Evaluating the usefulness of published data for estimating key parameters required in modelling global avian extinction risk

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Evaluating the usefulness of published data for estimating key parameters required in modelling global avian extinction risk

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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other University. The research reported within this thesis has been conducted by the author, unless indicated otherwise.

Summary

Despite the best efforts of conservationists worldwide, species extinction risks continue to rise. It is predicted that under intermediate climate warming scenarios 15-37% of species will be committed to extinction by 2050. This, coupled with limited funding and resources, means conservation management must be prioritised. Population viability analysis (PVA) models can help prioritisation by providing estimates of extinction risks for species. However, at present the availability of avian life history data and population data is limited, which makes this analysis challenging. Therefore, the aim of this thesis is to collate and calculate the necessary data so PVA models can be run for all bird species of the world.

We begin by looking at what density data is available for species because these underpin much of our understanding of the extinction risks, as they are directly linked to population sizes and population sizes are known to be highly correlated with extinction. We collate field densities for approximately 30% of all avian species and then implement a Generalised Linear Model (GLM) to calculate densities for the remaining species. In total, densities are modelled for 8,541 species with a 37% accuracy. We then use these densities, along with distribution polygons and habitat data, to calculate population sizes for 6,206 species with a 55% accuracy. Finally, as survival estimates are a key demographic parameter to include in PVA models, we calculate these for 5,291 species with a 36% accuracy.

Having calculated densities, population sizes and survival rates for over half of the worlds birds, we conclude that this is a huge step forward in being able to calculate extinction risks for many species. However, we highlight throughout that accuracy could be improved with more data collection, and fundamentally some data are still crucially missing if we want to run PVA models. Therefore, we suggest further research should aim to collect more avian data, such as fecundity, so simple PVA models can be run. For those species with the highest extinction risks we suggest even more data is collected, so more complex models, which include the effects of stochasticity, genetics and climate change can be run. We believe if robust and reliable data can be collected and included in PVA models, the results would be truly informative and insightful for conservation management and prioritisation.

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Contents

Chapter One: Understanding extinction threats and how these can be modelled

Abstract

In this chapter, we give a broad overview of the extinction threats species face and discuss how extinction responses can be studied. We suggest population viability analysis (PVA) models as a tool for quantifying extinction risks, and briefly discuss how these are used, giving examples of when PVA models have been successfully used and when they have been poorly implemented. We then consider the data necessary to run these PVA models, and conclude that the limited availability of life history data and population data are often what makes this type of analysis challenging and therefore this thesis must evaluate the usefulness of published data for estimating key parameters required in PVA modelling**.** We finish the chapter by outlining the aims of this thesis and the plan for the remaining chapters.

Species extinction

Species extinction is a natural process. Throughout geological time it has been occurring at a low and steady rate (the background extinction rate), and this has allowed species to diversify and evolve (Proença and Pereira 2013). However, when extinction rates increase beyond this background extinction rate it can have devastating impacts across the globe. This has happened five times in the last 540 million years, and each one resulted in the loss of at least 75% of all the existent species at that time (Barnosky *et al.* 2011). For example, only 5% of species survived the Permian mass extinction event, and it is thought to have taken 100 million years for global biodiversity to return to pre-extinction levels (Benton and Twitchett 2003).

Many scientists now believe we are experiencing the ‘sixth mass extinction event’ (Cellabos *et al.* 2015), as the number of recent species extinctions is much higher than what would be expected due to background extinction rates

(Mace *et al.* 2005). Since the 1500s there have been over 800 species extinctions (Proença and Pereira 2013), of which over 200 have been avian and mammalian species (Baillie and Cokeliss 2004 and Butchart *et al.* 2010). And since the twentieth century, there have been over 100 documented extinctions of amphibians, birds and mammals (Mace *et al.*, 2005), which is 30-120 times greater than the background extinction rate (Proença and Pereira 2013). Furthermore, this doesn’t include extinctions of undescribed species, so the actual number of extinctions may be much larger (Scheffers *et al.* 2012 and Costello *et al.* 2013), and perhaps more than double the recorded value for some taxa (Tedesco *et al.* 2014).

Unlike the past mass extinction events, the increase in current extinction rates is thought to be a direct consequence of increased anthropogenic disturbance. Any human activities which result either directly or indirectly in habitat destruction, introduce invasive species (such as predators, competitors or pathogens), or lead to the overexploitation of species and/or resources have all been cited as major drivers of species extinction (Proença and Pereira 2013). For example, it is well known that the Dodo (*Raphus cucullatus*) became extinct in the 16th century after humans overexploited it for food and introduced non-native species which predated it (Staud 1996). Recent examples of extinction due to anthropogenic habitat disturbance include the Atitlàn Grebe (*Podilymbus gigas*), Yunnan Lake Newt (*Hypselotriton wolterstorffi*) and the St. Helena Olive (*Nesiota elliptica*) (Baillie and Cokeliss 2004).

Climate change, which has dramatically increased over the last century due to anthropogenic activity, is also expected to be a major driver of species extinction (Thomas *et al. 2004,* Araújo *et al.* 2006 and Barnosky *et al.* 2011), and in fact over the next 100 years it is predicted to be a greater threat to global biodiversity than habitat loss (Leadley *et al.* 2010). Thomas *et al.* (2004) predict that, under intermediate climate warming scenarios, 15-37% of species will be committed to extinction by 2050, including up to 43% of endemic species becoming extinct (Malcolm *et al.* 2006). Furthermore, Sekercioglu *et al.* (2008) suggest that bird extinctions could increase by up to 500 species per degree increase in temperature. One species which is thought to already have suffered extinction due to climate change is the Monteverde golden toad (*Bufo periglenes*). This species is thought to have died out due to the abnormal severe droughts caused by the 1986–1987 El Niño event, and therefore it is often portrayed as first extinction as a direct consequence of global warming (Richards-Hrdlicka 2013). However, this is debated in the literature (for example see, Ochoa-Ochoa *et al.* 2013).

Extinction risks are generally higher in species which have limited adaptability, short generation times, low rates of reproduction or slow growth rates (Frankham *et al.* 2010). Risk of extinction is also high in species that are geographically restricted (due to having poor dispersal) and those with large home ranges (due to being harder to protect) (Purvis *et al.* 2000). There is also a positive correlation between extinction risk and adult mammalian body mass (Cardillo *et al.* 2005). Furthermore, species that occupy a high trophic level in the food chain are more at risk from extinction due to chains of extinction/ co-extinctions (Purvis *et al.* 2000, Dunne & Williams 2009 and Gilman *et al.* 2010).

Extinctions are arguably one of the most important species responses to predict as they may require more urgent interventions than other species responses, such as spatial or genetic responses. However, uncertainty in quantifying extinction is high and there is much debate over how reliable, and thus how useful, current predictions are. The International Union for Conservation of Nature (IUCN) has developed a Red List of all plant and animal species which are globally threatened and are at risk of becoming extinct (Vié *et al.* 2009). However, these assessments are rarely based on empirical methods, and species are assessed on an individual basis by different people. Assessments could therefore be considered subjective and might have low replicability. There is also further debate on how well the IUCN considers the effects of climate change on the listed species (Akcakaya *et al.* 2006 and Brook *et al.* 2009), which could further limit their utility. It is therefore clear that an approach is needed that allows extinction risks to be objectively quantified.

How are extinctions studied?

Extinction of birds and mammals can be inferred directly from site visits to known localities of a species. However, it is difficult to definitively record an absence from an area, and direct observations are time consuming and virtually impossible to complete for all species. Researchers therefore often use indirect methods to project future extinctions. For example, species distribution models (SDMs) are used to model current and future geographic ranges of species; the species-area relationship can then be applied to these models to extrapolate extinction rates (Thomas *et al.* 2004). However, this method has a number of caveats, which are reviewed extensively in He and Hubbell (2011) and He and Hubbell (2013). More recently, time budget models have been proposed to measure extinction rates. These link climate and survival rates to behavioural traits, and work on the principle that a species can only survive in a given area if it is able to carry out all of its essential activities (e.g. foraging) within the time available (Carne *et al.* 2012). Therefore, these models hypothesise that time constrains a species ability to survive (Dunbar *et al.* 2009). However, despite the merits of time budget models most researchers do not consider behaviour when calculating extinction risks. Therefore, amongst most scientists, the favoured method to calculate future extinction risks is population viability analysis (PVA). The sole purpose of these models is to predict the likelihood that a population will persist above a predetermined minimum size for a given time in the future, using basic life history variables or count data (Morris and Doak 2002).

Population viability analysis as a tool for studying extinction

Population viability analysis (PVA) estimates the extinction risks of species to inform conservation practices and policy decisions (Beissinger 2002). The first PVA developed was a population model incorporating environmental and demographic stochasticity to produce extinction probabilities (Shaffer 1981). This method was then updated by adding genetic stochasticity (e.g. the effects of inbreeding) to the model, allowing the more accurate determination of the viability of populations (Frankel and Soule 1981). Since the 1990s the use of PVAs has proliferated as computational advances have allowed the time-efficient running of more complex models (Beissinger 2002). To date, over 100 PVAs have been successfully run on a wide range of species, including large mammals, birds, fish, reptiles, invertebrates and plants (Keedwell 2004). For example, PVAs run on whooping crane (*Grus americana*) populations revealed that 10 to 20 birds could be sustainably harvested from the captive bred population per year in order to establish a new population in Florida (Mirande *et al.* 1991). Furthermore, PVAs run on of the threatened great Indian bustard (*Aredotis nigriceps*) revealed that the small population sizes caused by hunting and habitat destruction could not be sustained, and this led to tighter legislations and protections being enforced (Dutta *et al.* 2011). Similarly, the results from PVAs carried out on South African leopards were used to show that additional hunting would drive the population to extinction, and this allowed CITES (the Convention on International Trade in Endangered Species) to stop additional hunting permits being issued (Daly *et al.* 2005).

The IUCN currently uses PVA model predictions to classify endangered species under criterion E (Brook and Kikkawa 1998). To be listed as being critically endangered, quantitative analysis (such as a PVA model) must show that the species has a 50% chance of extinction within 10 years (Vié *et al.* 2009). It is interesting to note, however, that of the 4074 bird and mammal species listed on the IUCN as being threatened, only one species (*Hippocamelus antisensis*) has been assessed under criteria E (IUCN, 2014).This suggests that despite the perceived utility of PVA models, they have still not achieved their full potential, and lack of data is often cited as one of the main reasons for this (Fieberg & Ellner 2000). For example, VORTEX (a computer simulation model for PVA) requires 65 separate pieces of data, but it has been found that on average up to 43 of these parameters can be missing in a single PVA model (Morrison *et al.* 2016). When PVA models are conducted with missing data or if available data is poorly implemented, conclusions drawn from the models can be misleading and a greater hindrance to conservation efforts. For example, Theberge *et al.* (2006) conducted PVA on wolves (Canis lycaon) in Algonquin Provincial Park, and concluded that wolf harvesting must be banned to save the species from local extinction. However, Patterson and Murray (2008) later reviewed this study and found the results were much more pessimistic than the data warranted, and thus the diversion of resources from other conservation efforts to implement the ban on harvesting was unjustified. They concluded these results had been reached by Theberge *et al.* (2006) due to several flaws in the design and implementation of their model: lack of data, unrealistic estimates of demographic parameters, and lack of consideration into the effects of missing data on the model outcome. This highlights the importance of considering data availability when designing PVA models and when drawing conclusions from them, especially when they impact conservation management.

What data are required for PVA models?

One of the most useful demographic parameters used in PVAs are population sizes, as these are highly correlated to extinction risk (O'Grady *et al.* 2004). However, calculating population sizes is an inexact process (Lessios 1996), and even for well-known species there is high uncertainty in estimates (Newson *et al.* 2008). The most common methods used to estimate species abundance are distance sampling (Thomas *et al.* 2010) and mark-recapture sampling (Chao 1987). However, both these techniques require direct observations in the field, an impossible task to carry out for all species. Furthermore, neither provides a method to calculate or project future population sizes. An alternative approach for population estimation, in the absence of widespread density estimates, is to multiply the few available density estimates for a species by the estimated area over which the species occurs. If we assume that future densities remain similar to current densities in areas of suitable habitat and climate, this approach allows estimations to be made of future population sizes. Species distribution models can also be used to project future habitat suitability, and thus the area over which the species might occur under scenarios of climate change. New population sizes can then be recalculated using this new data. However, the reliability of population estimates calculated using such methods are dependent upon third party data. How these data have been calculated could therefore vary from species to species and source to source, making it difficult to make meaningful comparisons or further calculations with the data sets. These data may also not be available for all species of interest, further limiting the application of this method.

PVA models also typically require either count data or life history data for a species. Using count data, extinction risks are calculated through *Diffusion Approximation* PVA models (Elderd *et al.* 2003). This method estimates the variance and mean of the stochastic population growth rate and then uses these estimates to generate a range of predictions about the population, including extinction probabilities (Brigham *et al.* 2003). However, it has been suggested that this method provides unreliable measures of true extinction risks (Fieberg and Ellner 2000), even when data are collected over a long period (Brook *et al.* 2000). Instead, it is often beneficial to use life history parameters in the calculation of extinction probabilities. However, for most threatened species these data are difficult to acquire (O'Grady *et al.* 2004), often needing to be estimated with expert knowledge or data from closely related taxa. For each parameter, it is also good practice to evaluate its sensitivity and elasticity over a plausible range of values. This allows a better understanding of its influence on population dynamics; this is particularly true if parameters are extrapolated from other studies or species. It is important that the estimated range of values the parameter can take are sensible and not too large, otherwise the PVA could become meaningless, potentially hindering conservation efforts (Keedwell 2004). In order to estimate a sensible range of values, an in-depth understanding of the parameter and the species is required, which is often unattainable for most species (Fieberg and Ellner 2000). In addition to this, life history parameters should also try to incorporate stochastic events to increase the validity of PVAs. This requires many years of sampling, which is rarely feasible for threatened and endangered species. It is argued that extinction probabilities should only be predicted for the near future, and some research suggests that we can only reliably calculate extinctions for up to 10% of the time period over which they’ve been monitored (Fieberg and Ellner 2000).

Ideally, PVA models should also include data on catastrophic events since these have been shown to rapidly reduce population size and thus could have been responsible for many past extinctions (Coulson *et al.* 2001). For example, droughts and summer frosts have been shown to have caused the extinction of local populations the Edith's Checkerspot butterfly (*Euphydryas editha*) (Ehrlich *et al.* 1980 and Singer & Thomas 1996). However, it is hard to predict the frequency and severity of events such as these, so they are difficult to incorporate accurately in PVA models.

Genetic data should also be included in PVA models to increase the accuracy of extinction probabilities. However, since this information is only available for a limited number species, few studies integrate genetics into PVA models (Beissinger 2002). Even when the information is available, inbreeding depression is often the only genetic threat considered (Frankham *et al.* 2010). This is poorly defined in the analysis as it is usually only imposed on juvenile mortality, even though it has been shown to affect adult mortality and litter size (Beissinger 2002 and Frankham *et al.* 2010). Despite these limitations, inbreeding depression has been shown to increase the extinction probabilities of many species over time (O'Grady *et al.* 2004), and therefore it should be included in PVA analysis wherever possible to reduce the risk of underestimating extinction.

Most PVA models only consider climate change in terms of the variation in habitat availability and its impact on the size of the population (Akcakaya *et al.* 2006). However, climate change will also affect demographic variables such as survival rates, reproduction rates and dispersal ability (Brook *et al.* 2009). This information, however, is much harder to incorporate into PVA as it is difficult to predict exactly how these variables will change in the future. Caution must therefore be exercised when drawing conclusions from PVA models on the impact of climate change on extinction risks (Stanton *et al.* 2014).

Limited data availability can be seen as a hindrance to calculating potential extinction risks. However, conservation is a crisis discipline, with decisions needing to be made quickly, which often means making educated guesses and best use of limited data (Reed *et al.* 2003). Any research that aims to calculate extinction risks is likely to face the same problems. In addition to this, alternatives to PVA modelling often rely on subjective human decisions which do not make full use of the available data and do not include uncertainties in their conclusions (Brook *et al.* 2002). Therefore, despite their caveats, it can be argued that PVA models are the best tool we have at present for estimating extinction risks under climate change and therefore researchers should strive to use them wherever possible.

Birds as a model taxon for studying extinction risks

There are estimated to be around 10,300 extant species of birds across the globe, from 36 different orders and 203 families (Birdlife International 2014). The smallest orders such as the Cariamiformes, Eurypygiformes, and Opisthocomiformes, contain just a few extant families and species, whereas the largest order, the Passeriformes, contains over 50% of all the world's bird species (Birdlife International 2014). Within the Aves there is huge diversity and many birds have unique adaptations. Birds are also useful indicators of environmental change since they occupy almost every habitat globally (Gregory *et al.* 2003). As such, birds are one of the best studied and documented taxa across the globe.

It is estimated that 20% of people in the USA spend time observing and identifying birds (USFWS 2003), whilst in the UK 30% of people feed birds in their gardens or consider themselves to be bird watchers (Beolens 2010). Organisations such as the British Trust for Ornithology (BTO), the Royal Society for the Protection of Birds (RSPB) and BirdLife International utilise this army of amateur ornithologists to participate in citizen science monitoring schemes, such as the Breeding Bird survey (BBS), BirdTrack and various bird-ringing programmes. These schemes generate high quality data on bird populations, which can be used to highlight spatial and temporal population changes, and how birds are responding to environmental change. These monitoring programmes identify species of conservation concern, providing information for funding decisions and management strategies, and are therefore extremely valuable for conservation. Less than 1% of birds are insufficiently known for their threat status to be determined in International Union for Conservation of Nature (IUCN) Red List**,** whereas 16% of mammals remain unclassified, demonstrating how much data are available for avian taxa compared to other taxa (Vié *et al.* 2008).

Given that birds are some of the most well-studied species in the world, they are an ideal group to study for this thesis. Using available data, we should be able to estimate further key parameters required for PVA modelling, and thus gain a greater understanding into global avian extinction risks.

Aims of this thesis

The aims of this thesis are to:

- review and collate available densities, population sizes and life history data for all bird species, with the intention of using this data in population viability analysis (PVA) models;
- estimate densities of birds of the world, which can then be used to calculate population sizes;
- estimate population sizes for birds of the world, which can then be used in PVA models;
- estimate survival rates of birds of the world, which can then be used in PVAs; and
- make recommendations on further data to be collected in order to run the best possible PVA models for birds of the world.

Thesis plan

Chapter two will examine the density data available and impute densities for species for which no density estimates exist using general linear models. We will also explore the trends and patterns in these densities. Following this, in chapter three we will then estimate global population sizes for all the birds of the world using the density data collected and distribution data for each species. We will also consider trends and patterns in population sizes of birds across the world. Chapter four will examine what life history traits are necessary for population viability analysis models, and will attempt to calculate survival rates of birds, which could then be used in PVA models alongside the previously calculated population estimates. We conclude in chapter five by discussing the possibility of running basic PVA with the data available. We also discuss the further data required to be able to run improved PVA models. Finally, we outline why it's more important than ever before to collect and collate all this data under the threat of climate change.

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Chapter two: Estimating densities for the world's birds

Abstract

Population densities underpin much of our understanding of the extinction risks birds face since they are directly linked to population sizes. In this chapter we collate field density data for approximately 30% of all avian species. We then create a General Linear Model (GLM) to calculate densities for the remaining species. In total, we model densities for 8,541 species with a 37% accuracy. We conclude that further data collection is necessary in order to increase the accuracy and reliability of these modelled densities.

Introduction

Population densities underpin much of our understanding of the extinction risks birds face (Marsden *et al.* 2015). Densities directly affect the size of the population and are therefore a useful indicator of conservation status and extinction risk. For example, a low population density indicates a small population size, and a small population size can lead to higher extinction risks (see chapter three). Thus, collating and estimating densities for as many birds as possible is useful in order to calculate population sizes, which can then be used to prioritise conservation efforts.

Calculating densities in the field

Field densities can be calculated through territory mapping and distance sampling (Gregory *et al.* 2004). Territory mapping is generally only used in temperate, well defined study areas which are less than 4 km^2 in size (Bibby *et al.* 2004). Over at least eight visits to a study site, the exact locations and behaviours of birds in the area are recorded. This allows the total number of pairs or territories of each species in the area to be recorded (Svensson 1979). Although this method can produce highly accurate results, it is extremely time consuming (up to seven times slower than other field methods) and only works in small areas with temperate territorial species (Bibby *et al.* 2004). This method is rarely used in the tropics and is inefficient for sampling semi-colonial, non-territorial and non-monogamous species (Gregory *et al.* 2004); alternative field methods must be used for these species.

