Comparing adult abundance with productivity and survival show, that survival is the main factor driving the quantity of adults. Productivity show a positive but insignificant results for all three migratory groups and in total (short-distance ( $r=0.10$ ), medium-distance ( $r=0.28$ ), long-distance ( $r=0.24$ ), all groups ( $r=0.20$ )). Survival show significant positive results for short-distance migrants, long-distance migrants and all three groups, while medium-distance show nearly the same positive and insignificant result as in productivity (short-distance ( $r=0.29^*$ ), medium-distance ( $r=0.22$ ), long-distance ( $r=0.39^*$ ), all groups ( $r=0.31^*$ )).

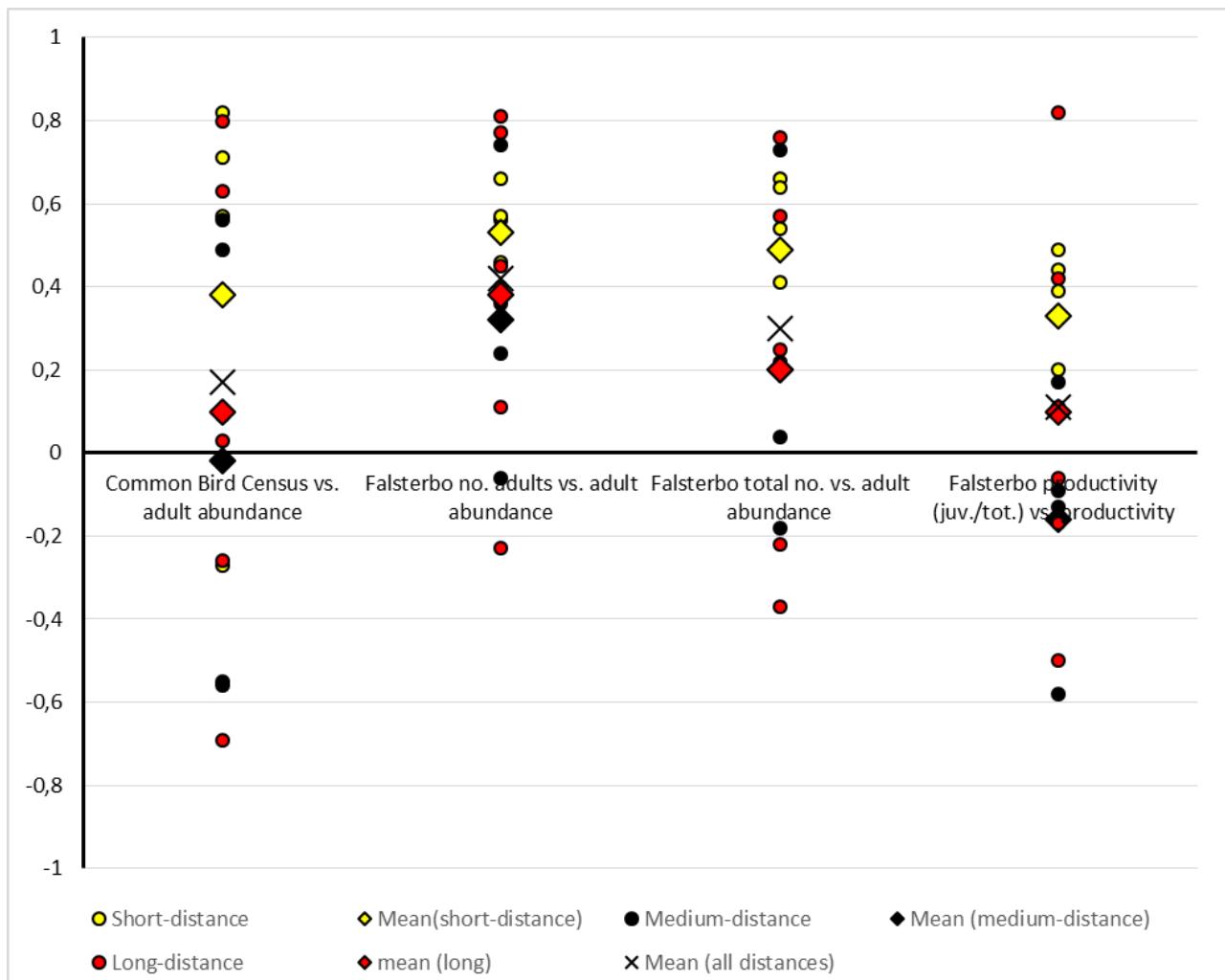
See Figure 4 for plotted mean r-values for each of the migratory groups and total mean for all groups.

## **Precipitations effect on productivity**

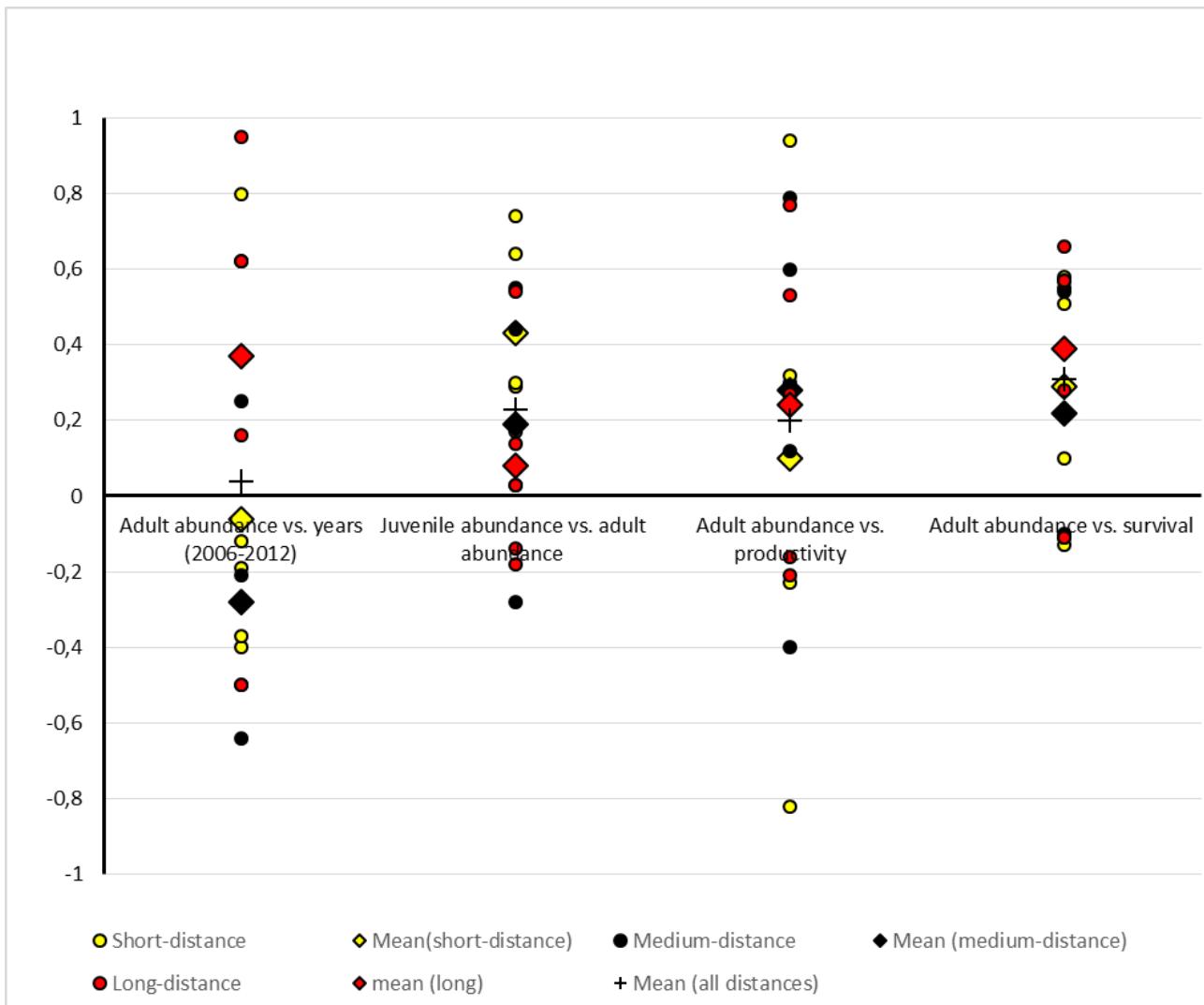
The mean precipitation from May-August show a negative correlation for each of the migratory groups, with significant results for long-distance migrants and all three groups in total (short-distance ( $r=-0.18$ ), medium-distance ( $r=-0.07$ ), long-distance ( $r=-0.60^*$ ), all groups ( $r=-0.29^*$ )). Medium-distance migrants show no correlation, which is also the case when comparing productivity with precipitation in May, whereas the rest of the groups are significant negative (short-distance ( $r=-0.35^*$ ), medium-distance ( $r=-0.01$ ), long-distance ( $r=-0.56^*$ ), all groups ( $r=-0.33^*$ )). June precipitation show no correlation for both short- and medium migratory groups while long-distance migrants continues to be significantly negative and all groups in total show a negative but insignificant result (short-distance ( $r=-0.03$ ), medium-distance ( $r=0.02$ ), long-distance ( $r=-0.68^*$ ), all groups ( $r=-0.25$ )). Precipitation in July show almost the same results for productivity in all three migratory groups, but the result for all groups in total is again significantly negative (short-

distance ( $r=-0.08$ ), medium-distance ( $r=0.01$ ), long-distance ( $r=-0.65^*$ ), all groups ( $r=-0.26^*$ )). In August, short- and medium distance migrants still show almost no correlation. The overall mean is positive but insignificant. This is caused by the interesting results for long-distance migrants which are still highly significant but positively correlated compared with all other months (short-distance ( $r=0.06$ ), medium-distance ( $r=-0.11$ ), long-distance ( $r=0.69^*$ ), all groups ( $r=0.24$ )).