An alternative field method is distance sampling, performed by carrying out line transects or point counts. Line transects involve travelling along a pre-determined route (a 'line') and recording all the birds present either side of the line. This highly adaptable method suits most accessible open habitats with mobile conspicuous species (Bibby *et al.* 2004) and is used in the UK Breeding Bird Survey (BBS) to gather data on UK breeding birds (Gregory 2000). In comparison, point counts often involve stopping at pre-determined points and recording all birds seen or heard from that point for up to 20 minutes (Jarvinen 1978). This method is used in the North American Breeding Bird Survey (Sauer *et al.* 2014). It is of greater use than line transects in areas that are less accessible, have dense habitat or are populated with cryptic species (Gregory *et al.* 2004). With both line transects and point counts it is essential that distance of the bird from the observer is recorded so population densities can be estimated (Rosenstock *et al.* 2002). Distance can be recorded as an absolute measure or in distance bands. For line transects, distances are estimated perpendicular to the transect, whilst for point counts the radial distance from the point is recorded. A key assumption of distance sampling, in order to get valid and reliable results, is that all birds at distance zero are detected (Buckland *et al.* 2001). Distance sampling calculates bird density, $\widehat{D}$, using:

$$\widehat{D} = \frac{n}{a\hat{P}_a} \qquad (1)$$

where n is the number of birds detected, a is the area covered and $\hat{P}_a$ is the probability of detecting a bird. For line transects a is the length of the transect multiplied by twice the half-width of the line, and $\hat{P}_a$ is calculated by:

$$\hat{P}_a = \frac{1}{w}\int_0^w \hat{g}(y)\,dy \qquad (2)$$

where w is the truncation distance, $g(y)$ is the detection function (y represents a perpendicular distance from the line or a radial distance from the point). For point counts a is the number of points multiplied by the area of the circle around the point (πw^2), and $\hat{P}_a$ is calculated by:

$$\hat{P}_a = \frac{2}{w^2}\int_0^w y\hat{g}(y)\,dy \qquad (3)$$

where w is the truncation distance, $g(y)$ is the detection function (y represents a radial distance from the point). These methods have been described and reviewed in detail elsewhere (Marques *et al.* 2007 and Buckland *et al.* 2008).

Although densities can be estimated through distance sampling, the results can be affected by the accuracy of the observers when identifying and recording the species present. Each observer may judge distances slightly differently, identify species incorrectly or miss individuals entirely. However, it is impossible to have one observer estimate the densities of all the species across the globe, and therefore when comparing densities this must be taken into consideration.

Calculating densities through modelling

In this chapter we collate and estimate densities for all the bird species in the world. This is an impossible task to complete using the field methods outlined above due to the sheer number of species and areas being studied. Therefore, alternative methods must be used which make best use of the density data that are already available and accessible, in order so density estimates can be predicted for the remaining species that have no available data. From an extensive literature search it is evident that no one source exists which brings together all available avian density estimates. It is also very apparent that many species do not have available density data, and therefore densities will need to be estimated for a large number of species.

Missing data can be estimated through imputation methods (Lajeunesse 2013). The aim of imputation is to estimate missing values in a dataset using data from other variables to create an imputed dataset. In multiple imputation this process is repeated several times to produce different imputed datasets (Ellington *et al.* 2015). Statistical analysis can then be run on each dataset, and the results pooled to create a single imputed dataset. There are a range of computational processes and analysis programmes that can carry out multiple imputations, including Multivariate Imputation with Chained Equations (MICE), missForest and Phylopars (Bruggeman *et al.* 2009, Azur *et al.* 2011 and Stekhoven *et al.* 2011). All three of these processes produce similar results. However, adding phylogenetic information (which can be done with phylopars) tends to improve the estimations, since closely related species tend to have similar traits (Pagel 1999 and Penone 2014) and a number of traits have been shown to be influenced by phylogeny (Blomberg, Garland & Ives, 2003). If a high number of values are missing from the original dataset, the accuracy of the imputations is lowered (Ellington *et al.* 2015). Furthermore, a high percentage of missing values means the imputation takes longer to run as it requires more computational power to 'fill in the gaps'. Even with small datasets, imputation can take a long time; imputations are almost impossible to run on datasets with over 20,000 values due to the computational power required (Penone 2014). This is perhaps why the use of imputation methods amongst researchers is currently low (Ellington *et al.* 2015). Consequently, although a promising method, imputation was not used in this chapter to estimate the missing density data. The avian density and trait database used in this chapter was too large and too many missing values across the predictor and multiple potential covariates. Although it has been suggested that the source code of some imputation programmes could be altered to handle larger datasets (Bruggeman, Heringa & Brandt 2009), amending code was beyond the time frame available here and so was not considered.

A simpler, but less robust, approach to estimate missing data, which requires less computational power than imputation, is to build general linear models (GLM) to predict known density values based on potential explanatory variables that are thought to drive avian density patterns. These models can then be applied to species which have no available density data, and density values can theoretically be modelled for each species.

Potential model parameters

Drivers of avian densities include many abiotic and biotic factors, which can operate at different spatial scales, but not all of these can be easily modelled (Zhang *et al.* 2015). For example, nest site availability can affect the density of birds but this information is hard to quantify and include in a model (Newton 1979). However, other factors such as body mass, habitat preference and feeding guild can all be easily measured and thus included in models. Body mass has shown to be related to population density, as predicted from allometric scaling laws (Jarman 1974). An inverse relationship between body size and population density has been demonstrated for a number of animals (e.g. Peters & Wassenberg 1983), including birds (Juanes 1986). However, the relationship is weaker in birds than in other animals suggesting further factors contribute to their density patterns (Juanes 1986). One such factor could be habitat preference. There is some evidence to suggest that in general wetland habitats have higher densities of birds than drier habitats (Hinojosa-Huerta *et al.* 2008). Similarly, bird densities in urban habitats are generally lower than in natural landscapes (Fuller *et al.* 2009). However, there are exceptions to these rules, some species have higher densities in drier habitats and some species react positively to human influence (Loe *et al.* 2007).

Latitude also influences density patterns: tropical regions have higher densities of birds than temperate regions (McArthur 1965). However, recently it has been shown that avian species are shifting their populations, and therefore their densities, towards the poles due to the changing climate (Lehikoinen *et al.* 2016). We would therefore expect the densities of birds in these northern latitude regions to increase as the climate warms, whereas the density of birds in tropical regions to potentially remain constant or even decrease.

The normalised differences vegetation index (NDVI), a measure of plant greenness/ photosynthetic activity of an area, could also contribute to bird density patterns. A high NDVI indicates greener areas, which we would assume to have higher resource availability (e.g. nest material and sources of food) than areas with a lower NDVI. We can therefore hypothesise that areas with a high NDVI can support a higher density of birds (Pettorelli *et al.* 2011).

Species richness of an area may also influence the density of individual populations: areas with a high species richness may be unable to support high densities of any one species due to narrow individual species niche breadths. Conversely, areas with lower species richness may be able to support higher densities of a species due to reduced inter-specific resource competition (McArthur 1965). The actual species present in an area can also affect the density of other species in the same area through potential roles as facilitators, competitors and predators. This is particularly true for predatory birds, whose presence in an area can reduce the density of prey species (Kosicki *et al.* 2015). Similarly, the feeding guild a species belongs to can also influence its density. For example, due to resource availability, carnivorous birds generally have lower densities than birds whose food source is more abundant, such as granivores or insectivores (Redpath *et al.* 1997). A final potential contributor to species densities is phylogeny, as closely related species tend to occur at similar densities (McArthur 1965).

Aims

The aim of this chapter is to predict population densities for all birds in the world. This will first involve compiling a database of trait data (such as body mass, feeding guild and habitat preference) and collating all density data that are already available, so GLMs can be created. Once densities have been estimated through GLMs, the results will then be analysed by comparing them to field density data. Densities will also be analysed on a global scale, across habitats and across feeding guilds to gain a deeper understanding of patterns in avian densities.

Methods

Compiling bird density estimates

Following the BirdLife Taxonomic Checklist v7.0 (BirdLife International 2014) an initial database was created with 10,455 accepted bird species (for the purpose of this thesis, subspecies were not included). An extensive literature search was then carried out to record all field density estimates for each bird. In total, 7,672 densities were recorded for just under 3,000 species. These estimates were collated from several sources of information: 1,719 were obtained from personal communication with Stuart Butchart at Birdlife International; 1,291 from the Handbook of Australian, New Zealand and Antarctic Birds (Higgins *et al.* 2006); 1,016 from the Handbook of the Birds of the World (del Hoyo *et al.* 2014); 312 from Birds of North America (Rodewald 2015); 283 form Birds of the Western Palearctic (Snow *et al.* 1998); 189 from Roberts Birds of Southern Africa (Hockey *et al.* 2005); 140 from unpublished point and line transect data from the Conservation Ecology Group, Durham University; and 24 from Holmes and Sherry (2001).

All estimates were collated, and if estimates were given as a range, these were recorded as the minimum and maximum densities of the species. All density estimates were converted into ‘individuals per km^2’, with any densities recorded in ‘territories or nests per km^2’ converted into ‘individuals per km^2’ by doubling the estimate. This follows the example outlined in many papers, for example see Juanes (1986) paper.

When species had more than one density estimate from more than one source, means and medians were calculated. Standard deviation, standard error of the mean (*sem*) and the absolute minimum and maximum density values were also recorded for each species.

All seabirds were removed from the dataset as most breed colonially and their distribution is dependent primarily upon non-terrestrial factors. Similarly, all colonial and semi-colonial nesting species were removed from the analysis in order to avoid skewing the density estimates, which could consequently cause model interference (Coulson 2001). Seabirds and colonial/ semi-colonial birds were defined using the classification system used by BirdLife International in their World Bird database, this classification is based on expert judgement. This resulted in a total of 9,025 species present in the database for further analysis.

Potential predictors of breeding bird densities

The following continuous explanatory variables were compiled as potential predictors of breeding bird densities: body mass (logged), breeding range latitude (recorded as the centre point of a species' breeding range), the mean annual NDVI across the breeding range, the mean breeding bird species richness of one degree cells within the breeding range and species generation length. The following potential categorical predictors of bird densities were also compiled: the taxonomic family to which a species belonged to (as a proxy for phylogeny), the feeding guild of each species and the primary habitat preference for each species.

These life history traits were acquired from several sources. Adult body mass was gathered from Birdlife International (2014), Tacutu *et al.* (2013) and Lislevand *et al.* (2007) (details on whether body mass data were from male or female birds was not available). Generation length was also gathered from Birdlife International (2014). Mean NDVI for half degree cells were compiled from the Global Inventory Modelling and Mapping Studies (GIMMS) dataset from the Global Land Cover Facility (Tucker *et al.* 2004 and Carroll *et al.* 2006). This dataset is an average of the monthly NDVI data from 1982-2002, with NDVI being calculated across each species' range extent. Mean species richness was calculated by gridding species range data from BirdLife International (2016), and then calculating the average richness of one degree cells within the breeding range. The centre point of species breeding ranges were calculated by finding the intercept of the mid-latitude and mid-longitude of each species range by mapping species distribution data from BirdLife

International (2016). Breeding distribution polygons were mapped using R statistical software. Polygons were overlaid onto a world habitat map (using a 10% minimum overlap threshold), and for all 50km grid cells within a species range it was assumed that any cell which contained suitable habitat was occupied. . Feeding guild data was collected from Birds of the World Online (del Hoyo *et al.* 2014), Breeding birds of North America (Rodewald 2015) and from Roberts Birds of Southern Africa (Hockey *et al.* 2005). Habitat preference data were collated from Birds of the World Online (del Hoyo *et al.* 2014), and standardised using the IUCN habitat classification scheme (IUCN 2012). When any of these traits had multiple values an average mean value was used. For categorical data, the value that was most common or most reliable was used.

In total, all species had data for order, family and habitat preference, 8,525 species had generation length data, 7457 species had mean species richness data, 7,390 species had centre point of breeding range data, 7,107 species had mean NDVI data, 7,044 species had feeding guild data and 6,966 species had body mass data. For some of these traits we were not able to use all the available data due to unresolved nomenclature mismatches. In total, 1,799 species had complete datasets, including an estimated field density value, and hence these were the species which were used to create the GLM to predict the densities for the remaining species.

Predicting avian breeding densities

To predict breeding bird densities, we used generalised linear models (GLM). These were run in R using the ‘glm’ function. The extracted density estimates were logged, resulting in a Gaussian distribution of log-density estimates. Model selection was performed to estimate densities from the assembled explanatory variables using the ‘dredge’ function in the R Package ‘MumIn’ (Barton 2016). The dredge function builds all possible model combinations from the candidate set of explanatory variables, and selects the most parsimonious models using the Akaike information criterion (AIC) (Barton 2016). Only species which had a full complement of explanatory variables and at least one density estimate were included in the model (n= 1,799). For each GLM, the most parsimonious model was considered to be the one with the lowest AICc value (Burnham *et al.* 2002). The ‘predict’ function was then used to predict the density values for all the species from this ‘best’ model.

To gain a better understanding as to whether these traits could predict densities more accurately for some types of bird species, the data were also split into several different biological subsets and a GLM was run on each of these subsets in turn. These subsets included: passerines and non-passerines, tropical and temperate species, and a further series of subsets for species associated with each primary global habitat type. Tropical and temperate species were defined by the mid latitude of their distribution; any species with mid-distributions between 23.5° N and 23.5°S were classed as tropical species, whereas any species with mid-distributions between 23.5° N to 66.5° N and 23.5° S to 66.5° S were considered to be temperate species.

Maps were also produced in R to understand how the field densities and modelled densities varied globally. To do this, the breeding distributions of species were mapped globally (at 0.5 degrees resolution), and the presence or absence of each species in each 50 km grid cell of the world was recorded. These were then combined to obtain a complete record of which species occurred in each cell. Initial maps were produced to show the percentage of species in each grid cell with a density estimate. Subsequent maps were then produced to show the total density and mean density of all avian species in each 50 km grid cell. Total densities were calculated by summing the densities for all species present in each grid cell, and mean densities were calculated by finding the average densities for all species present in each cell. Separate maps were produced for field and modelled densities.

Results

After an extensive literature search a total of 7,672 density estimates were identified for 2,942 species (28% of all bird species). After removing colonial nesting birds and seabirds 7,047 density estimates remained for 2,719 birds (30% of all the remaining species). These density estimates varied greatly both between species and within species. For example, one species with one of the smallest density estimates was the Tawny Eagle (*Aquila rapax*), whilst one species with one of the largest density estimates was the Red-billed Quelea (*Quelea quelea*). One species which had a large range of density estimates was the Grey Shrike-thrush (*Colluricincla harmonica*) which ranged from 2 birds per km^2 to 125 birds per km^2.

Density estimates were available for at least 20% of species in most orders, though coverage varied amongst orders (Figure 1). The orders Leptosomiformes and Opisthocomiformes had no density data available for any species. By contrast, density data were available for all species in the Coliiformes order. The passerines, which are by far the largest order of birds, had density data for approximately 30% of their species.

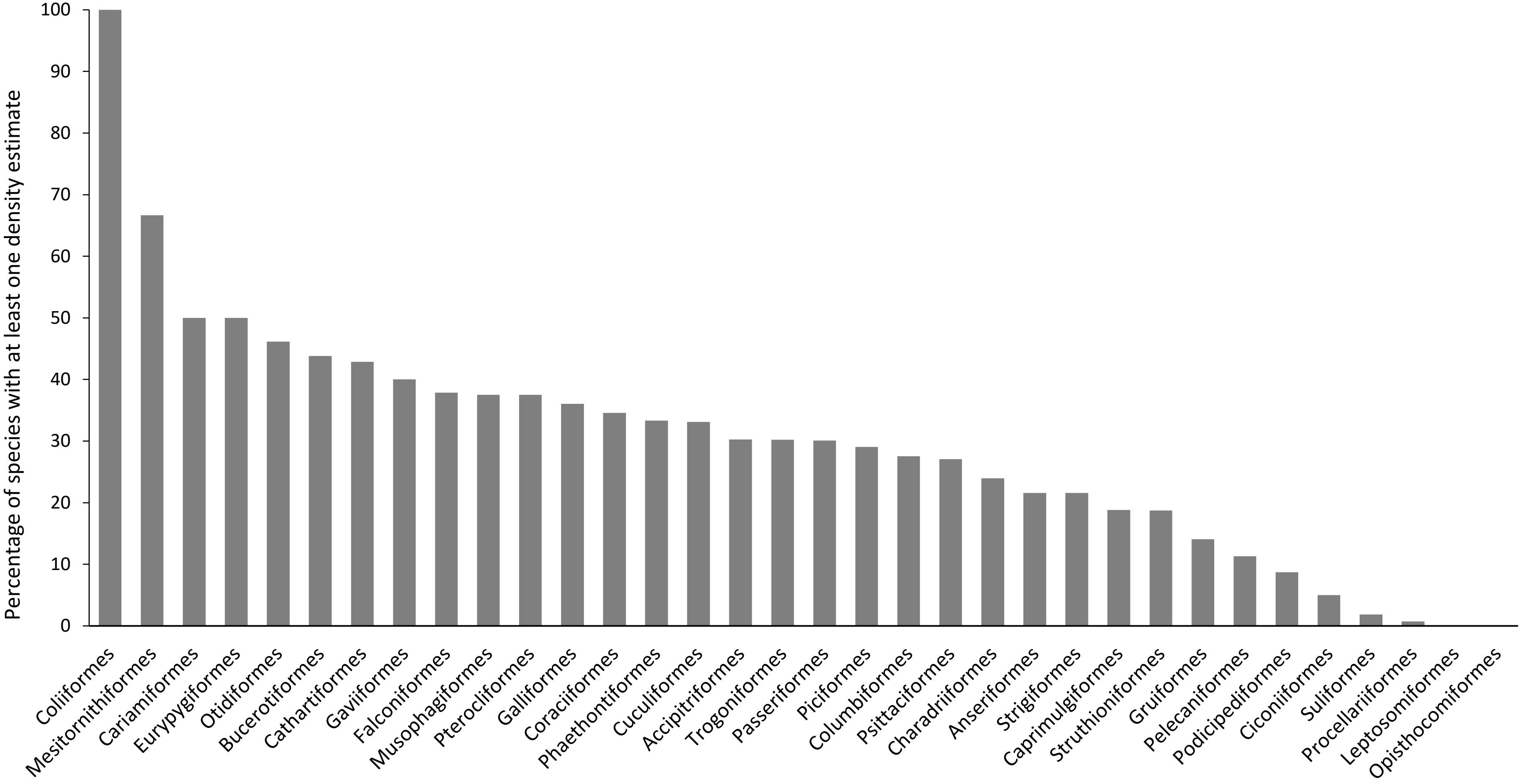


Figure 1: Percentage of species in each order with at least one recorded density estimate.

The number of species with field density data varied across the world (Figure 2A). Areas of low avian diversity, such as Greenland, had a high percentage of species with a density estimate. In contrast, areas of high biodiversity were more likely to have missing data, and thus have a lower percentage of species with density data. However, some biodiverse areas, notably parts of southern Africa and northern South America contained a high proportion of species which had field density estimates. This reflects regions of more intensive ornithological study but also regions for which density data have been collated in summary literature (Hockey *et al.* 2005 and Rodewald *et al.* 2014).

Due to the mismatch in data availability across the globe and since only 28% of species had available field density data, total densities across the globe were not calculated for the field data, as valid comparisons between areas would not have been possible. However, average avian densities were calculated across the globe using the field density data, as these are less sensitive to missing data. These averages differed across the globe. For example, birds found in Madagascar, parts of north-west Europe and the eastern half of North America were more likely to occur at higher densities than birds found in South America and northern Africa (Figure 2B).