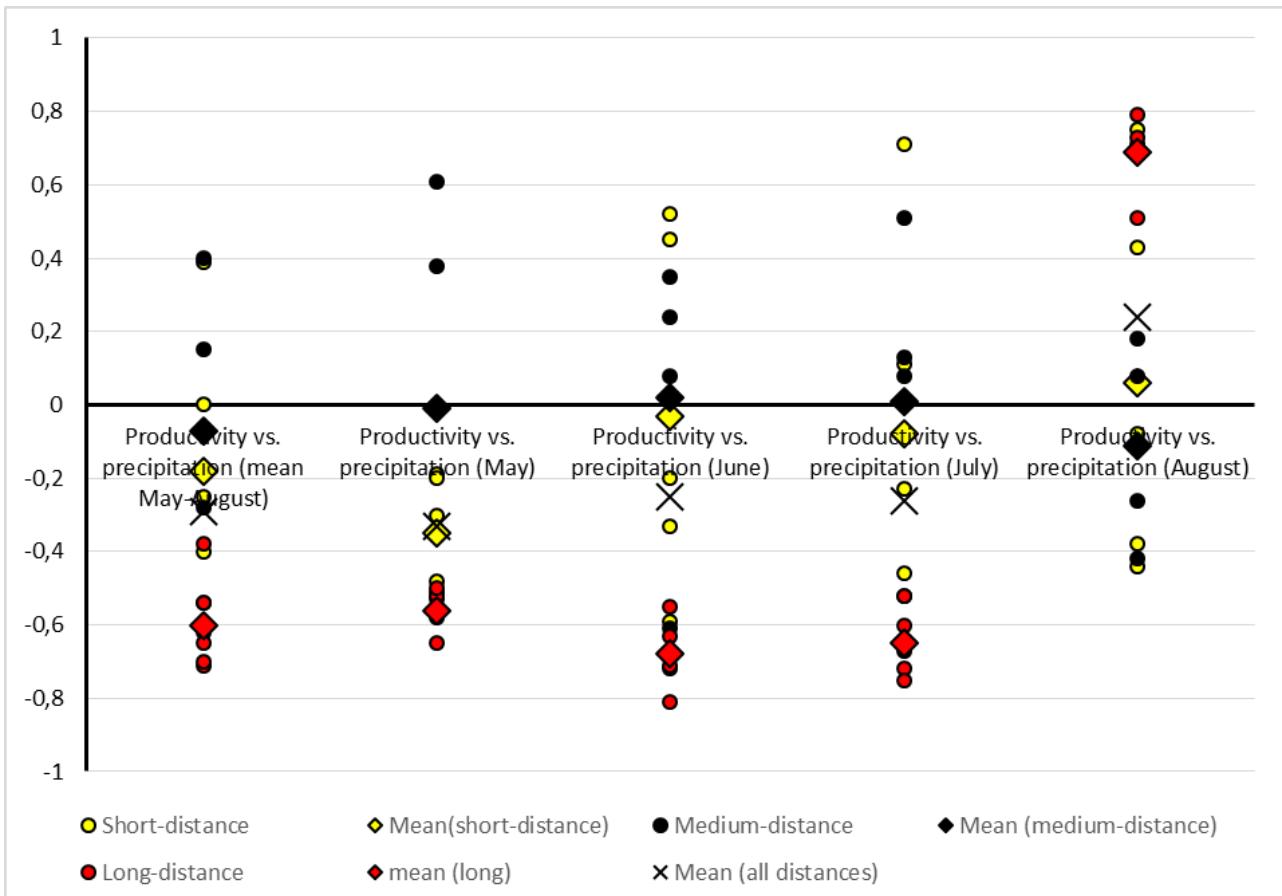
See Figure 5 for plotted mean r-values for each of the migratory groups and total mean for all groups.



**Figure 3.** Comparison among different indices of abundance and productivity between Constant Effort Sites and Danish Common Bird Census (CBC)/Falsterbo autumn ringing in the period 2006-2012. From left to right is shows plotted  $r$ -values calculated from linear regressions of respectively: adult abundance from CBC against adult abundance in CES, adult abundance at Falsterbo against adult abundance in CES, total of juvenile+adult abundance at Falsterbo against adult abundance in CES and productivity (ratio of juveniles to total catches of juveniles+adults) from Falsterbo against productivity at CES (ratio of juveniles to adults). Yellow legend shows plotted  $r$ -values for each species of short-distance migrants including a mean of  $r$ -values for each of the comparisons. Red legend shows the same plots for medium-distance migrants and black legend the same plots for long-distance migrants. For each comparison, there is also a total mean for all migratory groups plotted with a cross.



*Figure 4. Comparison among different indices of abundance, productivity and survival associated individually between Constant Effort Sites data in the period 2006-2012. From left to right is shows plotted r-values calculated from linear regressions of respectively: adult abundance against years showing increasing/declining tendencies for the period of seven years, juvenile abundance against adult abundance showing if the amount of juveniles is positively correlated with the amount of adults, adult abundance against both productivity (ration of juveniles to adults) and survival, to see which factor is most positively correlated with adults the following year. Yellow legend shows plotted r-values for each species of short-distance migrants including a mean of r-values for each of the evaluations. Red legend shows the same plots for medium-distance migrants and black legend the same plots for long-distance migrants. For each comparison, there is a total mean for all migratory groups plotted with a cross.*



*Figure 5. Comparison among indices of productivity compared to precipitation in the months CES is conducted (May-August) in the period 2006-2012. From left to right is shows plotted r-values calculated from linear regressions of productivity (ratio of juveniles to adults) to respectively: mean precipitation for May to August and against precipitation for each of the months May, June, July and August. Yellow legend shows plotted r-values for each species of short-distance migrants including a mean of r-values for each of the comparison. Red legend shows the same plots for medium-distance migrants and black legend the same plots for long-distance migrants. For each comparison is also a total mean for all migratory groups plotted with a cross.*

## Discussion

Results show that adult abundance in most cases show a positive relationship with other data monitoring methods, which points towards the fact that CES data is comparable with other data-methods and basically follows both a national and Scandinavian tendency. However, it is obvious that some species prevent the mean values from showing stronger positive results (Appendix 2). The question is if whether this is due to stochasticity or because there is a real difference in trends for some species between the monitoring methods. Other similar studies have shown overall significant correlation between CES and CBC when compared annually (e.g. Peach et al., 1998), but it is worth considering that other studies often correlate CES data with CBC conducted at the

CE-sites (Baillie et al. 1986, DeSante et al. 1995). This could suggest that these results are more consistent than comparing data across habitats and sites. Comparing CES trends with national CBC trend in Britain, have shown a high disparity for long-distance migrants (CES news 2013), which is a similar pattern to the obtained result for some species of long-distance migrants in this paper. Reed warbler and Willow warbler caused the big disparity here. These species could indicate that local populations of some species are doing better than the national trend shows, which indicates that CES-sites could tell us more about habitat-use and preferences of certain species. In fact, Harrison et al., 2000 showed that habitat change and management on CES sites affect Reed warblers (and Sedge warblers *Acrocephalus schoenobaenus*) compared to other species, and Peach et al. 1996, 1998 showed that Reed warblers and Sedge warblers are probably better monitored by CES than by other monitoring schemes in Britain, with high precision of annual changes. However, it is important to remember that the very low number of CE-sites in Denmark could affect the results. If just one or a few sites have very good breeding-conditions for birds like Willow warbler and Reed warbler, it could affect the overall results, compared to countries running far more sites. Different habitat-specific species have been shown not to occur in all suitable habitats (Baillie et al., 1986), so if just one site is extremely good for one species, it might drag the population trend towards an increase, even though this might not be the tendency for the rest of the sites or on a national scale. Nevertheless, these two species are the most abundant throughout the seven years (Reed warbler=2758, Willow warbler=1862) and should therefore show more reliable results than species caught in very low numbers. An example of this could be from the group of short-distance migrants, where the Yellowhammer also show an increase on CES compared to CBC. Since this species has only been caught 136 times during the seven years, it is more likely to be affected by stochasticity, but we cannot exclude the possibility that it actually increases. However, 14 out of 34 juvenile Yellowhammers were caught in 2012, which could have been due to a very good breeding season, but this one good year is not enough to drive a long-term population increase. Nevertheless, results suggest, at least for highly abundant species, that increasing populations of species at CES sites may provide valuable information of how habitats should be managed in order to conserve habitat-specific species in the best way.

Juvenile abundance seem to be consistent with adult abundance. The results show an overall positive relationship. What is interesting is that three species show a negative correlation suggesting that fewer adults equals more juveniles. Normally, this could be a matter of coincidence, but reports from two CES-sites (Jørgensen 2006, Ettrup et al. 2014) suggest that these three species;

Robin, Reed warbler and Garden warbler (*Sylvia borin*) can be caught in large numbers of juveniles in late August. The site at Brabrand caught a high number of juvenile Reed warblers (128) in August 2008 during one visit. The reed had previous that year been cut down leading to lower catches of adults due to breeding opportunities being scarce. This suggests that these juvenile Reed warblers mainly were migrants from other areas or countries, and high numbers of transient birds occurring on CES sites can sometimes affect data analyses (DeSante et al. 1995). A similar scenario occurred at Vestamager in 2006, where they caught a high number of juvenile Robins (28) and Garden warblers (16) during the last two visits in August after only catching maximum two individuals of each species at other visits that year. This also suggests a fall of migratory birds. The cesr analysis in R should take transient birds into account, but with such great numbers, it is possible that it will still affect the correlation. To explore this possibility it would be interesting to perform all analyses excluding August, especially since, as mentioned, only one or a few sites may affect the overall results, when the total of sites is so low. In general, the width of confidence intervals are reduced markedly for both juvenile abundance, adult abundance and productivity when more sites are added (Peach et al. 1996).

My results suggest that survival is the main factor driving the number of adults and thus population changes. Other studies support survival as the main factor determining adult abundance and thus population changes. Peach et al. (1995) suggested that survival is the main factor causing population decline of Willow warblers in Britain while Peach et al. (1991) showed that breeding productivity has no influence on population changes the next year. The same trend is seen inter-continentially where Gray catbirds in North America are more affected by survival than productivity (DeSante & Nott 2000). Anthropogenic habitat degradation and climatic conditions (mainly drought) in wintering grounds are playing an important role in the European decline of long-distance migrants (Vickery et al., 2013, Peach et al. 1995), while harsh winters will affect resident/short-distance migrants (Peach et al. 1995). These conditions might be the main factors influencing between-year survival and hence the number of adults in the next year with the ability to reproduce. However, it is also important to remember that both productivity and survival are vital parameters driving population dynamics and one thing does not exclude the other. If productivity is low, there will naturally be fewer individuals to survive until the next year and vice versa; productivity will most likely be affected if survival is low due to factors acting in non-breeding grounds. Furthermore, carry-over effects in form of reduced productivity due to lower individual fitness because of poor conditions in wintering areas, can also affect population negatively, even

though species have survived the winter. Sedge Warbler showed both reduced return rates and productivity on breeding grounds correlating strongly with drought (causing low food availability) in its non-breeding areas in the Sahelian region of West Africa (Peach et al. 1991). And Finch et al. 2014 likewise showed that poor conditions in non-breeding grounds affects productivity in three long-distance migrants. This urges the need for further analyses on the exact determinants of population fluctuations and links between them.

More precipitation had a negative impact on productivity. This is most likely due to lower chick survival and lower food availability for many species of birds (Boddy 1994, DeSante et al 1995, Harrison et al., 2000). Short-distance migrants are most affected by rainfall in May. This might be because of earlier breeding in short distance migrants compared with species having a longer journey to breeding grounds (Baillie et al. 1986). Medium-distance migrants show almost no correlation with rainfall in any months. Some species might be positively correlated to rainfall since most or parts, of their food supply, consists of earthworms, snails, berries or seeds that can be more plentiful in rainy periods, but I have not investigated this further. For both short- and medium-distance migrants it could have been interesting to see how big an influence March and April's precipitation has on these species due to earlier breeding compared to long-distance migrants. Exactly the general later arrival and breeding of long-distance migrants could be the reason why they seem to be negatively affected by rainfall in both May, June and July. In addition, long-distance migrants rely more heavily on flying insects as the main food supply for both adults and juveniles, which is consistent with lower numbers during rainy periods (CES news 2013). For long-distance migrants there is not only a problem with carry-over effects due to poor conditions in non-breeding grounds. Poor conditions in wintering-grounds affecting both arrival dates and adult fitness, will lead to delayed egg-laying and extreme low productivity, when conditions furthermore is poor in breeding grounds due to high precipitation (CES news 2013). The strong positive significance of the August correlation implies that more than just stochasticity cause it, but the result is hard to interpret and it will take further analyses to discover a possible reason for this. A suggestion could be that many migratory birds will stop-over on the CE-sites if there is rainfall in August. Generally, it could be interesting to analyze the correlation between both juvenile and adult abundance and precipitation for all of the months. Precipitation and fog is known to force migratory birds to stop-over and therefore rainfall could actually be positively correlated with abundance if, in fact, many migratory birds pass through some of the sites in August, where Denmark throughout the

autumn is a major migration funnel for birds migrating from mainly other Scandinavian countries to non-breeding grounds in south.