A)

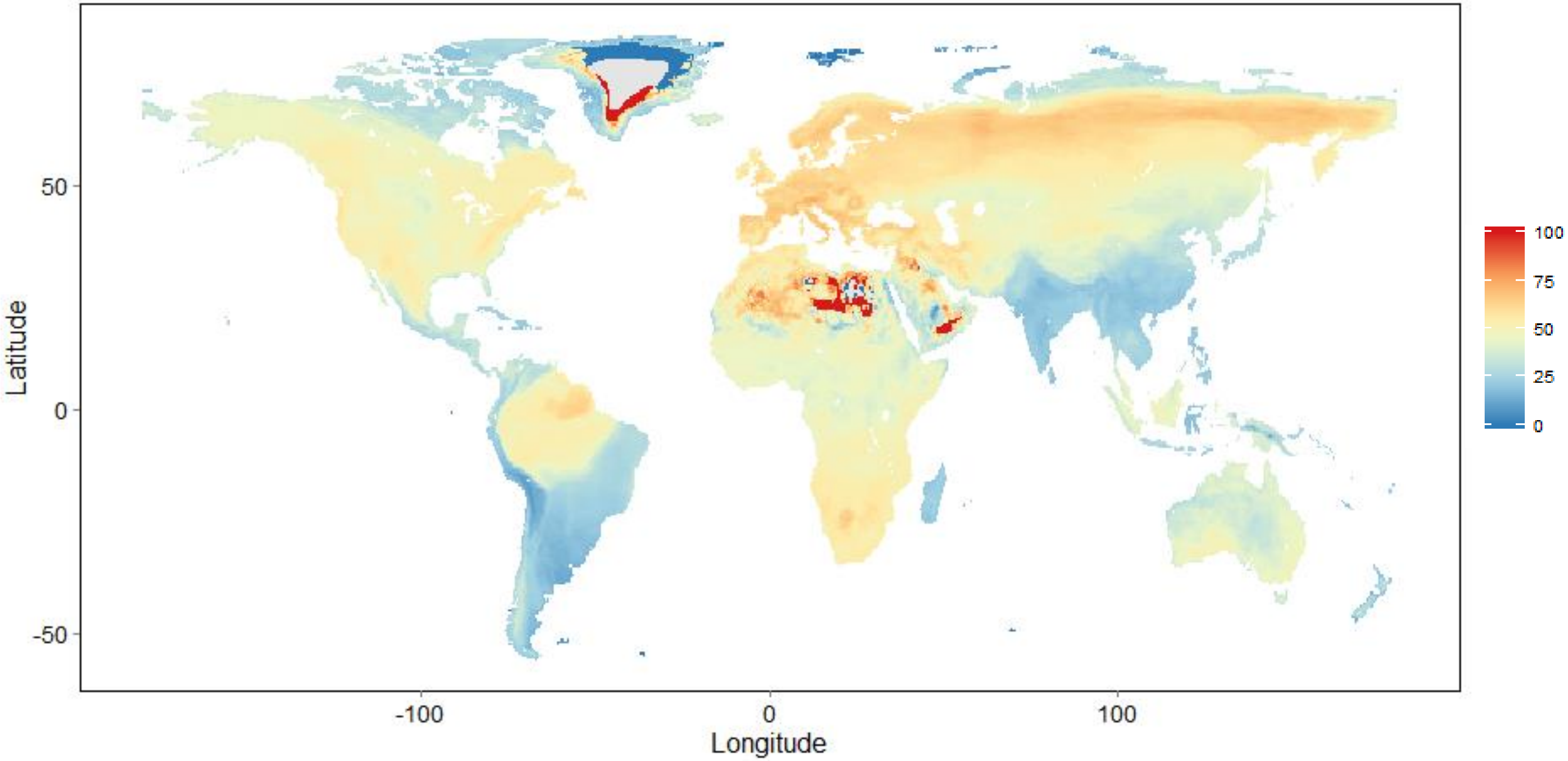


Figure 2A: The geographic distribution of the field density data. A) The percentage of all species occurring within each 0.5 degree terrestrial grid cell which had at least one recorded field density value.

B)

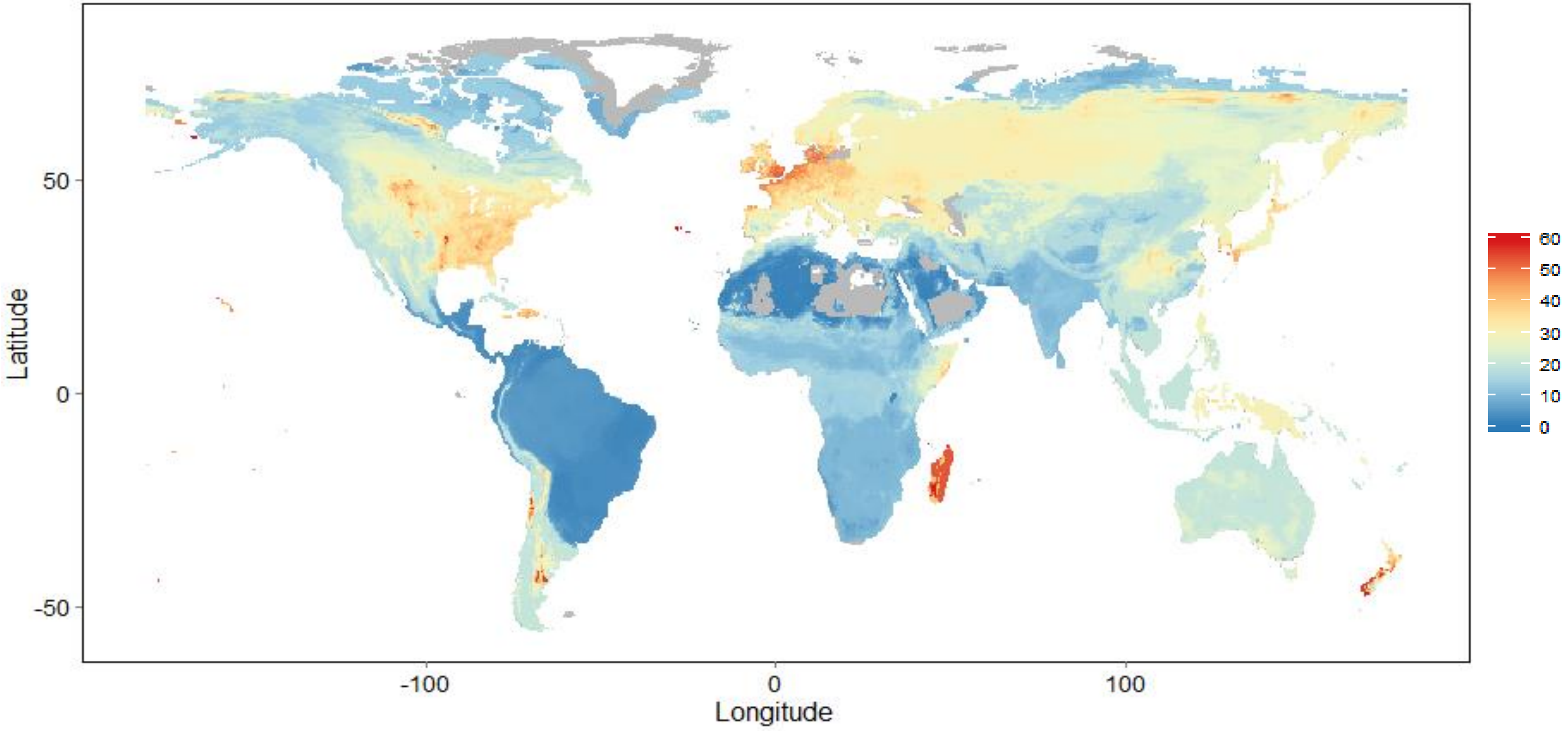


Figure 2B: The geographic distribution of the field density data. B) Median density (birds/km^2) for all species (which had a field density estimate) occurring in each 0.5 degree grid cell.

Densities were estimated for 8,541 species. Note, it was not possible to predict data for 484 species, as these species had categorical data which were not present in the original dataset used to create the GLM, and therefore they could not be modelled. The model with the lowest AICc value, and therefore the model that was used, included the predictors: body mass, family, mean NDVI, mean species richness and primary habitat type (Table 1).

Table 1: Performance of the GLM with body mass, taxonomic family, taxonomic order, mean NDVI, mean species richness and habitat type as predictors for population densities.

Model	**DF**	**Log-Likelihood**	**AIC$_C$**	**Delta AIC$_C$**
Body mass + Family + Mean NDVI + Mean species richness + Habitat type	146	-1168	2655	0.00
Body mass + Family + Order + Mean NDVI + Mean species richness + Habitat type	148	-1154	2667	1.83
Body mass + Family + Order+ Mean NDVI + Generation length + Mean species richness + Habitat type	148	-1132	2669	2.03

There was a positive correlation between field densities and their respective modelled densities calculated from the GLM (R^2= 0.37) (Figure 3). Although the modelled density values of some species laid within the range of field densities recorded for that species, many species had modelled estimates which were considerably higher or lower than their field density values. Comparing modelled and field densities amongst certain groups of species highlighted that the model performed worst for passerines (R^2= 0.27) (Figure 4), temperate species (R^2= 0.34) (Figure 5) and bare area species (R^2= 0.29) (Figure 6). However, it performed better for tropical species (R^2= 0.47) and forest species (R^2= 0.42) (Figure 6).

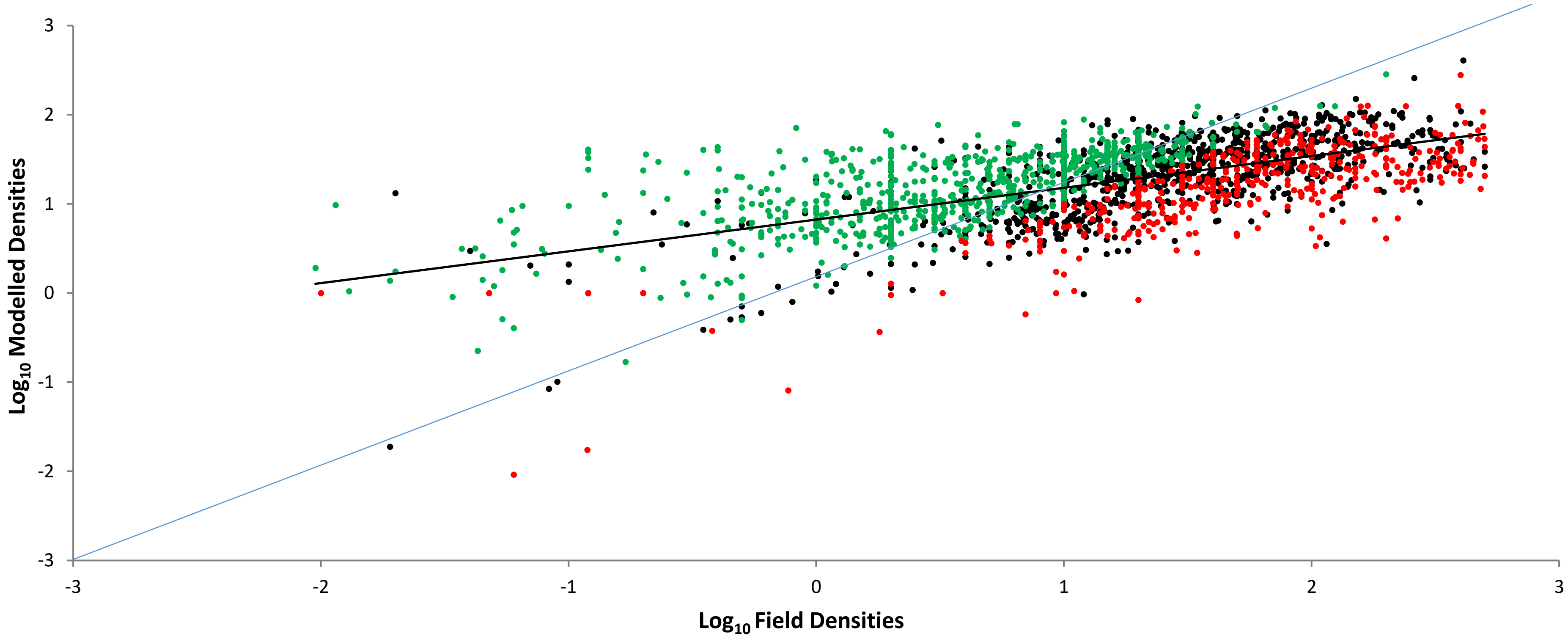


Figure 3: Median field densities for each species plotted against their respective modelled densities from the GLM. Black points represent species whose modelled density value lies within the range of field density estimates for that species. Green points represent species whose modelled density value is greater than the maximum recorded field density value for that species. Red points indicate species whose modelled density value is less than the absolute minimum field density value collected for that species. The black line represents the best fit line of all the data ($R^2 = 0.39$), whilst the blue line represents a line of $\log_{10}$ modelled densities = $\log_{10}$ field densities.

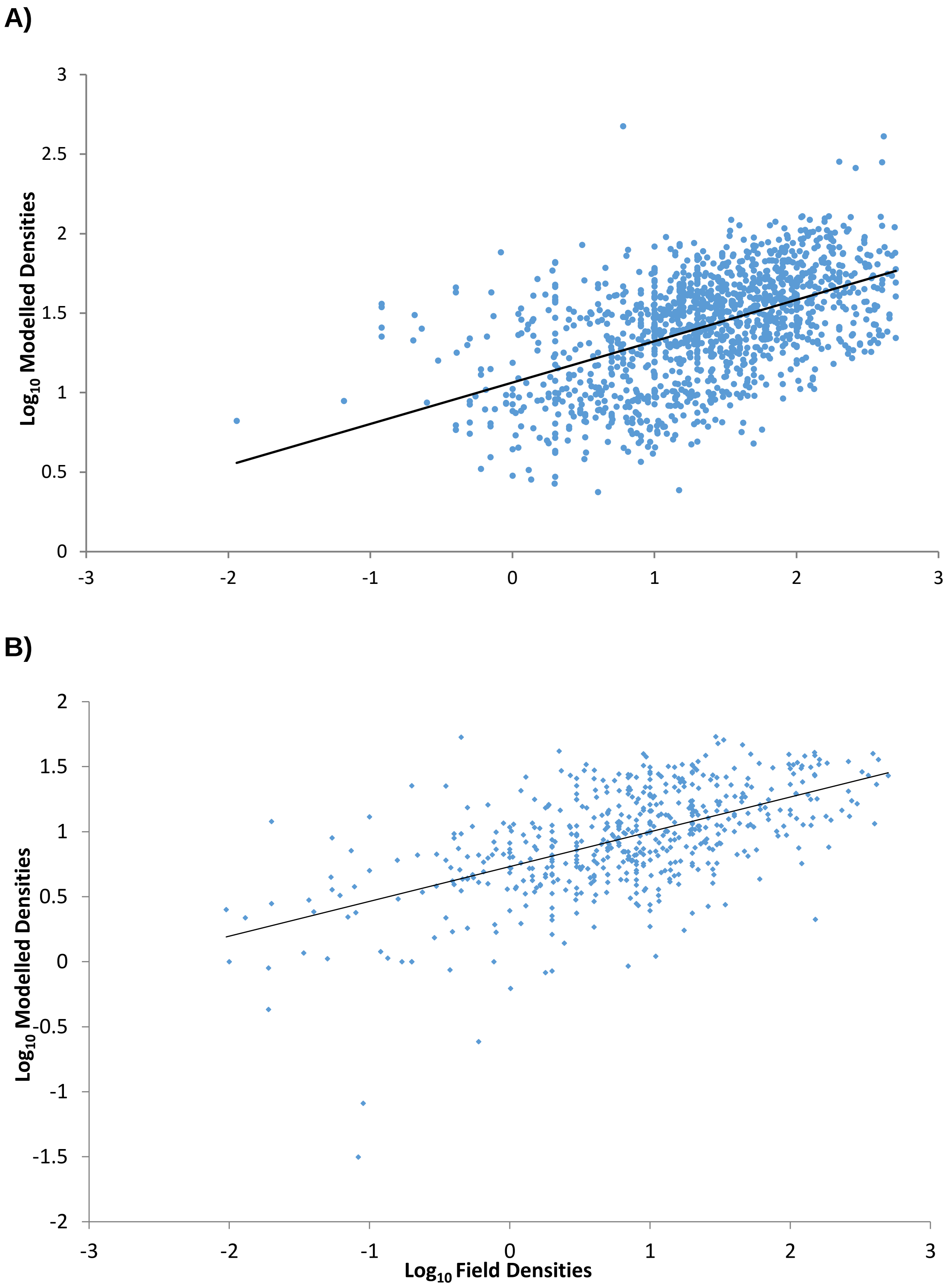


Figure 4: Modelled densities from the GLM against each species respective field density estimate, grouped into passerines and non-passerines. **A)** Passerines, $R^2 = 0.27$. **B)** Non-passerines, $R^2 = 0.31$.

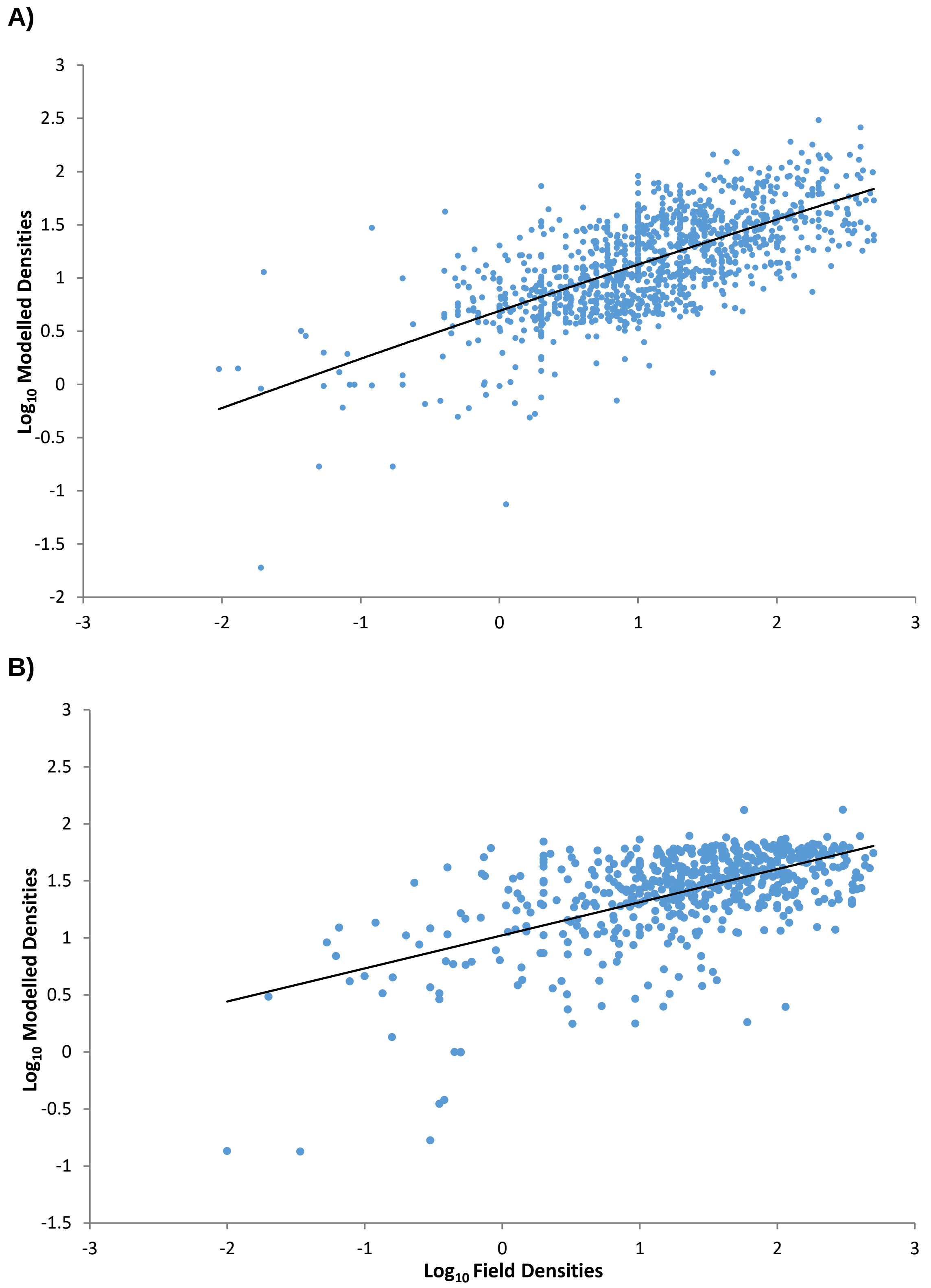
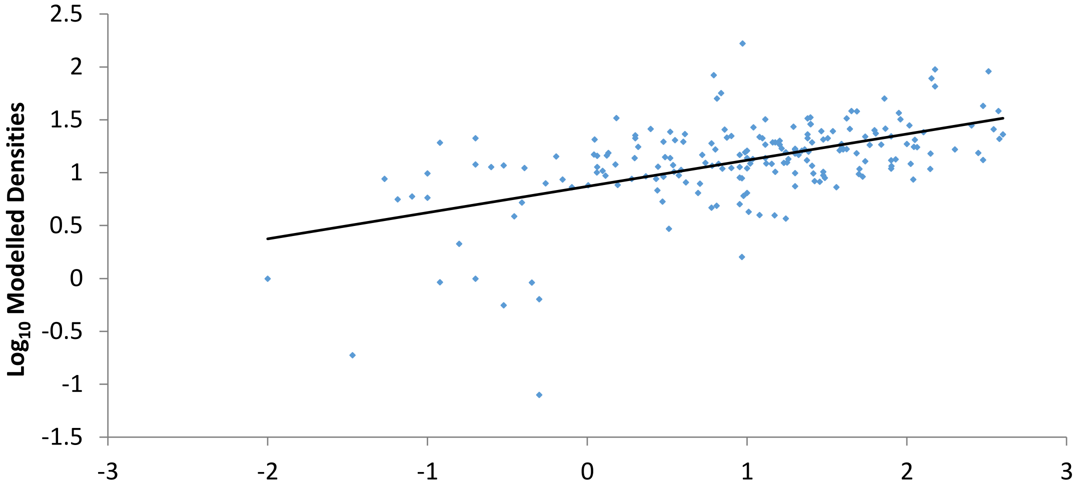


Figure 5: Modelled densities from the GLM against each species respective field density estimate, grouped into tropical and temperate species, as defined by the mid latitude of their distribution. **A)** Tropical, R^2 = 0.47. **B)** Temperate, R^2 = 0.34.