## Future perspectives

### Expanding the Danish CE-sites

The preliminary results provide possibilities for expanding research on the Danish CES data. First it should be noticed, that a major priority is to enter more sites into the CES monitoring scheme. With more CE-sites, the pooled dataset will automatically be both more interesting and valuable in analyses, especially when focused on abundance and productivity. With more sites, the capture data will increase to a level where analyses can be conducted on more species than this paper has investigated. Species like the southern Bluethroat (*Luscinia svecica cyanecula*) and Red-backed Shrike (*Lanius collurio*) are breeding on existing CE-sites, but their abundances are still too low for reliable analyses. The European Birds Directive (Directive, E. E. C. 2009) protects these species and we have a special obligation to protect them and their habitats. Here, CES could contribute by adding to the, currently scarce, demographic information on the species and their habitat-preferences. Another way of assessing demographic rates for more species is performing analyses over more years. Two years of data-collection has been added to CES data since analyses for this paper started, and this probably already leads to more species that are reliable for analyses. Furthermore, more sites and years will make habitat-analyses more reliable too, since the number of specific habitats are increased.

### Expanding the recent data analyses

Although, more sites and years will strengthen habitat-analyses, results from this paper already suggest that some species are doing better in CE-sites compared to national trends, which emphasizes the need for further analyses on specific species and their habitat-preferences. A first step could be to look at the differences between habitats, to see how specific populations differ in abundance, productivity and survival between and within habitats. Population dynamics do differ within CES habitats (Baillie et al. 1986, Peach et al. 1996, 1998) and habitat-analyses will provide us with unique knowledge about how important certain habitats are for different species. Testing the habitats against each other, will demonstrate if CES trends are positive in specific habitats compared to national population trends. Gaining knowledge about habitats will provide us with a

tool for further investigating how environmental factors and habitat succession affects population size. However, as long as the number of sites is low, it could be worth investigating if specific sites affect overall results, because of extremely good habitat conditions for specific species. If this is the case, then more years of data are required before testing of habitats against each other.

Survival has been proven to be a key factor determining population size, underscoring the need for linking environmental factors affecting population dynamics at both breeding and non-breeding grounds, to find the direct causes of changes. The fact that we already know that factors such as e.g. drought in Africa affects the return rates of Sedge warblers in breeding areas (Peach et al. 1991), is a big step in this direction. Also, the increasing field of tracking birds with technology, such as radio-transmitters and geolocators, improves our knowledge about migration patterns of species. This gives us an idea about where to focus the investigation of environmental factors affecting species at non-breeding grounds. CE-sites could be excellent sites for choosing individuals for this technology due to the high recovery rate compared to other monitoring schemes. Nevertheless, information about habitat requirements at non-breeding grounds are also necessary. Conducting a form of CE-ringing in the non-breeding grounds during the winter period could further strengthen our knowledge about the causes of population declines. However, this requires that we know exactly where the local populations winter, such information could be obtained with tracking technology but also with collection of feathers for stable isotope analyses at CE-sites.

Climate change is a likely cause of changing weather patterns and rising temperatures. It has been linked to a change in seasonal timing of species affecting productivity negatively, due to a mismatch between food-preference and offspring rearing (Burger et al. 2012). This suggests that further analyses on the feeding ecology of birds is necessary, which will require a different kind of analyses than what CES can provide. Notwithstanding, it is possible to collect reliable data of incubation patches and post-breeding moult from CE-sites, which can provide us with very important knowledge about breeding periods and even brood numbers. Thereby providing information on breeding phenology over time. Furthermore, biometric measures of weight, wing, length and fat scores could, when measurements are standardized, be correlated to survival (Evans et al. 1999) and probably productivity, to see how general body condition affects individuals and populations.

The further potential of CES both on a Danish and European scale is enormous and new research methods that are improving the analyses of data emerge with higher speed than ever before, making the results even more powerful and precise. CES data is an indispensable tool for

future conservation strategies in both temporal and spatial scales locally and on a national, Pan-European and inter-continental scale, both as a tool itself and in tandem with other monitoring methods.

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## Appendix 1

Species used in analyses of CES-data in the period 2006-2012 including their migratory strategies and the total number of adults and juveniles caught on the six sites contributing with data.

Species	Migratory Strategy	Adults	Juvs.	Total
Wren ( <i>Troglodytes troglodytes</i> )	Short (resident/Europe)	94	77	171
Blackbird ( <i>Turdus merula</i> )	Short (resident/Europe)	223	101	324
Blue tit ( <i>Cyanistes caeruleus</i> )	Short (resident/Europe)	194	551	745
Great tit ( <i>Parus Major</i> )	Short (resident/Europe)	283	411	694
Yellowhammer ( <i>Emberiza citrinella</i> )	Short (resident/Europe)	102	34	136
Dunnock ( <i>Prunella modularis</i> )	Medium (SW Europe)	170	82	252
Robin ( <i>Erithacus rubecula</i> )	Medium (SW Europe)	65	172	237
Song thrush ( <i>Turdus philomelos</i> )	Medium (SW Europe/ N Africa)	38	23	61
Reed bunting ( <i>Emberiza schoeniclus</i> )	Medium (SW Europe)	575	544	1119
Sedge warbler ( <i>Acrocephalus schoenobaenus</i> )	Long (trans-Saharan)	117	142	259
Reed warbler ( <i>Acrocephalus scirpaceus</i> )	Long (trans-Saharan)	1354	1400	2754
Whitethroat ( <i>Sylvia communis</i> )	Long (trans-Saharan)	304	308	612
Garden warbler ( <i>Sylvia borin</i> )	Long (trans-Saharan)	271	193	464
Willow warbler ( <i>Phylloscopus trochilus</i> )	Long (trans-Saharan)	974	888	1862
Total	All	4764	4926	9690

## Appendix 2

Slopes, r-values,  $r^2$ -values and p-values for each species in three different migratory groups, for each comparison made with linear regressions. Furthermore is mean r-values for each migratory group and overall mean for all three migratory groups in each of the comparisons.

### Common Bird Census vs. Adult abundance

	Short-distance			
	Slope	r	$r^2$	P-value (95%)
<i>Wren</i>	22.4	0.82	0.68	0.02
<i>Blackbird</i>	19.68	0.71	0.50	0.07
<i>Blue tit</i>	29.25	0.57	0.33	0.18
<i>Great tit</i>	6.39	0.09	0.008	0.85
<i>Yellowhammer</i>	-0.38	-0.27	0.07	0.55
<b>Mean</b>		0.38	0.32	
	Medium-distance			
	Slope	r	$r^2$	P-value (95%)
<i>Dunnock</i>	13.66	0.49	0.24	0.26
<i>Robin</i>	-11.68	-0.55	0.30	0.21
<i>Song thrush</i>	-7.33	-0.56	0.32	0.19
<i>Reed bunting</i>	18.36	0.56	0.32	0.19
<b>Mean</b>		-0.02	0.30	
	Long-distance			
	Slope	r	$r^2$	P-value (95%)
<i>Sedge warbler</i>	0.3	0.03	0.0009	0.95
<i>Reed warbler</i>	-7.56	-0.26	0.07	0.57
<i>Whitethroat</i>	26.12	0.80	0.64	0.03
<i>Garden warbler</i>	44.21	0.63	0.4	0.13
<i>Willow warbler</i>	-9.65	-0.69	0.47	0.09
<b>Mean</b>		0.10	0.32	
<b>Mean (all groups)</b>		0.17	0.31	

### Falsterbo caught adults vs. Adult abundance

	Short-distance			
	Slope	r	$r^2$	P-value (95%)
<i>Wren</i>	8.75	0.56	0.32	0.19
<i>Blackbird</i>	21.12	0.57	0.33	0.18
<i>Blue tit</i>	633.41	0.46	0.21	0.3
<i>Great tit</i>	652.58	0.66	0.43	0.11
<i>Yellowhammer</i>	0.56	0.4	0.16	0.38
<b>Mean</b>		0.53*	0.29	
	Medium-distance			
	Slope	r	$r^2$	P-value (95%)
<i>Dunnock</i>	-1.52	-0.06	0.004	0.89
<i>Robin</i>	71.73	0.24	0.06	0.6
<i>Song thrush</i>	21.64	0.74	0.55	0.056

<i>Reed bunting</i>	35.8	0.36	0.13	0.43
<b>Mean</b>		0.32	0.19	
<b>Long-distance</b>				
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Sedge warbler</i>	20.68	0.45	0.20	0.31
<i>Reed warbler</i>	470.44	0.81	0.66	0.03
<i>Whitethroat</i>	5.91	0.77	0.59	0.04
<i>Garden warbler</i>	-16.03	-0.23	0.05	0.61
<i>Willow warbler</i>	14.88	0.11	0.01	0.82
<b>Mean</b>		0.38	0.30	
<b>Mean (all groups)</b>		0.42*	0.26	

#### Falsterbo total captures vs. Adult abundance

	<b>Short-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Wren</i>	67.24	0.54	0.27	0.22
<i>Blackbird</i>	57.1	0.66	0.43	0.11
<i>Blue tit</i>	24576.16	0.64	0.41	0.12
<i>Great tit</i>	5225.42	0.41	0.16	0.37
<i>Yellowhammer</i>	0.84	0.22	0.05	0.64
<b>Mean</b>		0.49*	0.26	
	<b>Medium-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Dunnock</i>	-67.37	-0.18	0.03	0.70
<i>Robin</i>	75.45	0.04	0.001	0.94
<i>Song thrush</i>	120.42	0.73	0.53	0.06
<i>Reed bunting</i>	60.4	0.21	0.05	0.65
<b>Mean</b>		0.20	0.15	
	<b>Long-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Sedge warbler</i>	70.01	0.25	0.06	0.59
<i>Reed warbler</i>	1201.63	0.57	0.32	0.18
<i>Whitethroat</i>	67.1	0.76	0.57	0.05
<i>Garden warbler</i>	-163.58	-0.37	0.13	0.42
<i>Willow warbler</i>	-378.91	-0.22	0.05	0.64
<b>Mean</b>		0.20	0.23	
<b>Mean (all groups)</b>		0.30*	0.22	

#### Falsterbo caught juvenile/total catches vs. Productivity

	<b>Short-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Wren</i>	0.06	0.44	0.19	0.33
<i>Blackbird</i>	0.18	0.39	0.15	0.39
<i>Blue tit</i>	0.5	0.11	0.01	0.81
<i>Great tit</i>	0.1	0.2	0.04	0.67
<i>Yellowhammer</i>	1.58	0.49	0.24	0.27
<b>Mean</b>		0.33*	0.13	

	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
Dunnock	0.003	0.17	0.03	0.72
Robin	-0.004	-0.09	0.008	0.85
Song thrush	-0.008	-0.58	0.33	0.18
Reed bunting	-0.06	-0.13	0.02	0.78
<b>Mean</b>		-0.16	0.1	
	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
Sedge warbler	0.08	0.82	0.67	0.02
Reed warbler	-0.05	-0.17	0.03	0.72
Whitethroat	-0.02	-0.5	0.25	0.26
Garden warbler	-0.007	-0.06	0.003	0.9
Willow warbler	0.02	0.42	0.17	0.35
<b>Mean</b>		0.10	0.22	
<b>Mean (all groups)</b>		0.11	0.15	