A)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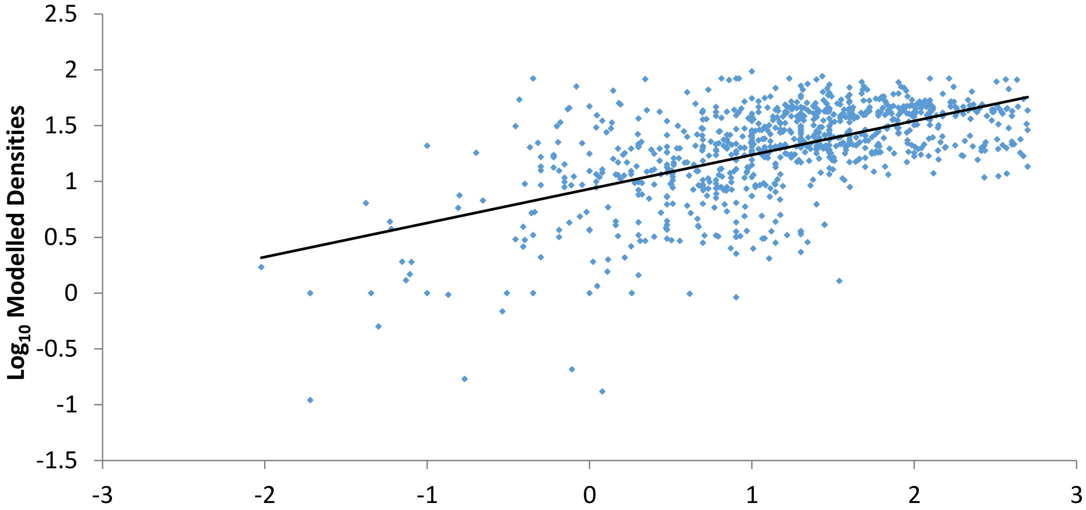
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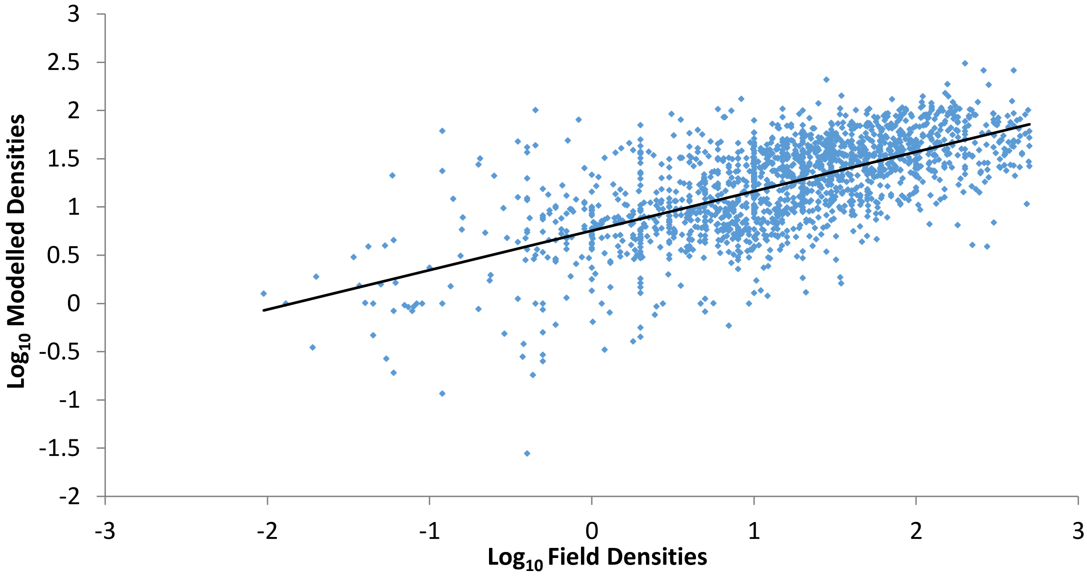
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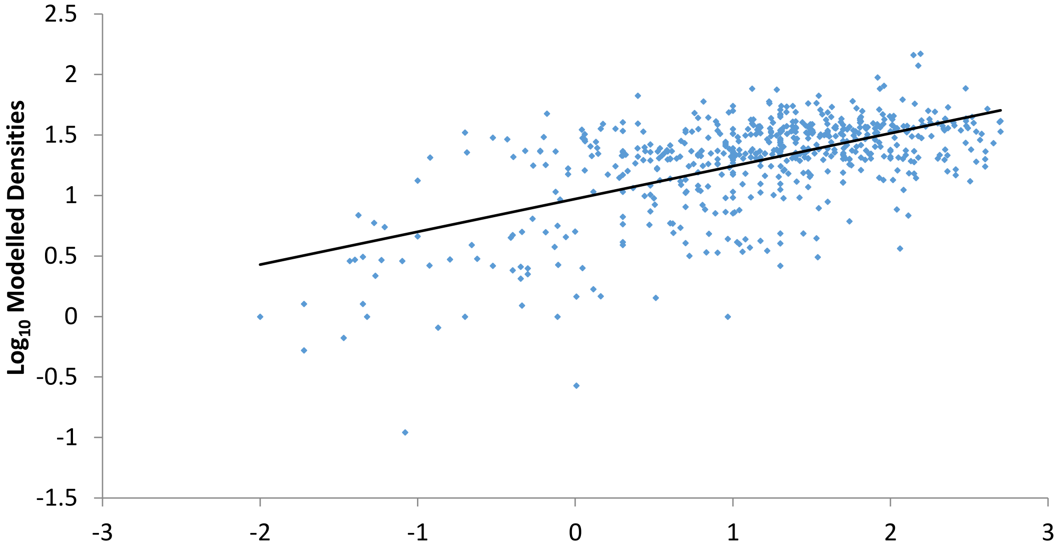
D)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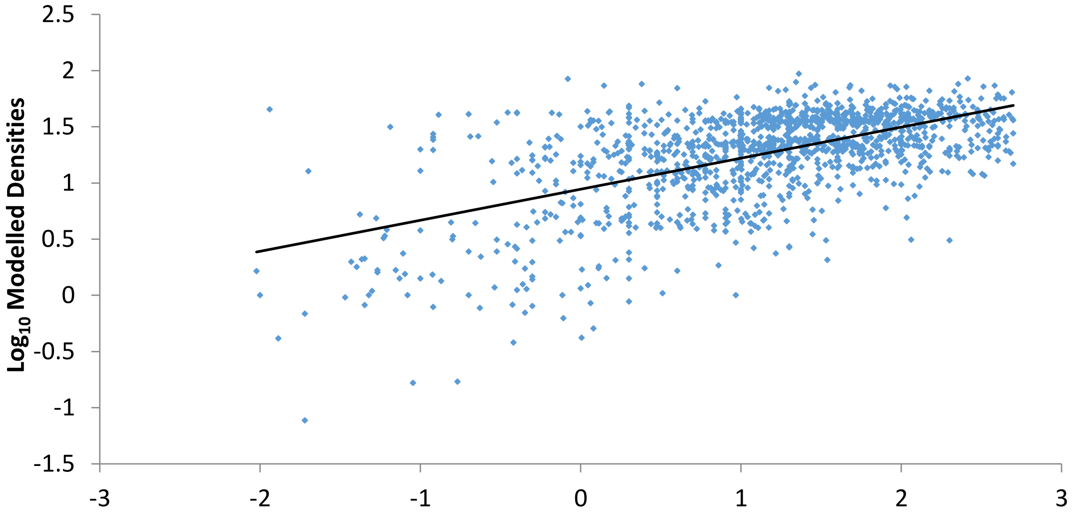
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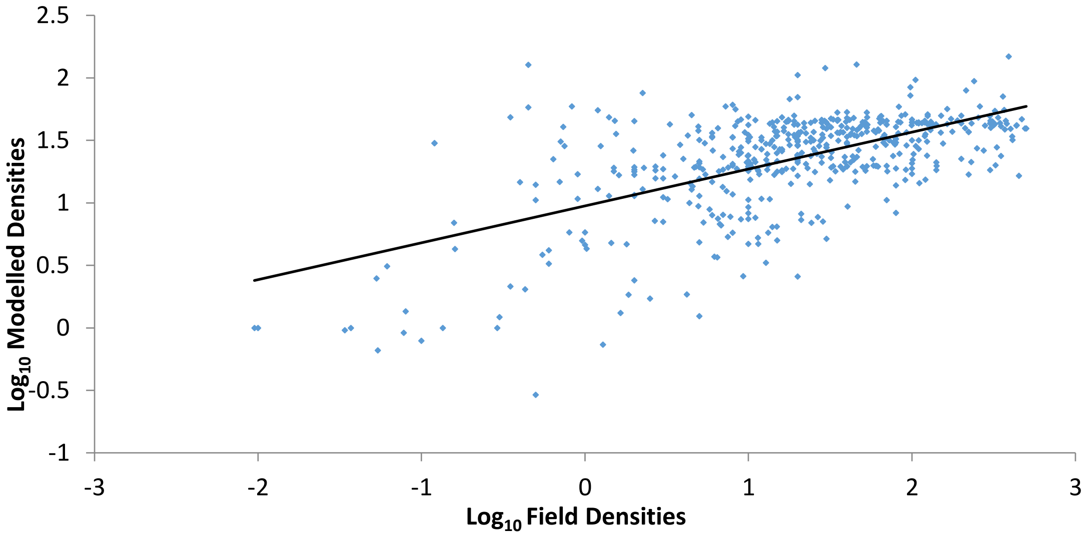
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G)

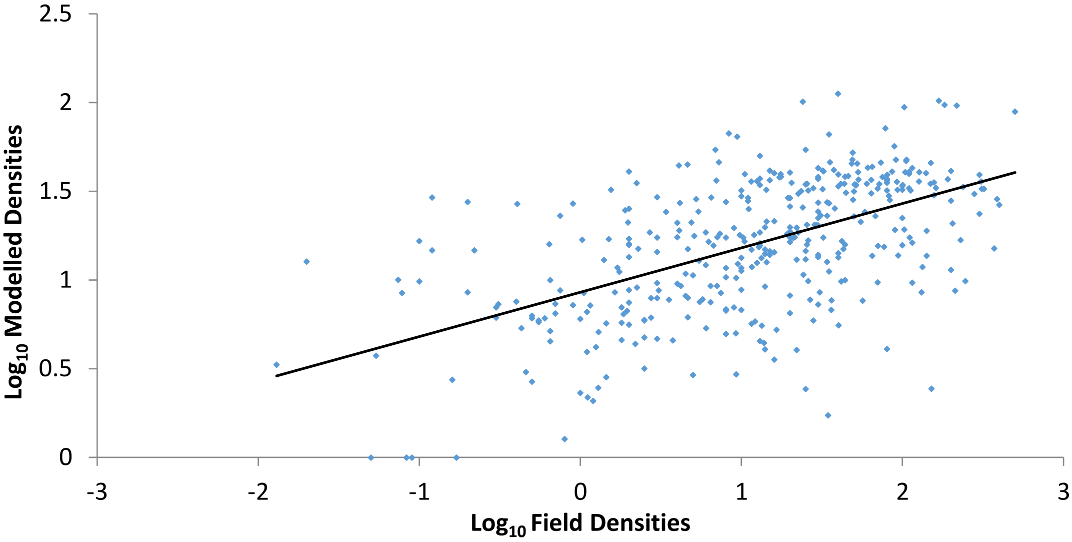

Figure 6: Modelled densities from the GLM against each species respective field density estimate, grouped by habitat preference. **A)** Bare area species, R^2 = 0.29. **B)** Cropland species, R^2 = 0.33. **C)** Forest species, R^2= 0.42. **D)** Grassland species, R^2= 0.35. **E)** Shrubland species, R^2= 0.34. **F)** Urban area species, R^2= 0.37. **G)** Inland water species, R^2= 0.31.

The GLM produced estimated modelled densities for many species which had no prior field density measurements: almost all regions had density data for over 75% of their avian inhabitants (Figure 7A). In parts of northern Africa population densities were modelled for every species in that cell. However, this is most likely due to a low number of species occurring in that area (Figure 7A). In contrast, the Arctic had modelled densities for fewer than 50% of its species (Figure 7A). In general, modelled densities were lower than field densities (for example Figure 2B versus Figure 7C).. The total modelled densities of birds in the Albertine rift area, east Africa and Southeast Asia were high compared to the rest of the world (Figure 7B), however the average densities in these areas were not higher compared to other parts of the world (Figure 7C), suggesting these areas are very species rich, but that each species occurs at low densities.

A)

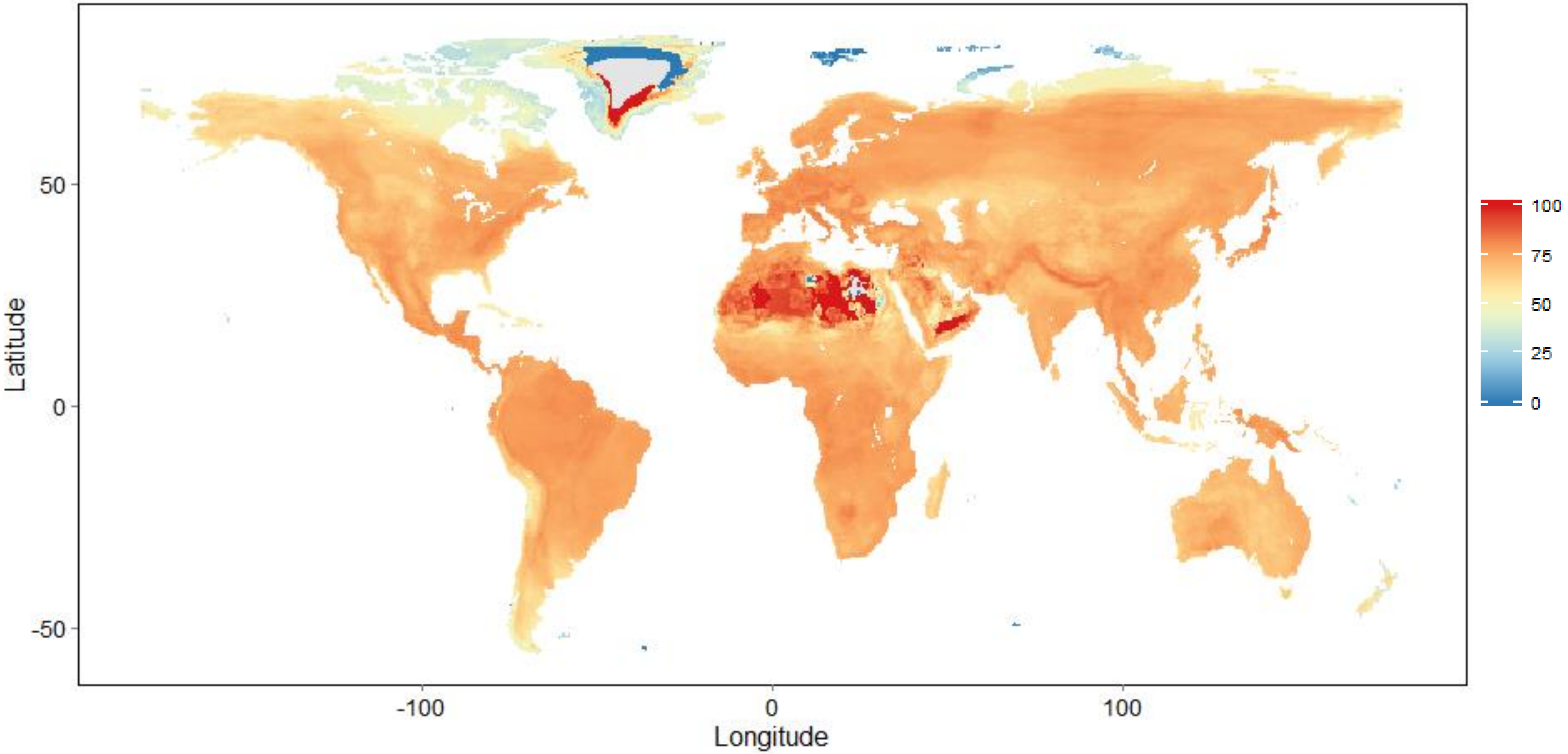

Figure 7A: The geographic distribution of the modelled density data. A) The percentage of all species occurring within each 0.5 degree terrestrial grid cell which had at least one recorded modelled density value.

B)

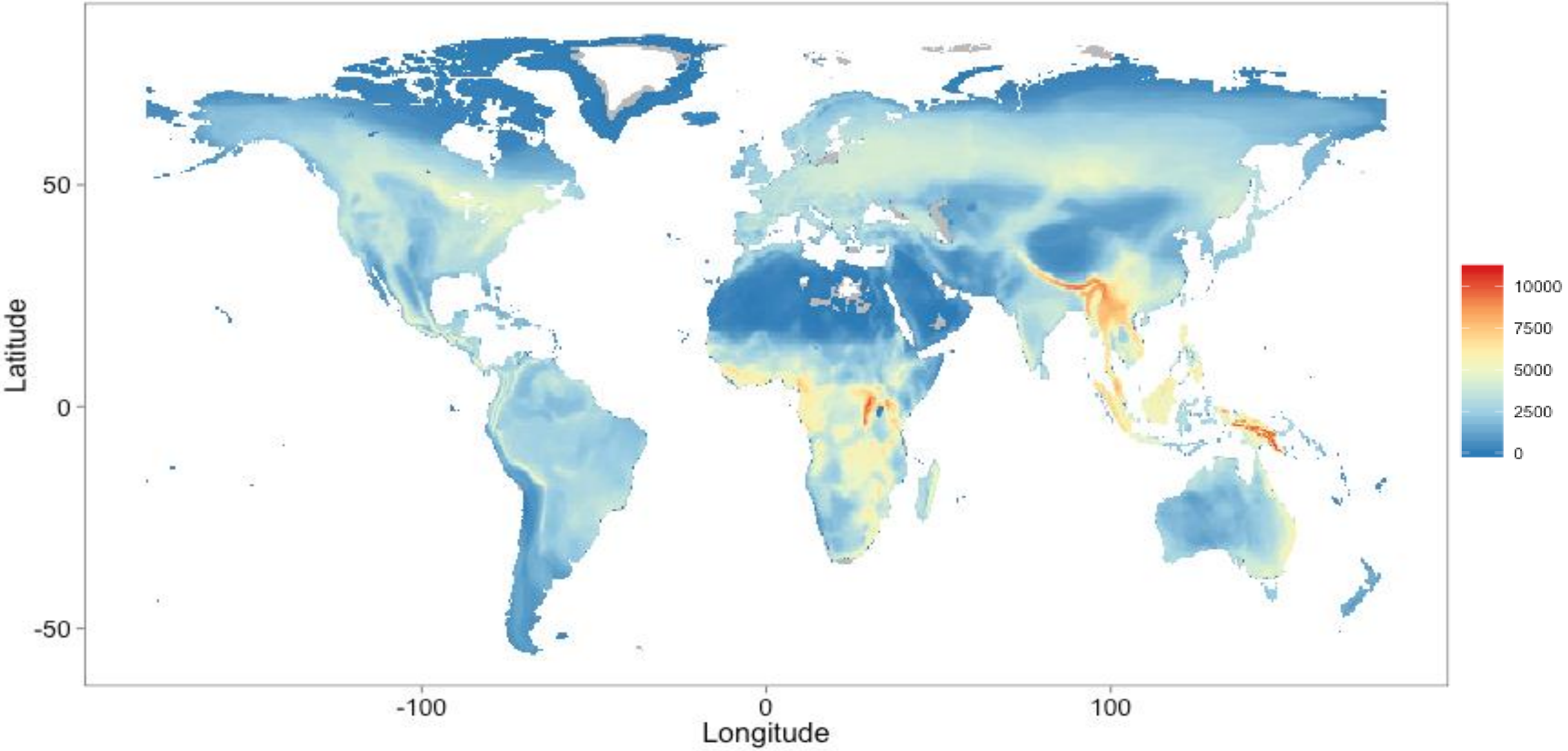

Figure 7B: The geographic distribution of the modelled density data. B) Summed density values (birds/km^2) for all species (which had a modelled density estimate) occurring in each 0.5 degree grid cell.

C)

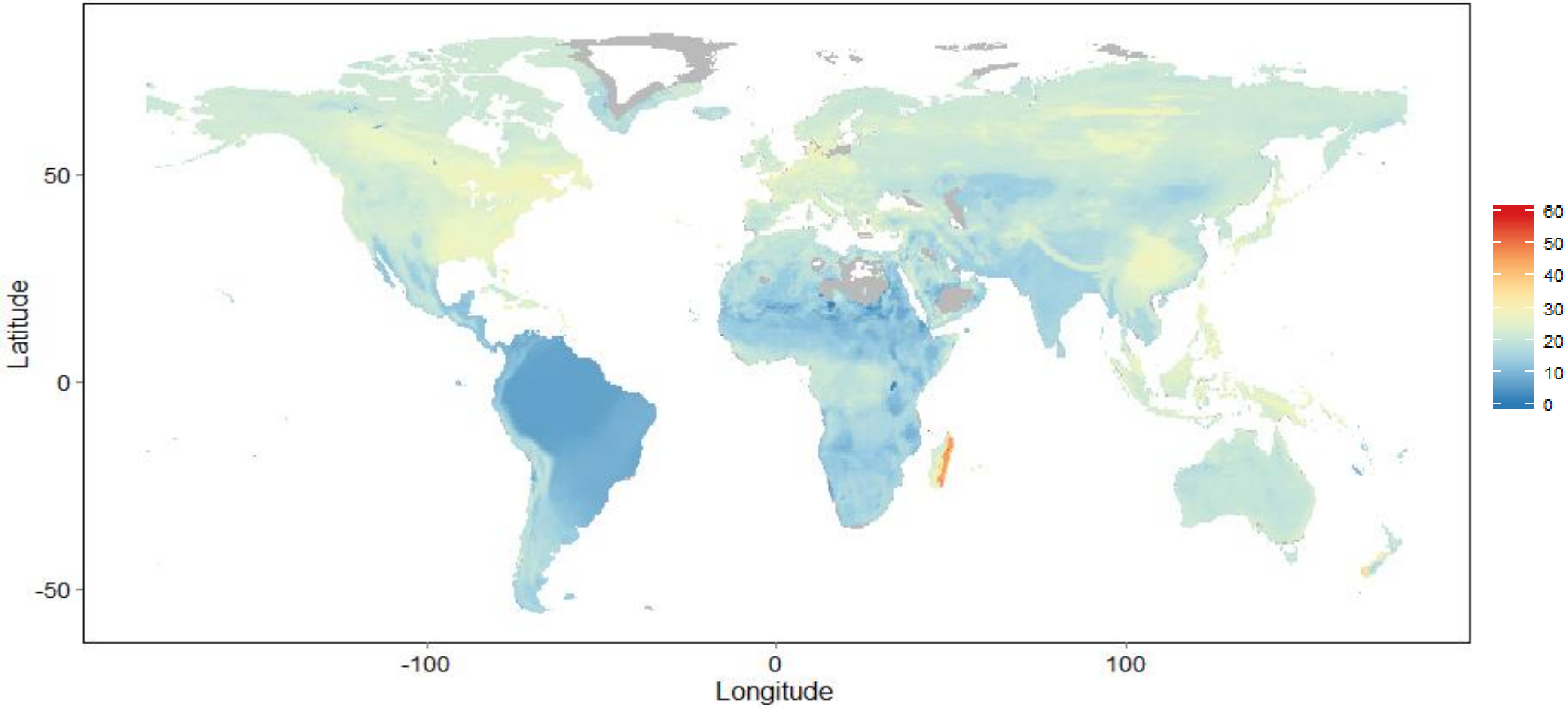

Figure 7C: The geographic distribution of the modelled density data. C) Median density (birds/km^2) for all species (which had a modelled density estimate) occurring in each 0.5 degree grid cell.

Discussion

Overall, we were able to gather field density estimates from the literature for approximately 30% of all avian species. This was considerably fewer than expected, however, there are a number of reasons why this number could be so low. For example, it is likely that density data collection is a secondary goal in many research projects. This may be due to the time consuming and logistically challenging nature of recording densities in the field. It is highly probable that more density estimates exist, but because they remain unpublished or are included in individual species papers, they are difficult to collate without much more time and resources.

Although we were only able to collect estimates for 30% of avian species, it is still possible to analyse these data to see if they provide any useful insights for future research or conservation. Initial analysis highlights which species are well studied, typically those with multiple density estimates. Eight species each had over 30 different density estimates from multiple sources. These were the Ground Parrot (*Pezoporus wallicus*), the Grey Fantail (*Rhipidura fuliginosa*), the Striated Thornbill (*Acanthiza lineata*), the Black-faced Cukooshrike (*Coracina novaehollandiae*), the Grey Shrike-thrush (*Colluricincla harmonica*), the Australian Magpie (*Gymnorhina tibicen*), the Rufous Whistler (*Pachycephala rufiventris*) and the Spotted Pardalote (*Pardalotus punctatus*). These species are likely to be so well studied due to either having wide distributions, being ecologically interesting or because they are of conservation concern. Knowing the species that have multiple density estimates is useful as it implies that we don’t need to focus research efforts on these species, and instead should focus on gathering data for those with no data. This is especially true if these species are rare or of conservation concern.

We can also look at geographical areas which are well studied in terms of avian densities (Figure 2A). A high proportion of birds in Europe and north America have available density data; this is most likely due to these regions having a high number of professional and amateur ornithologists, and are therefore more likely to have the resources needed to collect density estimates. In contrast, biodiversity hotspots such as Madagascar, the Atlantic forest and Indo-Burma, have very low numbers of species with recorded data. These areas have been designated as important areas to conserve since they contain a high number of endemic species, making the lack of data concerning. It is therefore important we know the density of bird species in these areas to enable improved conservation of these areas and the species within them.

Looking at the median field densities across the globe (Figure 2B), it is evident that Europe and North America have relatively high median densities. This is somewhat surprising as these regions have large areas of agricultural land and frequently experience anthropogenic disturbance, so we would therefore expect this to result in low median densities. However, these relatively high median densities could be due to observation bias in the field data we have collected, i.e. species that occur in non-disturbed habitats are over represented in the literature and therefore densities are higher than expected. In contrast, South America has considerably lower median densities (despite having approximately the same percentage of species with field density estimates as Europe and North America, Figure 2A). This is likely to be because species richness is very high in this area and therefore species can only occur at low densities.

It is also important to consider the effectiveness of the generalised linear model (GLM) in predicting density data for the remaining 70% of species. Overall, the model used was able to predict densities for nearly all these species (Figure 7A), with approximately 40% of the variation in the modelled density values explained by the linear trend (Figure 3, R^2=0.39). This suggests that other explanatory variables not included in the model are contributing to the population densities of birds. This could include variables such as nest availability and presence of predators. However, as no reliable data are available for these variables across the extent of the species studied, it was not possible to include these in the GLM. Although a weak correlation was found, this is expected as it is near impossible to predict variables such as these with a high level of accuracy. Furthermore, despite being unable to predict perfect density estimates for the majority of species, there were a number of species which we were able to model a density estimate for within their range of field density estimates (Figure 3); this model clearly works for some species. For species which do not have a range of field density estimates it is difficult to judge the accuracy of the modelled estimates, as it is possible that the solitary field estimate is not representative. This may be particularly true if some single estimates of field density data come from the highest quality site for a species, such as within protected areas.

Considering specific groups of species, we found that the model performed best for tropical species (Figure 5A, R^2=0.47) and forest species (Figure 6C, R^2= 0.42). This indicates that the explanatory variables used in the model were slightly better predictors or were more well defined for these two groups of species. Therefore, when analysing these results we can be more confident in the accuracy of the modelled densities for tropical and forest species.
Across the globe, the modelled densities varied less than the field density estimates (for example compare Figure 2B to Figure 7C). This could be a cause for concern, as less differentiation in the density data could be an indication that we are losing or masking important and interesting variation, which could ultimately hinder conservation efforts. Alternatively, this could better reflect the true variation in densities. For example, in Europe and North America, the median modelled densities were significantly smaller than the median field densities (Figure 2B versus Figure 7C). However, this is more in line with what we would expect given the high levels of anthropogenic disturbance across Europe and North America.

Reliability and validity of the model

In addition to interpreting the results of the GLM, it is also important to consider the reliability and validity of the model in order to understand the credibility of the results. A major caveat of the model is that we are most likely predicting too many density estimates. Research has highlighted that you can only accurately predict missing density data if there are less than 60% of the values in the original dataset missing, and the more values that are missing the lower the accuracy of predicted data (Penone *et al.* 2014). In the dataset used, over 70% of species were missing density data, and many were also missing data for a number of explanatory variables. This will have reduced the accuracy of the predictions the model made, which therefore reduces the reliability of the results and conclusions.

It could also be argued that there are biases in the data that are missing. For example, species could have limited life history trait data because they occur at low densities or are inconspicuous and hard to study, therefore meaning they are more likely to be missing from our model. This biases the model towards species which are easier to study and therefore skews the results. Furthermore, due to time constraints it was not possible to look at every monograph for every area of the world; some areas and species within those areas could thus be underrepresented in the data. This introduces bias towards species that occur in the areas that were specifically investigated. These biases in the missing data are likely to decrease the variability in the datasets and will thus lower the variability in our modelled estimates, which will consequently lower the accuracy of the results (Nakagawa *et al.* 2008). If we compare Figure 2B to Figure 7C, we can see that variation in median densities across the world has been lost, which may be a result of this issue.

We could also question the accuracy of the data used within the model. For simplicity, we only used one density value per species. This could be argued to lower the accuracy of the results, since in reality it is likely that species will have different densities in the different areas they inhabit (for example see Cook 1969). Not including this in the model results in a lowered variability in the data and the accuracy of the modelled predictions. Furthermore, we must concede that no data collected in the field is perfect. Conservation is an imprecise science and therefore it is likely that at least some of the life history trait data used in the model will have inherent uncertainty (Murphy 1989). This is especially true with climate change, as research has shown that the changing climate is altering the life history traits of many species, both directly and indirectly (Winkler *et al.* 2002). For example, increasing temperatures are causing declines in the body sizes of many mammals and birds (Gardner *et al.* 2011). It is very unlikely that any of these recent changes in trait data have been captured in our dataset, so even if the data are accurate now they will be inaccurate in the near future which limits the usefulness of the conclusions we can draw. If these data aren't accurate, then when they are used in the model these inaccuracies will be magnified and the modelled values will be inherently wrong. However, there is little we can do to alleviate this problem, so we must be aware of this limitation when drawing conclusions from the results.

The accuracy of the results is also influenced by the explanatory variables included in the model. We were only able to predict densities with 40% accuracy, despite including multiple drivers of density in our model. This suggests that there may be other variables contributing to density patterns. For example, biotic interactions, nest availability and current climate and land use change have all been shown to influence density patterns either directly or indirectly (Jarman 1974, Juanes 1986 and Zhang *et al.* 2015). These variables are difficult to quantitatively measure, placing modelling on these variables beyond the scope of this thesis, owing to constraints in computational power and time. However, this is not an impossible task; recent research on species distribution models (SDMs) have been able to include some of these variables in their models with success (Keith *et al.* 2008 and Wisz *et al.* 2012). Therefore, if we can apply these learnings to GLMs there is scope to improve the accuracy of modelled density predictions.

Concluding thought

In conclusion, regardless of the limitations of the model, we were able to predict a number of bird densities with moderate success. We will use this data in the next chapter to help predict population sizes for all the birds of the world and ultimately we hope this data will contribute to extinction risk calculations. This chapter has highlighted the need for more data collection, not only of density data but also other life history variables. At the time of writing, less than 30% of species have readily available field density data, and even fewer species had density data and a full set of life history traits. Therefore, research efforts should be focused on acquiring these missing data, either through field methods or through robust modelling methods (such as multiple imputation). These data would improve our understanding of each species, ultimately aiding conservation of not only the species in question, but also the species its interacts with or the area it occupies. Once these data have been collected, researchers can consider mapping the data to gain informative insights. For example, by mapping densities we have been able to highlight areas where conservation should be prioritised. We believe priority should be given to areas with low densities of endemic birds: if an area undergoes rapid or drastic land change (which is becoming more likely with climate change) there is a greater risk of local extinction in areas with low species densities, since they have no buffering capacity. Whereas, areas with species at high densities are more likely to be able to withstand these land changes as they can afford potential loss of their population without becoming locally extinct, therefore their conservation need is not as critical.

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Chapter three: Estimating population sizes for the world's birds

Abstract

Population sizes are fundamental for use in conservation science as they can provide useful insights into species and can help inform conservation priorities. Although population sizes have been estimated for a number of species, an accessible and comprehensively populated database of avian population estimates is crucially not available. In this chapter, we use the density estimates from the previous chapter, along with distribution polygons and habitat data, to calculate population sizes for 6,206 species. After comparing these to 3,177 independent population size estimates gathered from the literature, we find that our model consistently over predicts population sizes. However, we conclude that there is still utility in our results, and suggest that future research should focus on using multiple density estimates for each species and should aim to clip distribution areas by future habitat change scenarios, climatic suitability and altitudinal suitability, to ensure future work produces as accurate population sizes as possible.

Introduction

It is well known that there are approximately 10,000 species of bird globally, but the number of individual birds across the globe remains relatively unknown: bird numbers are inherently dynamic, fluctuating within and between years due to reproduction, mortality, immigration and emigration (Newton 1998). Natural events and anthropogenic interactions can also cause population sizes to vary dramatically. This highlights some of the challenges of estimating population sizes and is perhaps why much research focuses on population trends rather than total numbers of individuals. However, the absolute size of a population is important in conservation terms, especially for rare species which may be under threat of extinction (Mace 1994), and therefore population estimates are still vitally important.

In 1996, Gaston and Blackburn attempted to estimate how many individual birds there were on the planet, and to the best of our knowledge this work has not been replicated or refined. This research, which trialled several different methods, estimated a total of between 200 and 400 billion individuals. One method which yielded promising results involved scaling up bird densities from local study sites to areas across the globe. This resulted in a global estimate of 333 billion individuals. This estimate, however, was based on very limited density data taken from forest study sites only. This is likely to have led to an overestimation of the number of birds globally: the density of birds in forested areas is generally considerably higher than the density of birds in other habitats, such as urban landscapes or agricultural areas. Furthermore, although estimating the total number of individuals globally can provide a broad understanding of biodiversity, Gaston and Blackburn (1996) did not consider population sizes of individual species, which would have provided more useful data for conservation purposes.

In the UK, as in many developed countries, population data for individual species are often available for native species due to the work of organisations such as British Trust for Ornithology (BTO) (Newson *et al.* 2005) and The Royal Society for the Protection of Birds (RSPB) (Cannon 1999). For example, Musgrove *et al.* (2013) collated and presented population estimates for over 250 UK birds using data collected by thousands of volunteers who had participated in monitoring schemes and programmes hosted by the BTO and RSPB. BirdLife International have also collated population estimates for approximately 2000 species. These BirdLife estimates come from a variety of sources including: research publications that derive single species estimates, species monographs, and ‘best guess’ estimates by specialists in the BirdLife network (BirdLife International 2004*).* Further population estimates are provided in ‘Handbook of Birds of the World’ (del Hoyo *et al.* 2014) and in country specific monographs. However, an accessible and comprehensively populated database of avian population estimates is crucially missing.

The importance of population data

Population sizes can provide useful insights for species and groups of species. Amongst all the avian taxonomic orders we would expect passerines to have the largest number of total individuals, as this order comprises of over 50% of all avian species. We can also hypothesise that abundant species are most likely to be classified as Least Concern on the IUCN Red List, whilst species with smaller population sizes are more likely to be listed under one the threatened categories, due to their higher risk of extinction (Lande 1993). Some research has also shown that frugivores and insectivores are more abundant than carnivores on wetland reserves (Zakaria & Rajpar 2010); however, there is little research to confirm if this pattern holds true for all areas. By understanding patterns and trends such as these, we can gain greater insight into population estimates, which ultimately will help inform conservation efforts. For example, if we know the average population size of species in each IUCN category, then we might be able to make predictions as to what classification a species should belong to based on this information alone. In addition, if we know which are the most abundant feeding guilds, then conservationists can use this information to ensure there is a sustainable source of food to meet the needs of the entire population.

Population estimates are perhaps most importantly used to help prioritise conservation decisions and resource spending. Wildlife populations can be used as an indicator of environmental health as, among comparable habitats, we might expect more individuals in areas where habitats are rich and healthy (Fewster *et al.* 2000 and Gillings and Fuller 2001). Thus, if fewer individuals are present in an area then habitat restoration and conservation might be necessary. On an individual species scale, population information can be used to assess the conservation status of a species, since population sizes are known to be highly correlated with extinction risk (O’Grady *et al.* 2004). This makes population sizes one of the most useful demographic parameters to include in Population Viability Analysis (PVA) models (O'Grady *et al.* 2004). PVA models are a powerful tool for predicting the extinction risks of individual species. They have been used with great success and much research is currently being devoted to determining the most appropriate parameters to include in order to ensure accurate reflections of extinction risks are calculated (Stephens 2016); accurate population sizes are pivotal to this. Musgrove *et al.* (2013) concluded that most population size estimates could be improved upon, with only 31% classified as reliable. However, this work established that rarer species were more likely to have reliable population estimates, and since rare species are usually the species in most urgent need of conservation interventions due to their higher risk of extinction, this is particularly useful.

In general, the bigger the population size, the lower the extinction risk and thus conservation priority. In contrast, smaller populations are at greater risk of becoming extinct due to processes such as genetic drift, demographic stochasticity and environmental stochasticity having a greater proportional effect (Lande 1993). Random variation in reproductive success and survival has a bigger influence on smaller populations since only a few individuals will remain unaffected; it is therefore harder to recover the population. These processes can interact to create a positive feedback loop called an extinction vortex (Gilpin and Soule 1986). For example, a random environmental change could decrease the size of a population. This smaller population would then have less allelic diversity, and any further environmental and demographic stochasticity would have an increased impact on the population, further reducing the population size and genetic diversity. This could lead to inbreeding depression and reduced fertility, which would lead to an even smaller population. Such chains of events potentially result in very high extinction probabilities for small populations. This is one of the main motivations for knowledge of population sizes, so priority can be given to the conservation of smaller populations before they enter the 'vortex'. However, there is great debate as to the definition of a 'small' population size. Shaffer (1981) coined the term 'minimum viable population' (MVP), which is defined as the smallest population size with a 99% chance of persistence for at least 1,000 years or a defined number of generations. Despite subsequent research attempting to calculate MVP for many species (Reed *et al.* 2003), ultimately without the knowledge of the current population size there is no way of knowing if the population has reached its MVP.

Interestingly, recent research suggests that we should be focusing conservation efforts on larger populations (Gaston & Fuller 2007, Lindenmayer *et al.* 2011 and Inger *et al.* 2015). Inger *et al.* (2015) found that common European birds were declining more rapidly than less abundant species, which were actually increasing in numbers. This is a concern since common birds play a key role in ecosystem functioning; so declines in their numbers are likely to affect ecosystem services such as seed dispersal, pollination and pest control (Sekercioglu *et al.* 2004; Whelan *et al.* 2008; Wenny *et al.* 2011). However, regardless of whether conservation of small or large populations should be prioritised, we first fundamentally need to know the population size of the species.

Estimating population sizes

It is impossible to count the total number of birds in a population with absolute certainty: population sizes are constantly changing due to births, deaths and migration. Therefore, researchers must instead estimate population sizes as accurately as possible. As outlined in the previous chapter, distance sampling methods such as line transects and point counts can be used to estimate density and subsequently population sizes by multiplying the density by the area studied. Population sizes can also be estimated through capture-mark-recapture (CMR) methods. These methods work by capturing and marking a number of individual birds in a natural population which are then returned to the population to remix and at a second capture event some of these individuals are recaptured by chance (Gregory *et al.* 2004). Population sizes can then be calculated using the Cormack-Jolly-Seber model, which encompasses year specific estimates of survival and capture probability to estimate the number of individuals in a population (see Seber 1965, Jolly 1965 and Lebreton 1992 for detailed methods). Although CMR has yielded some promising results (for example see Baker *et al.* 2004) there are many assumptions that need to be met, including that the study population is closed which is unrealistic for most populations (Gregory *et al.* 2004). Furthermore, this method is very time consuming and costly since special licenses are required to handle and ring birds, which means this method is limited to trained researchers only (Sutherland *et al.* 2004). In addition, if knowledge is needed of the size of several populations or the population size of an entire species, instead of the population size in a specific habitat or location, these methods are rarely suitable. This is perhaps one reason why much research investigates relative changes in population indices rather than absolute abundances. However, although calculating population indexes is much less resource-intensive, they are arguably less useful since they reveal nothing about the size of the population (Anderson 2001).

A method that allows for population sizes to be estimated across many species, and which is robust, reliable and easy to implement is therefore needed. Several methods have been suggested, including using reporting rates from bird atlas data (Robertson *et al.* 1995) and count data in binomial models (Royle 2004). However, one possible means of estimating an entire species' population size, that has not been explored fully, is to multiply typical densities of the species in their preferred habitats by the area of those habitats within the species global range. This approach has been considered previously (for example see Newson *et al.* 2005), but has never been realised at a large scale, perhaps in part due to limited availability of density data. In this chapter, we propose to combine the density estimates calculated in the previous chapter with habitat and range data for individual species to permit a first exploration of estimating global population sizes of bird species. We will then validate our estimates against published population estimates derived by other means.