#### Adult abundance vs. Years

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
Wren	-0.40	-0.40	0.16	0.37
Blackbird	-0.06	-0.37	0.14	0.41
Blue tit	-0.02	-0.19	0.04	0.68
Great tit	-0.01	-0.12	0.02	0.79
Yellowhammer	0.68	0.80	0.63	0.03
<b>Mean</b>		-0.06	0.20	
	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
Dunnock	-0.02	-0.21	0.05	0.65
Robin	0.04	0.25	0.06	0.58
Song thrush	-0.14	-0.50	0.25	0.25
Reed bunting	-0.05	-0.64	0.40	0.13
<b>Mean</b>		-0.28	0.19	
	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
Sedge warbler	0.27	0.62	0.39	0.13
Reed warbler	0.06	0.62	0.38	0.14
Whitethroat	0.11	0.95	0.90	0.001
Garden warbler	-0.04	-0.50	0.25	0.25
Willow warbler	0.02	0.16	0.03	0.73
<b>Mean</b>		0.37	0.39	
<b>Mean (all groups)</b>		0.03	0.26	

### Juvenile abundance vs. Adult abundance

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	0.07	0.29	0.08	0.53
<i>Blackbird</i>	0.37	0.64	0.41	0.12
<i>Blue tit</i>	0.16	0.17	0.03	0.72
<i>Great tit</i>	1.03	0.30	0.09	0.52
<i>Yellowhammer</i>	0.12	0.74	0.54	0.06
<b>Mean</b>		0.43*	0.23	
	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Dunnock</i>	0.45	0.03	0.0008	0.95
<i>Robin</i>	-2.09	-0.28	0.08	0.54
<i>Song thrush</i>	0.17	0.44	0.19	0.32
<i>Reed bunting</i>	1.32	0.55	0.30	0.20
<b>Mean</b>		0.19	0.14	
	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Sedge warbler</i>	0.01	0.03	0.0009	0.95
<i>Reed warbler</i>	-0.33	-0.14	0.02	0.77
<i>Whitethroat</i>	3.41	0.54	0.29	0.21
<i>Garden warbler</i>	-0.34	-0.18	0.03	0.69
<i>Willow warbler</i>	0.76	0.14	0.02	0.76
<b>Mean</b>		0.08	0.07	
<b>Mean (all groups)</b>		0.23*	0.15	

### Adult abundance vs. Productivity

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	-3.47	-0.23	0.05	0.66
<i>Blackbird</i>	1.75	0.94	0.88	0.006
<i>Blue tit</i>	0.9	0.3	0.09	0.57
<i>Great tit</i>	0.16	0.32	0.10	0.54
<i>Yellowhammer</i>	-49	-0.82	0.68	0.04
<b>Mean</b>		0.10	0.36	
	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Dunnock</i>	0.02	0.12	0.01	0.83
<i>Robin</i>	0.50	0.60	0.36	0.21
<i>Song thrush</i>	2.10	0.79	0.63	0.06
<i>Reed bunting</i>	-0.38	-0.40	0.16	0.43
<b>Mean</b>		0.28	0.29	
	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Sedge warbler</i>	-0.58	-0.21	0.04	0.69
<i>Reed warbler</i>	-0.15	-0.16	0.03	0.76
<i>Whitethroat</i>	0.07	0.27	0.07	0.60

<i>Garden warbler</i>	0.28	0.53	0.29	0.28
<i>Willow warbler</i>	0.35	0.77	0.6	0.07
<b>Mean</b>		0.24	0.21	
<b>Mean (all groups)</b>		0.20	0.29	

#### Adult abundance vs. Survival

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	2.64	0.58	0.34	0.22
<i>Blackbird</i>	0.51	0.51	0.26	0.30
<i>Blue tit</i>	0.41	0.10	0.01	0.85
<i>Great tit</i>	0.15	0.39	0.15	0.44
<i>Yellowhammer</i>	-0.80	-0.13	0.02	0.80
<b>Mean</b>		0.29*	0.16	
Medium-distance				
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Dunnock</i>	-0.14	-0.11	0.01	0.84
<i>Robin</i>	-0.09	-0.10	0.01	0.85
<i>Song thrush</i>	9.97	0.54	0.29	0.27
<i>Reed bunting</i>	0.73	0.55	0.3	0.26
<b>Mean</b>		0.22	0.15	
Long-distance				
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Sedge warbler</i>	1.26	0.57	0.32	0.23
<i>Reed warbler</i>	0.73	0.28	0.08	0.59
<i>Whitethroat</i>	0.61	0.66	0.44	0.15
<i>Garden warbler</i>	-0.07	-0.11	0.01	0.83
<i>Willow warbler</i>	1.74	0.57	0.33	0.24
<b>Mean</b>		0.39*	0.24	
<b>Mean (all groups)</b>		0.31*	0.18	

#### Productivity vs. Precipitation (mean May-August)

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	-0.003	-0.25	0.06	0.59
<i>Blackbird</i>	-0.01	-0.62	0.38	0.13
<i>Blue tit</i>	-0.002	-0.40	0.16	0.38
<i>Great tit</i>	0.03	0.39	0.15	0.39
<i>Yellowhammer</i>	8.75E-07	0.0003	1.02E-07	1
<b>Mean</b>		-0.18	0.15	
Medium-distance				
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Dunnock</i>	-0.03	-0.28	0.08	0.54
<i>Robin</i>	-0.02	-0.54	0.29	0.21
<i>Song thrush</i>	0.003	0.15	0.02	0.75
<i>Reed bunting</i>	0.01	0.40	0.16	0.37
<b>Mean</b>		-0.07	0.14	

	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Sedge warbler</i>	-0.02	-0.65	0.43	0.11
<i>Reed warbler</i>	-0.01	-0.71	0.5	0.08
<i>Whitethroat</i>	-0.05	-0.7	0.49	0.08
<i>Garden warbler</i>	-0.01	-0.54	0.29	0.21
<i>Willow warbler</i>	-0.01	-0.38	0.14	0.4
<b>Mean</b>		-0.60*	0.37	
<b>Mean (all groups)</b>		-0.29*	0.23	

#### Productivity vs. Precipitation (May)

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	-0.003	-0.48	0.23	0.28
<i>Blackbird</i>	-0.002	-0.30	0.09	0.52
<i>Blue tit</i>	-0.001	-0.57	0.32	0.18
<i>Great tit</i>	-0.01	-0.19	0.04	0.68
<i>Yellowhammer</i>	-0.0003	-0.20	0.04	0.67
<b>Mean</b>		-0.35*	0.14	
	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Dunnock</i>	-0.03	-0.51	0.26	0.24
<i>Robin</i>	0.01	0.38	0.15	0.39
<i>Song thrush</i>	0.01	0.61	0.37	0.15
<i>Reed bunting</i>	-0.004	-0.53	0.28	0.22
<b>Mean</b>		-0.01	0.27	
	Long-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Sedge warbler</i>	-0.01	-0.57	0.32	0.18
<i>Reed warbler</i>	-0.01	-0.58	0.34	0.17
<i>Whitethroat</i>	-0.02	-0.52	0.27	0.23
<i>Garden warbler</i>	-0.01	-0.50	0.25	0.25
<i>Willow warbler</i>	-0.01	-0.65	0.42	0.11
<b>Mean</b>		-0.56*	0.32	
<b>Mean (all groups)</b>		-0.33*	0.24	

#### Productivity vs. Precipitation (June)

	Short-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)
<i>Wren</i>	-0.001	-0.33	0.11	0.47
<i>Blackbird</i>	-0.001	-0.20	0.04	0.66
<i>Blue tit</i>	-0.001	-0.59	0.35	0.16
<i>Great tit</i>	0.01	0.52	0.27	0.23
<i>Yellowhammer</i>	0.001	0.45	0.21	0.31
<b>Mean</b>		-0.03	0.20	
	Medium-distance			
	Slope	r	r <sup>2</sup>	P-value (95%)

<i>Dunnock</i>	0.003	0.08	0.01	0.86
<i>Robin</i>	-0.01	-0.61	0.37	0.15
<i>Song thrush</i>	0.002	0.24	0.06	0.61
<i>Reed bunting</i>	0.002	0.35	0.12	0.44
<b>Mean</b>		0.02	0.14	
		<b>Long-distance</b>		
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Sedge warbler</i>	-0.01	-0.72	0.35	0.07
<i>Reed warbler</i>	-0.004	-0.63	0.40	0.13
<i>Whitethroat</i>	-0.02	-0.81	0.66	0.03
<i>Garden warbler</i>	-0.05	-0.71	0.50	0.08
<i>Willow warbler</i>	-0.01	-0.55	0.31	0.2
<b>Mean</b>		-0.68*	0.44	
<b>Mean (all groups)</b>		-0.25	0.27	

### Productivity vs. Precipitation (July)

	<b>Short-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Wren</i>	-0.001	-0.23	0.05	0.62
<i>Blackbird</i>	-0.003	-0.46	0.21	0.30
<i>Blue tit</i>	-0.001	-0.52	0.27	0.24
<i>Great tit</i>	0.02	0.71	0.50	0.07
<i>Yellowhammer</i>	0.0001	0.11	0.01	0.81
<b>Mean</b>		-0.08	0.21	
	<b>Medium-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Dunnock</i>	0.01	0.13	0.02	0.79
<i>Robin</i>	-0.01	-0.67	0.45	0.10
<i>Song thrush</i>	0.001	0.08	0.006	0.86
<i>Reed bunting</i>	0.003	0.51	0.26	0.25
<b>Mean</b>		0.01	0.18	
	<b>Long-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Sedge warbler</i>	-0.01	-0.72	0.51	0.07
<i>Reed warbler</i>	-0.004	-0.65	0.42	0.12
<i>Whitethroat</i>	-0.02	-0.75	0.57	0.05
<i>Garden warbler</i>	-0.01	-0.60	0.36	0.16
<i>Willow warbler</i>	-0.01	-0.52	0.27	0.24
<b>Mean</b>		-0.65*	0.43	
<b>Mean (all groups)</b>		-0.26*	0.28	

### Productivity vs. Precipitation (August)

	<b>Short-distance</b>			
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Wren</i>	0.002	0.43	0.18	0.34
<i>Blackbird</i>	-0.0004	-0.08	0.006	0.87
<i>Blue tit</i>	0.001	0.75	0.56	0.05

<i>Great tit</i>	-0.01	-0.44	0.19	0.32
<i>Yellowhammer</i>	-0.0003	-0.38	0.15	0.40
<b>Mean</b>		0.06	0.22	
<b>Medium-distance</b>				
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Dunnock</i>	-0.01	-0.26	0.07	0.58
<i>Robin</i>	0.002	0.18	0.03	0.69
<i>Song thrush</i>	-0.003	-0.42	0.18	0.35
<i>Reed bunting</i>	0.0004	0.08	0.007	0.86
<b>Mean</b>		-0.11	0.07	
<b>Long-distance</b>				
	<b>Slope</b>	<b>r</b>	<b>r<sup>2</sup></b>	<b>P-value (95%)</b>
<i>Sedge warbler</i>	0.01	0.71	0.50	0.08
<i>Reed warbler</i>	0.003	0.51	0.26	0.24
<i>Whitethroat</i>	0.02	0.73	0.53	0.06
<i>Garden warbler</i>	0.01	0.7	0.49	0.08
<i>Willow warbler</i>	0.01	0.79	0.63	0.03
<b>Mean</b>		0.69*	0.48	
<b>Mean (all groups)</b>		0.24	0.27	