Methods

Densities were modelled for 6,206 species using the methods described in the previous chapter. A breeding distribution range polygon for each of these species was obtained from Birdlife International (BirdLife International 2016) and these polygons were gridded at a 0.5-degree resolution to obtain the breeding range area, assuming an equal area of grid cells globally. Habitat preference data was collected for each species from Birdlife international (personal communication with Stuart Butchart, BirdLife October 2014) and Handbook of Birds of the World (del Hoyo *et al.* 2014). If more than one habitat was listed for a species, then all habitats were recorded. These habitats were then standardised to match the level one IUCN habitat classifications (for details on each habitat see IUCN 2007). Independent estimates of population sizes were collated through an extensive literature search. In total, we collected 3,705 population estimates for 3,177 species (these estimates came from Handbook of the Birds of the World (del Hoyo *et al.* 2014), Handbook of Australian, New Zealand and Antarctic Birds (Higgins *et al.* 2006), Roberts Birds of Southern Africa (Hockey *et al.* 2005), Birds of North America (Rodewald 2015), and Birdlife International (2015)). Finally, data on taxonomic order, feeding guild and conservation status for each species were taken from sources discussed in the previous chapter.

To try to estimate realistic population sizes, the distribution polygon of each species breeding range was clipped by their habitat preference. To do this, distribution polygons for each species were overlaid onto the 2010 ESA Global Land Cover Map of the same resolution (ESA Climate Change Initiative 2014), and the habitat in each polygon was determined to be suitable or not by comparing the habitat types present in each polygon to the habitat preferences for each species. (see Table 1 for details on how IUCN Level one habitat classifications and ESA landcover variables Once all the habitats had been matched, each species polygon could then be clipped accordingly so only suitable areas of habitat remained in each distribution polygon. For example, species with a Marine Intertidal IUCN habitat, had their distribution polygons clipped to only include areas of Grassland, Bare areas, Consolidated bare areas or Water bodies. Once the new distribution area had been calculated for each species it was then multiplied by the species predicted mean density to generate an estimated population size. We additionally calculated population sizes using the 2,719 field density estimates (collated in the previous chapter), to investigate how the limitations of the previous chapter might affect the results.

Table 1: IUCN Level one habitat classifications matched to ESA landcover variables. Each of the 11 IUCN habitat classifications were converted into at least two of the 36 ESA landcover variables.

IUCN Level one habitat classifications	ESA landcover variables
Forest and woodland	Tree cover (evergreen and deciduous) Flooded tree cover
Savanna	Mosaic tree and shrub (>50%) / herbaceous cover (<50%) Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
Shrubland	Shrubland (evergreen and deciduous) Sparse vegetation (tree, shrub, herbaceous cover <15%) Sparse shrub (<15%)
Grassland	Grassland Sparse herbaceous cover (<15%) Flooded shrub/ herbaceous cover
Wetlands	Mosaic herbaceous cover (>50%) / tree and shrub (<50%) Sparse vegetation (tree, shrub, herbaceous cover <15%) Flooded shrub/ herbaceous cover Water bodies
Rocky Areas	Bare areas Consolidated bare areas
Desert	Sparse herbaceous cover (<15%) Bare areas Unconsolidated bare areas
Marine Intertidal	Grassland

	Bare areas Consolidated bare areas Water bodies
Marine coastal	Bare areas Consolidated bare areas Water bodies
Artificial Terrestrial	Cropland Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) Urban areas
Artificial Aquatic	Cropland (irrigated) Water bodies

To explore the variation in population estimates amongst groups of species, mean population size estimates (and standard errors) were calculated for species in each taxonomic order (total of 26 groups), feeding guilds (total of 7 groups) and conservation category (total of 5 groups). The total percentage of individuals in each of these groups (as a percentage of all individuals) were also calculated to see which group contributed the largest number of individual birds to the total estimated populations. To explore the variation in population estimates across geographical areas, global maps were produced of the total percentage of species with population estimates and the total number of individuals across the globe. These maps were produced using the same method as outlined in the previous chapter.

To gauge the accuracy of the estimated population sizes for each species they were compared to independent population size estimates. Both these estimates were binned into $\log_{10}$ categories: 1-9, 10-99, 100-999, 1000-9999, 10000-99999, 100000-999999, 1000000-9999999, 10000000-99999999, 100000000-999999999 and 1000000000+. Comparisons were then made between the frequency of our estimated population sizes and the frequency of the independent population size estimates in each bin group.

For species which had both a modelled and independently estimated population size, a ratio between the estimates was calculated. For each species, the log of this ratio was plotted against the log of their range size, modelled density, independent population size estimate and modelled population size estimate to see if any of these variables were influencing any discrepancy between the modelled and independently estimated population sizes.

Results

In total, we modelled population sizes for 6,206 species from across the globe (Figure 1). Through the summation of all these estimates, we predict there to be a total of 183 billon birds across the globe, excluding sea birds, colonial nesting birds or birds which we were not able to estimate a mean density for (this equates to excluding about 38% of species). Therefore, we can assume that this is the absolute minimum number of birds and in reality we would expect significantly more individuals; perhaps up to 295 billon (from proportionally scaling our estimate for the 62% of species accounted for (183/62) x100). Individual species estimates varied from under 100 individuals (for example, the the White-collared Kite, *Leptodon forbesi*) to over 1 $x10^9$ individuals (for example, the Willow Warbler, *Phylloscopus trochilus).* The most abundant order was the Passerine order, which we predicted to contain over 77% of all individuals (Figure 2). We also found that species classified as ‘Least Concern’ were likely to have larger population sizes than species in all other IUCN categories (Figure 3). Furthermore, although 66% of all birds were classified as insectivores, granivorous species had the largest population size estimates (Figure 4). We also mapped the total number of individuals in each grid cell across the world and found that the areas with the largest number of individual birds were predicted to be parts of South-East Asia and the Albertine Rift area of East Africa (Figure 5).

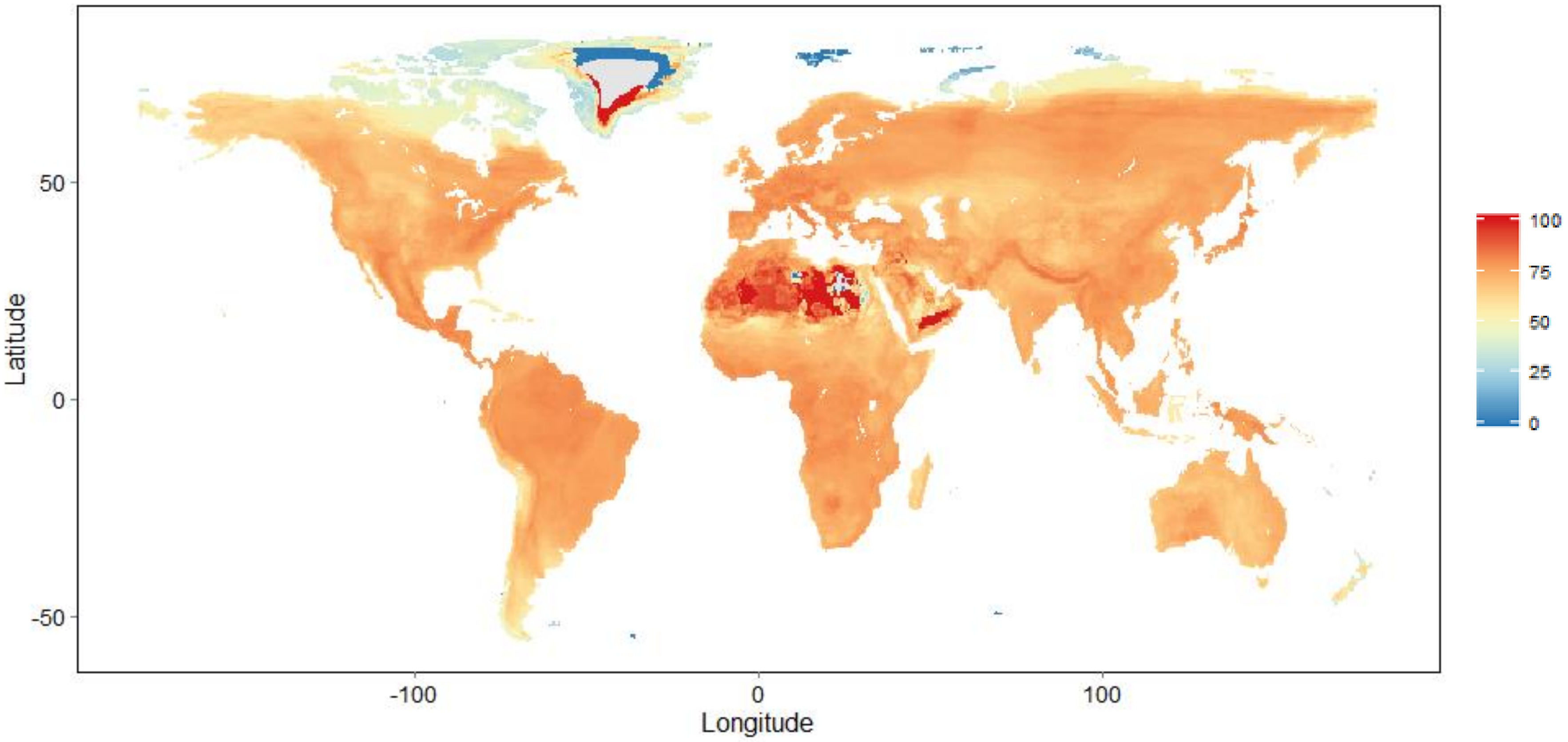

Figure 1: Percentage of species in each cell with at least one modelled population estimate. Red colours represent a high percentage of species in that area with a modelled estimated population size, whereas blue colours indicate that few species in that area had a modelled population size. Grey areas indicate no species were present in these areas.

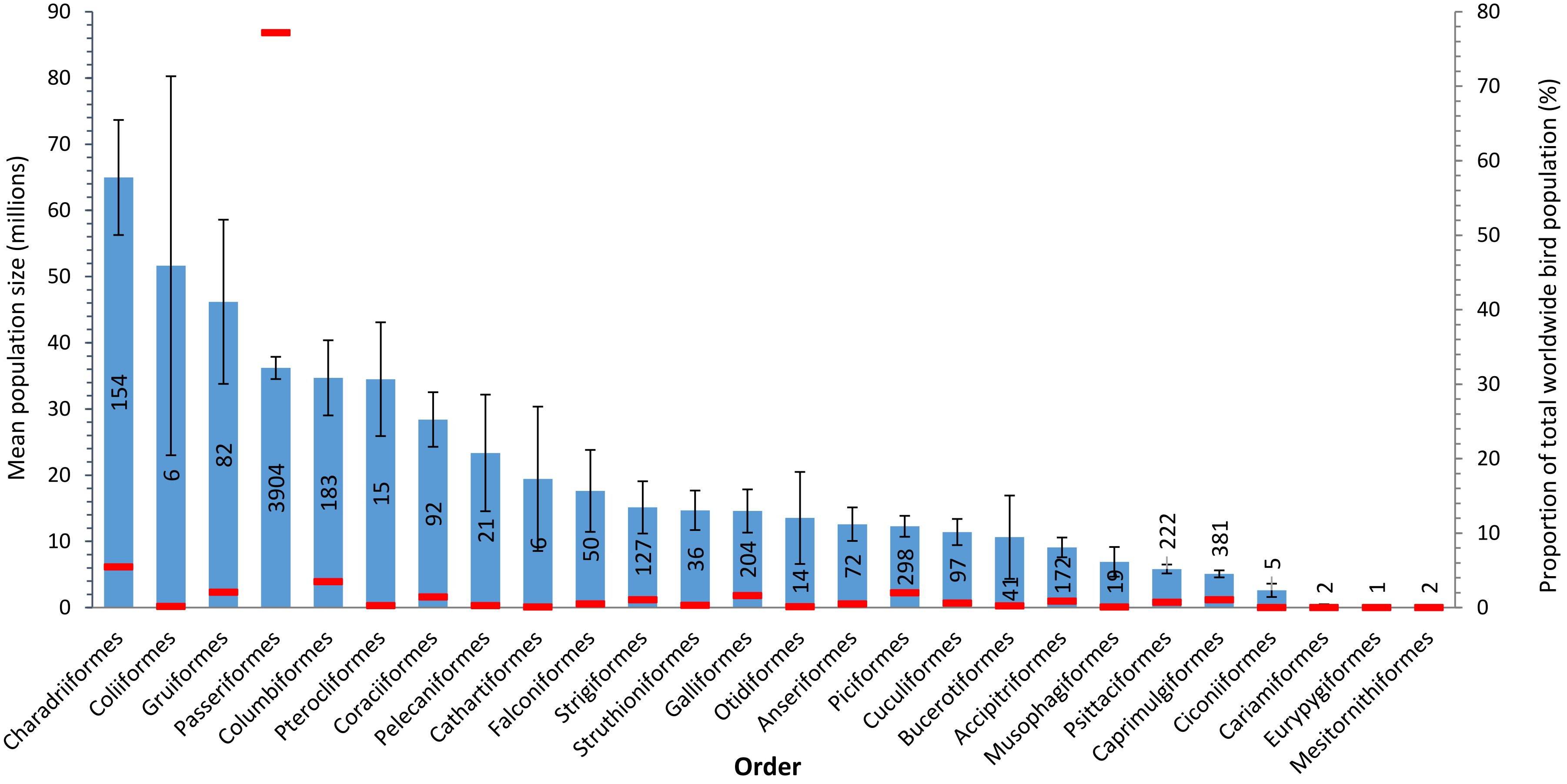

Figure 2: The mean population size (in millions) of species in each order (blue bars) and the total number of individual birds in each order as a percentage of all the birds in the world (red dashes). The error bars show the standard error of the mean (*sem*), and the number within each bar represents the sample size (i.e. the number of species in each order with a modelled population size).

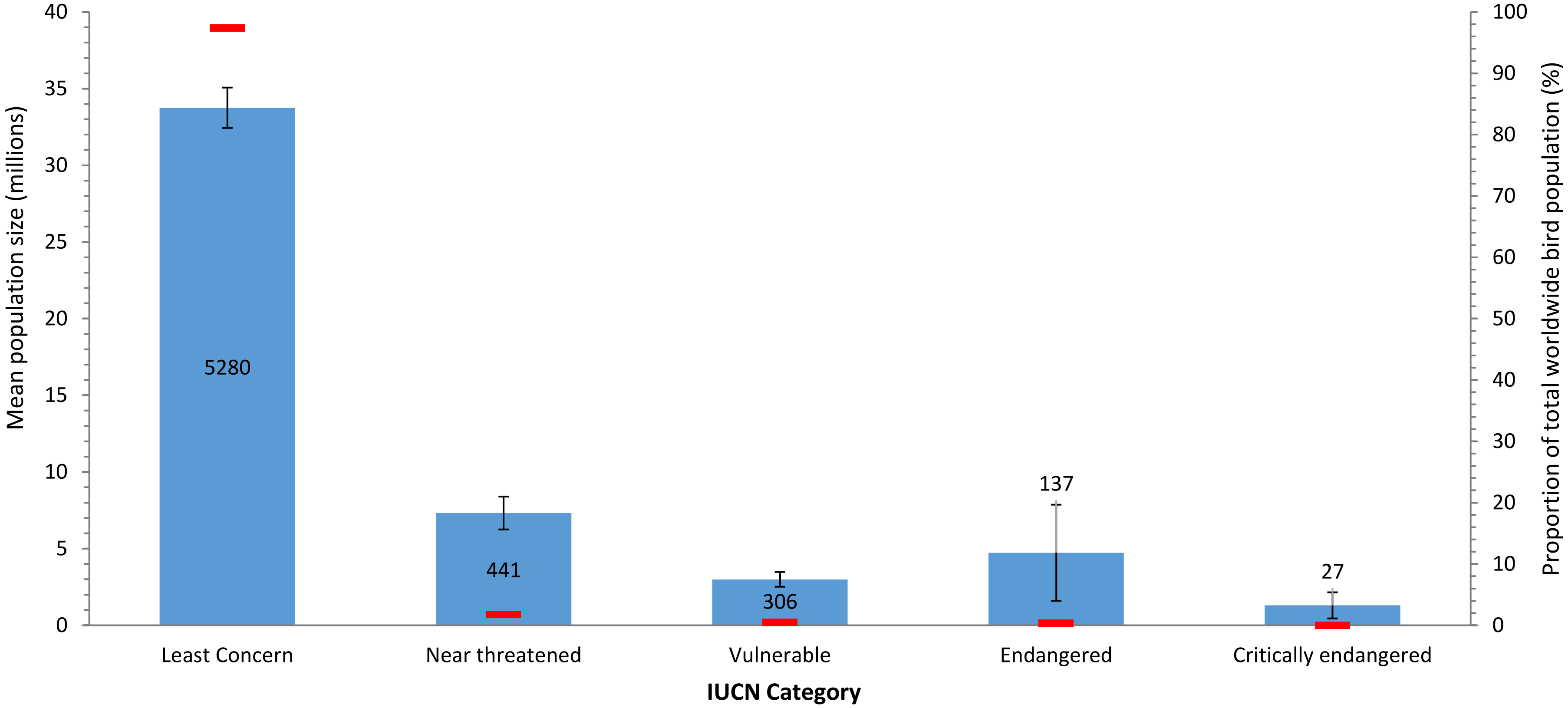

Figure 3: The mean population size (in millions) of species in each IUCN category (blue bars) and the total number of individual birds in each category as a percentage of all the birds in the world (red dashes). The error bars show the standard error of the mean (*sem*), and the number within each bar represents the sample size (i.e. the number of species in each category with a modelled population size).

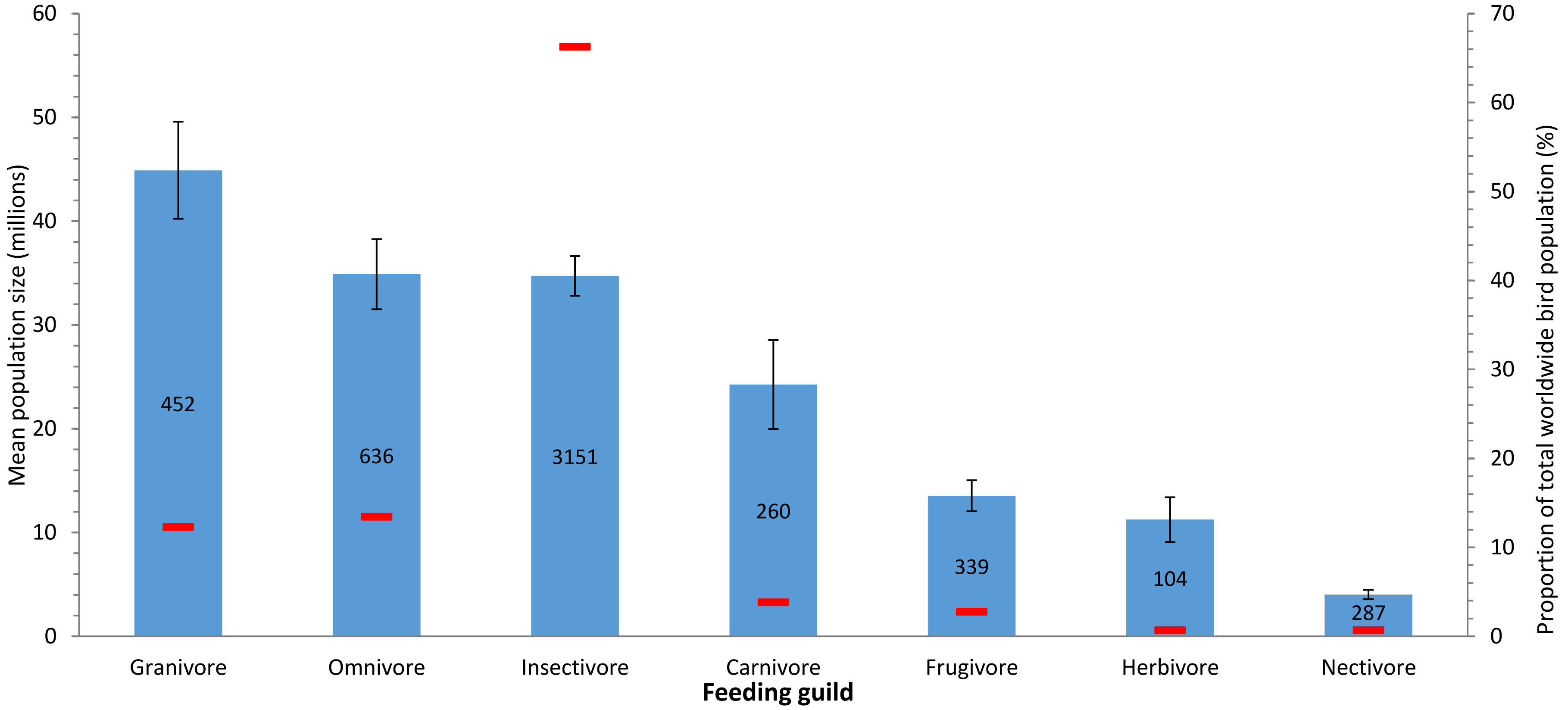

Figure 4: The mean population size (in millions) of species in each feeding guild (blue bars) and the total number of individual birds in each guild as a percentage of all the birds in the world (red dashes). The error bars show the standard error of the mean (*sem*), and the number within each bar represents the sample size (i.e. the number of species in each guild with a modelled population size).

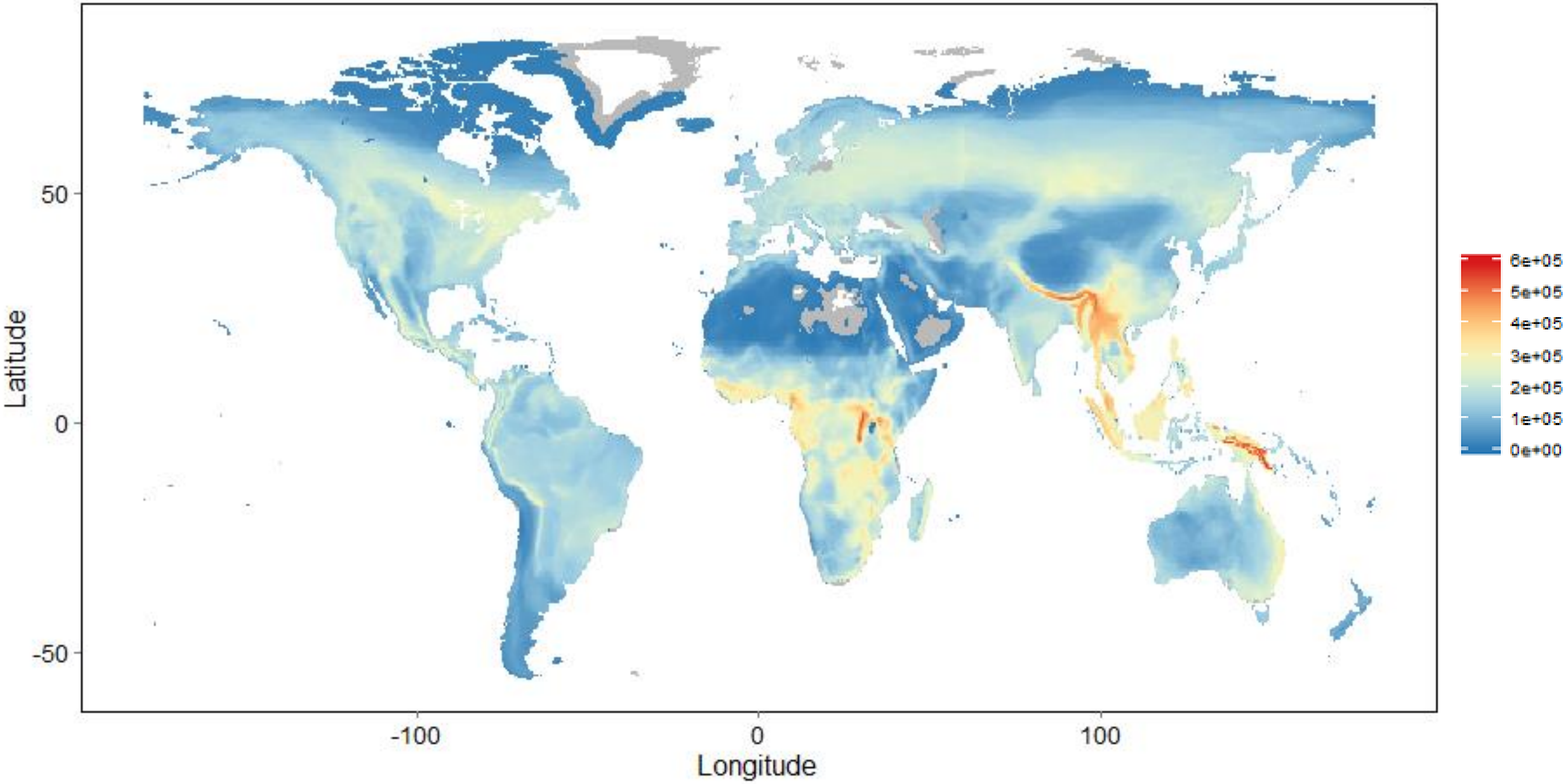

Figure 5: The total number of individual birds (for all species studied) per 0.5-degree grid cell. Red colours indicate high numbers of individual birds, whereas blue colours suggest the area has a lower number of birds.

To estimated population sizes were found to be moderately correlated to the independently estimated population sizes (R^2=0.55, Figure 6). When the population estimates were calculated using field density data (as opposed to the modelled density data calculated in the previous chapter) the correlation between the modelled and independently estimated population sizes was similar (R^2= 0.53, Figure 7), suggesting the limitations of the previous chapter were not hindering the estimation of the population sizes.

The most common modelled population size estimates were in the ‘millions’, whereas the most common independently estimated population sizes were in the ‘tens of thousands’ (Figure 8). Modelled population sizes exceeded the independently estimated population sizes for 90% of species. On average, population sizes were overestimated by a factor of 103. To understand the potential correlates of population overestimation, the overestimation factor (the modelled to independent population size ratio), f, for each species was compared to a number of variables: the range size, r (Figure 9); the modelled density, d_m (Figure 10); the modelled population size, p_m (Figure 11); and the independently estimated population size, p_i (Figure 12). Although correlations were weak, species with larger range sizes were more likely to have overestimated modelled population sizes (Figure 9). In contrast, species with smaller ranges were more likely to have underestimated population sizes (Figure 9). Furthermore, the larger the range of the species, the more variable the modelled population size estimates were (Figure 9). In addition, the model tended to be more accurate for those species with large *independently* estimated population sizes (Figure 11), but despite this, species with large *modelled* population sizes were not necessarily more accurate (Figure 12).

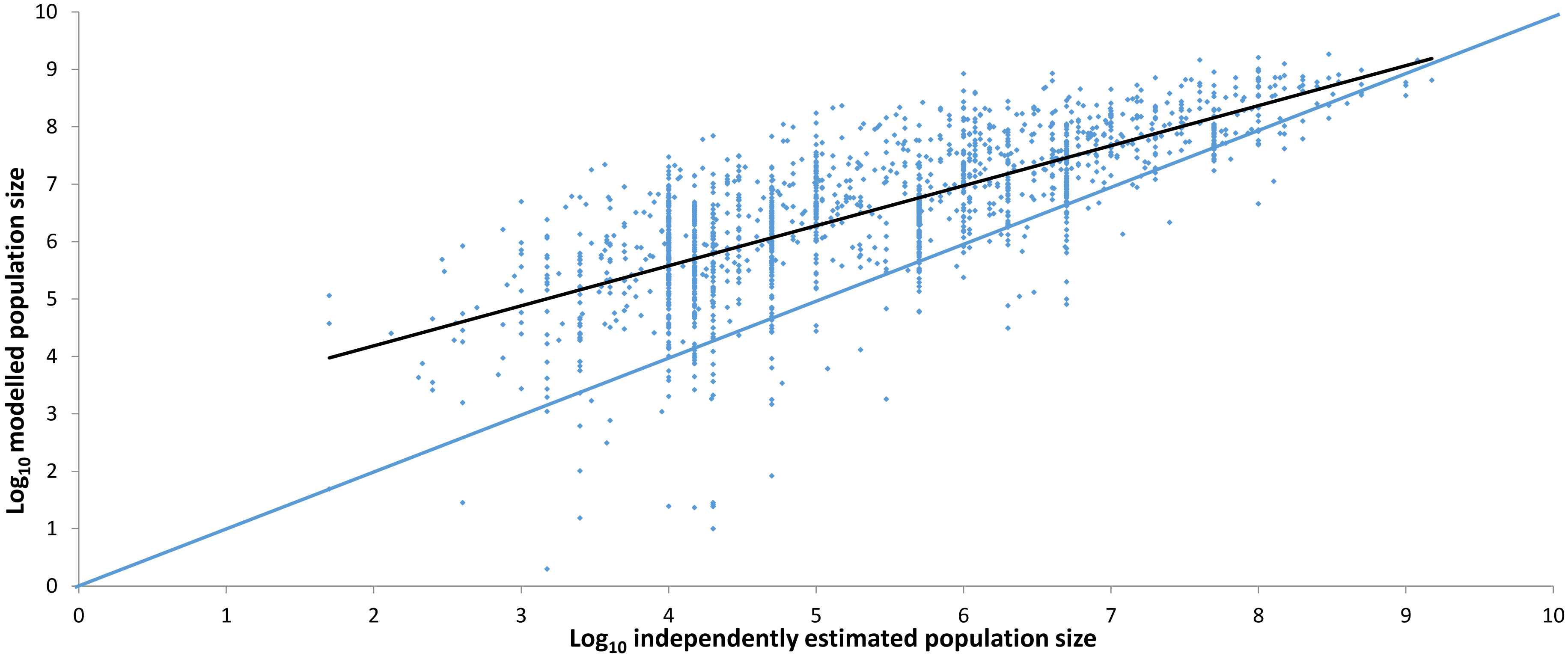

Figure 6: Species modelled population sizes against their independently estimated population sizes. Modelled population sizes were calculated using modelled densities, which were calculated in the previous chapter. The best fit line is represented by a black line, $R^2=0.55$. The blue line shows the expected trend if the modelled estimates were to replicate the independent estimates. The majority of the modelled population sizes are above this line, implying a tendency for the model to produce overestimates.

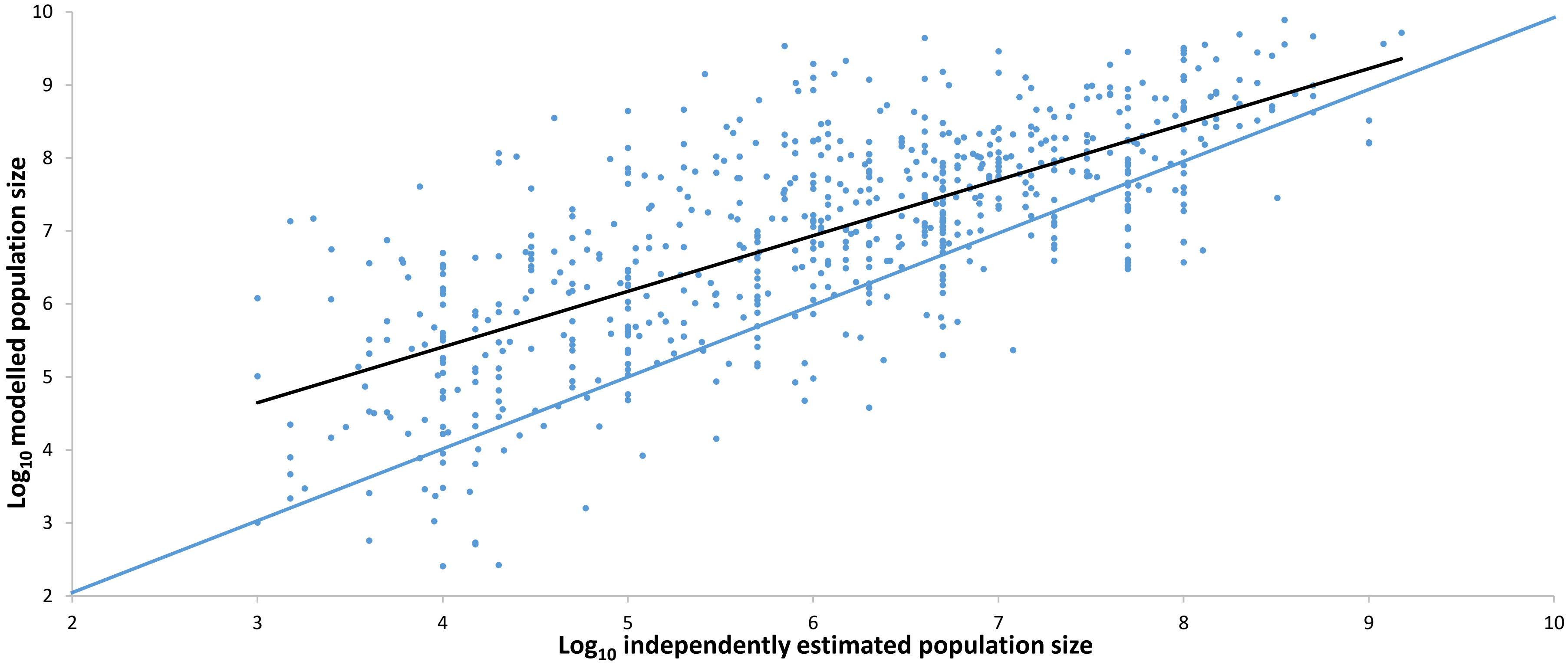

Figure 7: Species modelled population sizes against their independently estimated population sizes. Modelled population sizes were calculated using field densities, which were collated from the previous chapter. The best fit line is represented by a black line, R^2=0.53. The blue line shows the expected trend if the modelled estimates were to replicate the independent estimates.

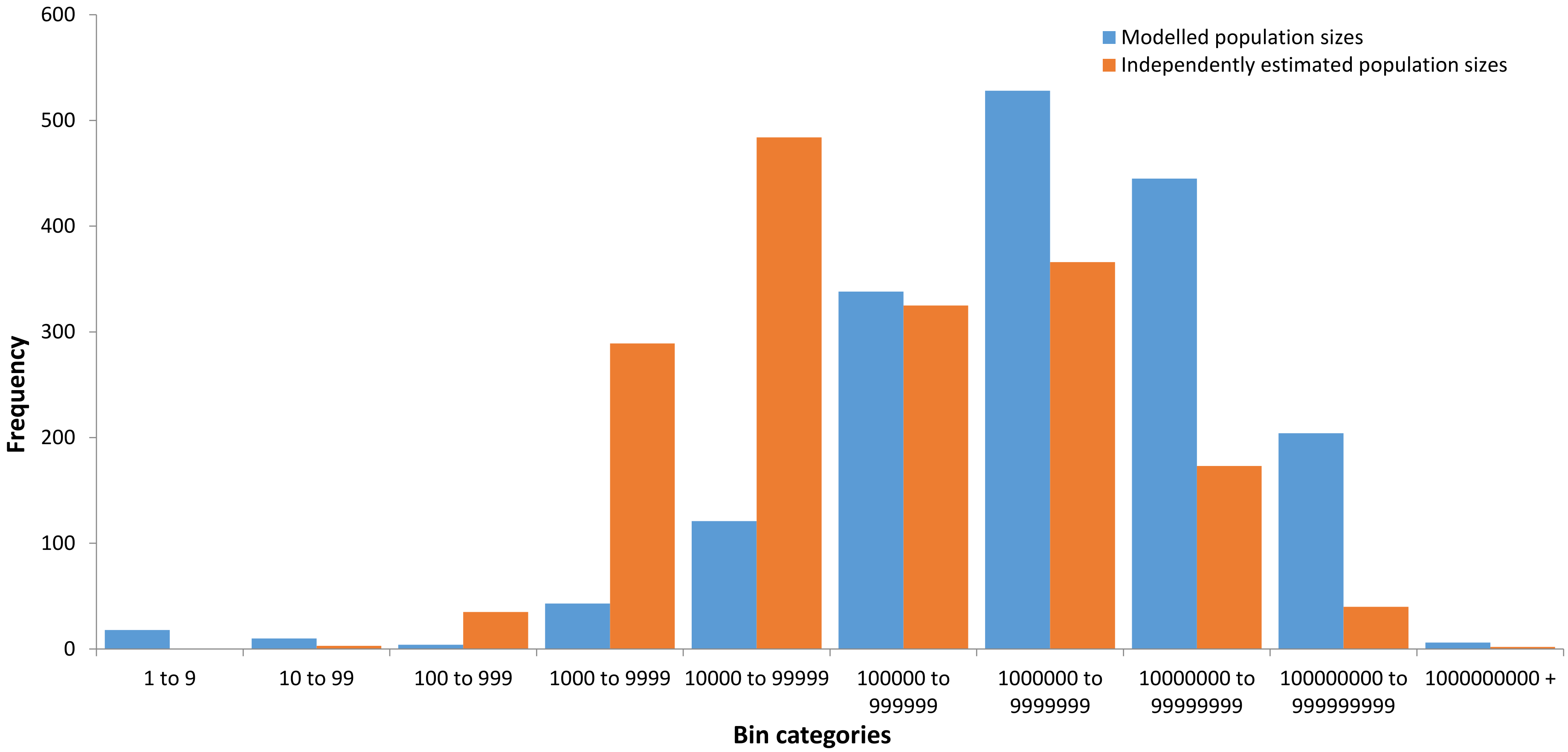

Figure 8: The frequency of all independently estimated population sizes and modelled population sizes, for the same subset of species (n=1717), binned into $\log_{10}$ categories.

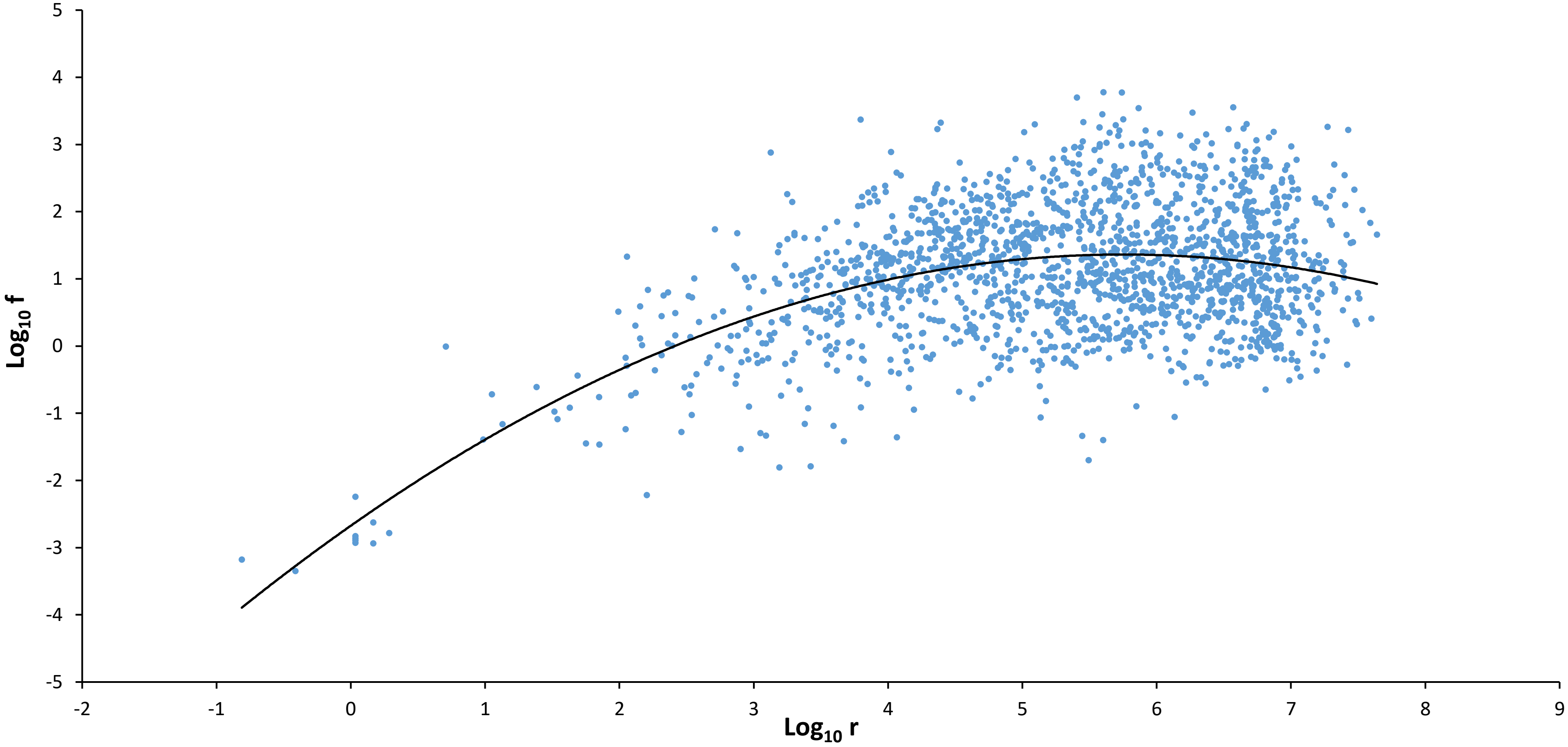

Figure 9: The overestimation factor, *f*, relative to the range size, *r*, for each species. The black line shows a polynomial line of best fit, which has an R^2 value of 0.2.

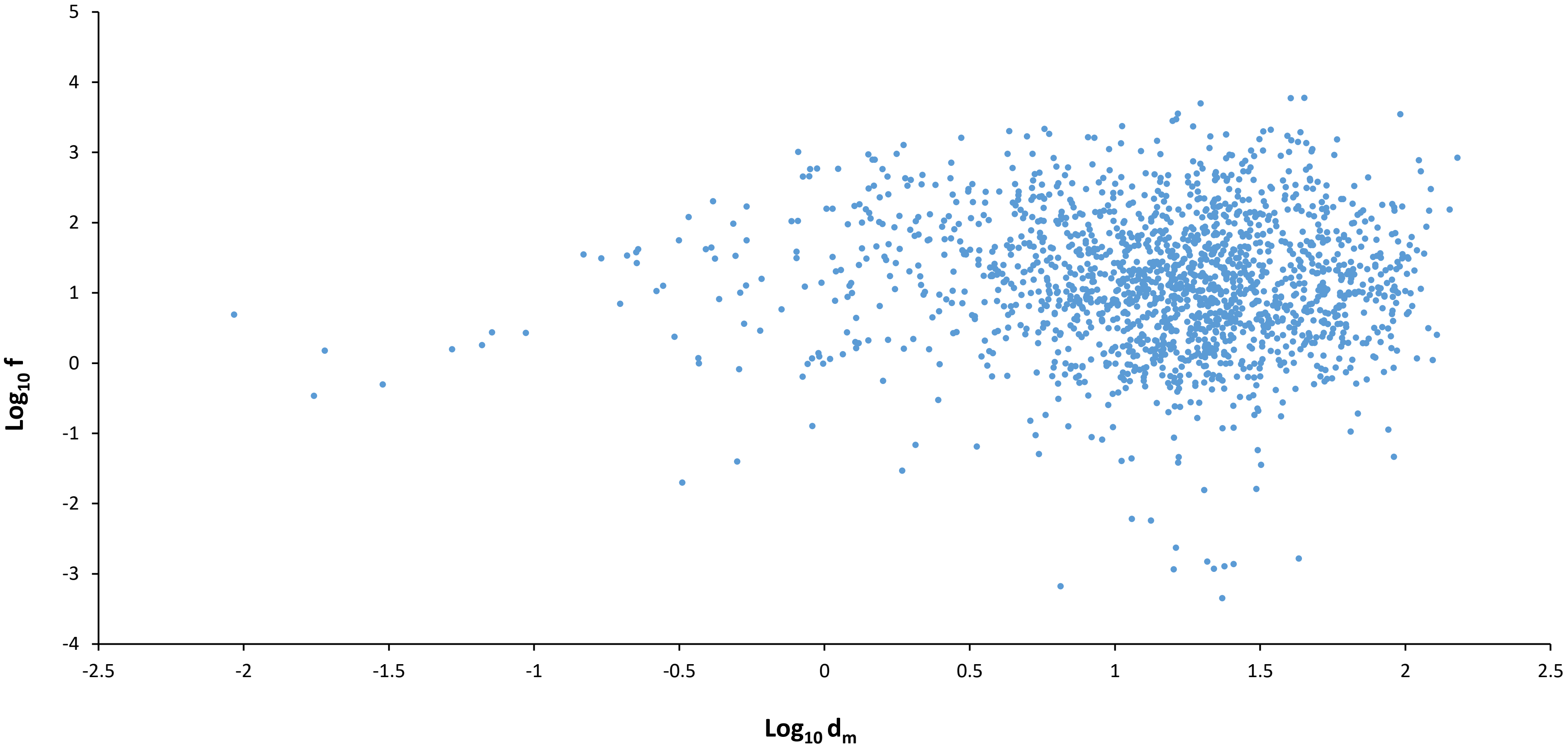

Figure 10: The overestimation factor, f, relative to the modelled density, d_m, for each species.

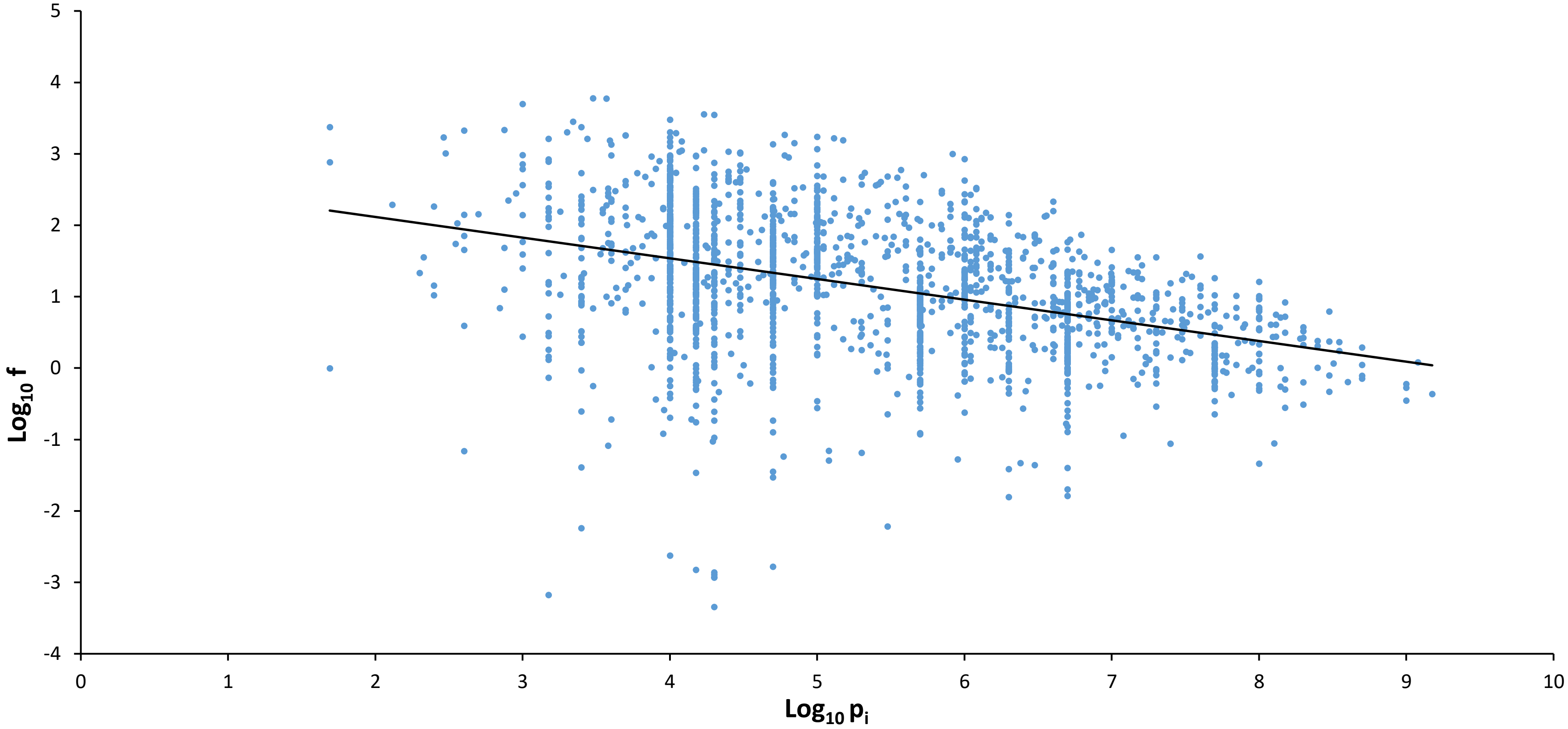

Figure 11: The overestimation factor, *f*, relative to the independent population size estimate, *P_i*, for each species. The black line shows a line of best fit, which has an R^2 value of 0.2.

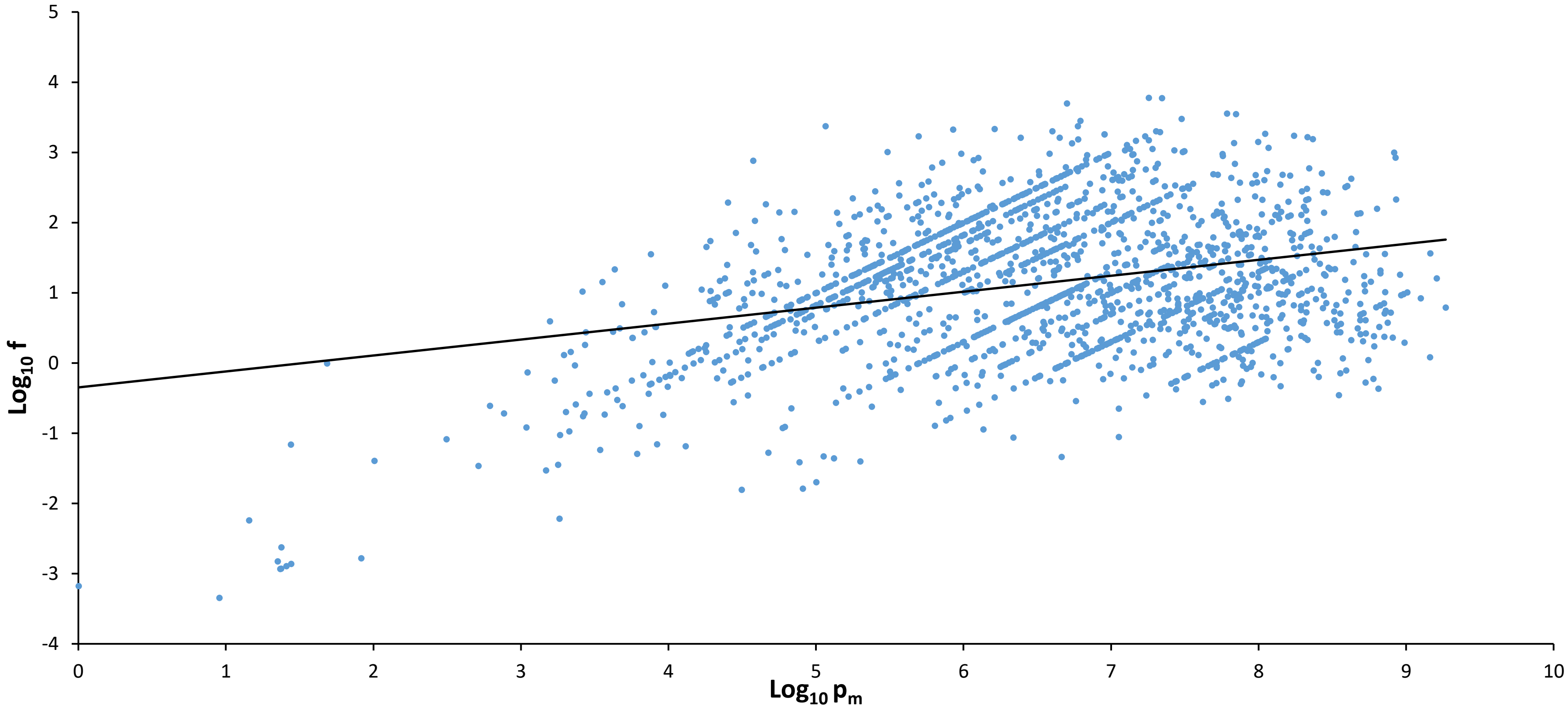

Figure 12: The overestimation factor, *f*, relative to the modelled population size estimate, P_m, for each species. The black line shows a line of best fit, which has an R^2 value of 0.1.

Discussion

Model reliability and accuracy

Overall, we found only a moderate correlation between the modelled and independently estimated population estimates, indicating that the modelled population sizes aren't as accurate as they could be (Figure 6). This is most likely because our model consistently over predicts the population sizes by an average factor of 103 (Figure 12). The density at which species occur had no effect the degree of overestimation (Figure 10). For species with small distribution areas, population sizes are less likely to be overestimated as methods for calculating population sizes are more likely to be accurate than in larger areas (Meadows *et al.* 2012). This means we can be more confident that the independently estimated population sizes, which we are comparing our modelled estimates to, are accurate. Species with large independently estimated population sizes are also less likely to have overestimated modelled population sizes as the larger the independently estimated population size, the bigger the margin of error can be in the modelled population size before it has a significant impact on the results. However, it is interesting to note that Musgrove *et al.* (2013) found that larger population sizes were more likely to be inaccurate compared to smaller population sizes, and therefore perhaps we cannot have much confidence in the large independently estimated population sizes that we are comparing our modelled estimates to, even though they appear to be more accurately correlated to our estimates than the smaller population sizes are.

To understand further why the model works well for some species but not for others, there are several methodological issues we must consider. One fundamental flaw of this method is that only one density estimate per species was used to calculate population sizes. However, much research has highlighted that species are found at different densities in different areas due to the presence or absence of other species and the availability of resources (del Hoyo *et al.* 2014). For example, we predicted the Speckled Mousebird (*Colius striatus*) to have a density of 155 individuals per km^2 and therefore this is the value we used to calculate its population size (which we estimated to be approximately 680 million). However, research has shown that densities of this Mousebird can range from as small as two individuals per km^2 in mixed woodland in Zimbabwe (Vernon *et al.* 1985) to up to 300 individuals per km^2 in Gabon (del Hoyo *et al.* 2006): these densities would give population estimates ranging from 8 million to 1 billion individuals. This analysis could be argued as being more informative as it provides more than just one population estimate. Furthermore, if we know which densities are most likely to reflect the true densities in each area a species occupies, we can include this variance in our model to produce even more accurate and reliable population size estimates, tailored to each specific area. This approach would be more useful for conservation efforts as it would allow specific areas to be targeted rather than just applying a ‘blanket cover’ to the whole of the species distribution, which could waste vital resources and money. However, trying to replicate this process for approximately 10,000 species would be a huge undertaking and was therefore outside the scope of this thesis. Furthermore, for some species the required data are not available, and thus even more data collection would be required before a comparison of results between species could be made.

Another methodological issue was in relation to how the distribution polygons were clipped to account for species habitat preferences. Due to the mismatch in the resolution of the IUCN level one habitat classifications and the ESA landcover variables, multiple ESA landcover variables had to be allocated to each IUCN habitat to ensure the entire ESA Global Land Cover Map was covered. Furthermore, to ensure the matching was as realistic as possible, the ESA landcover variables were overlapped across the IUCN habitats. This mismatch and overlap between the ESA variables and IUCN habitats could have reduced the key differences between the distinct habitat groups. Therefore, even though the polygons were clipped by the presence of suitable habitat, they could still be overestimating the amount of actual suitable habitat, and this could have ultimately contributed to the overestimation of the population sizes.

Further to the point above, another methodological issue with the distribution ranges used for each species was that they were treated as static. Due to limited time and resources we were unable to consider how human land-use practices or climate change might be influencing the range sizes, and thus the population sizes, of each species (Lehikoinen *et al.* 2015). For example, much research has demonstrated that climate change is altering range sizes of birds (Walther *et al.* 2002, Parmesan & Yohe 2003 and Sekercioglu *et al.* 2008). It is generally well confirmed that species have moved their distribution ranges towards the poles and to higher altitudes to avoid rising temperatures (Thomas and Lennon 1999, Hickling *et al.* 2006 and Hitch and Leberg 2007). In some cases, this has resulted in reduced range sizes, whilst in other scenarios range sizes are increasing (Thomas *et al.* 2004 and Walther *et al.* 2002). However, the rate at which this occurs is not uniform amongst species and is highly dependent on their body mass and migration ecology (Valimaki *et al.* 2016). For example, large species are more likely to change their distribution at a slower rate due to their longer generation time and slower reproduction rate, both of which reduce their dispersal capabilities (Valimaki *et al.* 2016). Similarly, full migratory species are also likely to change their distribution range at a slower rate than partial migratory or resident birds (Valimki *et al.* 2016). Therefore, although Birdlife endeavour to keep their distribution maps as accurate and up-to-date as possible, as of yet there is no hard and fast rule that can be accurately applied to all species, and therefore each species must be looked at individually. However, this is again a huge undertaking and so was not possible for this masters. This means the population sizes calculated in this chapter are only valid for the distribution ranges we have used, and this caveat must be taken into consideration when using these data in conservation research. As an interim method of understanding the impacts of climate change, it would be possible to generate a new global habitat map based on future climate change projections (Hallegatte *et al.* 2016). This would give us a snapshot into how the population size could change with the specified habitat change, but it would not include the effects of changing resources, competitors or predators. This is therefore unlikely to give us the full story of how the population will change with climate change.

As well as looking at the limitations of the methodology it is also important to look at the limitations of the data. For example, the independently estimated population sizes were collated from a number of primary and secondary sources. However, it was not always apparent from these sources exactly how the population sizes were calculated, and therefore we have no way of knowing exactly how accurate they are. Furthermore, even when the methods used are known, such as distance sampling, these methods have their own limitations and are ultimately just another form of estimation. Musgrove *et al.* (2013) found that all population estimates calculated through distance sampling were of ‘poor’ or ‘moderate’ quality. This therefore provides little confidence in the independently estimated population data we have gathered, and it is therefore understandable that the correlation between the modelled estimates and the independently estimated estimates is not high. In addition to this, it is important to remember that population sizes are not static; they are constantly fluctuating due to births, deaths, immigration and emigration. These in turn are influenced by resource availability, natural disasters, anthropogenic interactions and climate change (Baker *et al.* 2006). Therefore, if there is a considerable time difference between when these independently estimated population sizes were calculated and when the data we used to model our estimates were generated, then again we would not expect a perfect correlation between these estimates.

Observations from the model

For what is possibly the first time since Gaston and Blackburn’s 1996 paper the total number of terrestrial birds across the globe has been estimated. Although this method predicts fewer individuals than Gaston and Blackburn’s original estimate, this estimate is based on only 60% of all individuals due to data limitations. Therefore, it is likely that the actual number of individuals is much greater, and possibly as many as 295 billon birds, which is in the middle of Gaston and Blackburn’s range of estimates.

When looking at the modelled population estimates, we have not found anything particularly surprising. For example, over 77% of all terrestrial birds are predicted to be passerines. This is unsurprising as this taxonomic order contains over 50% of all known species; therefore, we would expect a high proportion of the world's birds to be passerines (Figure 2). Furthermore, we found that, in general, species with the lowest priority conservation status (Least Concern) had the most abundant populations. This again is expected as a criterion of being classified in this category is that the species is widespread and abundant (IUCN 2001) (Figure 3). We have also shown there to be a high abundance of individuals in areas which are known to be rich in avian fauna, such as Albertine Rift area of tropical east-Africa (Myers *et al.* 2000) (Figure 5). Species of lower trophic levels also tend to have larger population sizes (Figure 4). Interestingly, we have shown that Granivores have the largest mean population size, but Insectivores make up a higher percentage of all the birds studied (Figure 4). This could be due to bias in the data or it could be an actual trend indicating that although insectivores are very abundant, their individual population sizes are limited due to their dependence on a food source which is itself more limited than seeds or grains (Martin 1987). Similarly, the population sizes of Frugivores, Herbivores and Nectivores could be so small as these food sources are very ephemeral and therefore limit the population.

We can also examine the results at an individual species level to see which species have small or large populations, and therefore which species might need conserving. For example, one of the smallest population sizes we modelled was for the Yellow-throated Woodland-warbler (Phylloscopus ruficapilla). According to Birdlife International, the population size of this species is unknown; however, it is suggested that the size is decreasing due to ongoing habitat destruction (BirdLife International 2012). In contrast, del Hoyo *et al.* (2006) describe the Yellow-throated Woodland-warbler as 'locally common' and therefore for conservation purposes is classified as Least Concern. Our results indicate that population size of this individual could be as few as a couple of hundred individuals. This is because we predict the actual area of suitable habitat the species can inhabit to be much smaller than the assumed area of occupance. Research has shown that much of its known range size has undergone serve habitat destruction (Korfanta *et al.* 2012), therefore it is not unreasonable to predict a reduction in population size as a consequence. If we predict, as in this example, that a population size of a species is extremely small, it highlights that conservation of that species might be necessary. At the very least further research is needed to understand if the species is under imminent threat and if its population size is truly as small as we modelled. In contrast, if there is no information on population sizes, the conservation of these species could get overlooked especially if they are currently classified as Least Concern on the IUCN Red List. This begs the question as to how accurate the IUCN Red List assessments are when significant changes, such as habitat destruction and climate change are rapidly impacting species. At the time of writing, the most recent Red List assessment for the Yellow-throated Woodland-warbler was published in 2012 (Birdlife international 2012) and therefore this will not capture any changes to the habitat structure or population size since 2012. However, the method we have used in this chapter to model population sizes has the potential to overcome this problem as we can easily manipulate the distribution area of a species to reflect how changes in habitat availability (caused by climate change or anthropogenic interactions) could affect area of occupancy. In turn, this will tell us how the population size could change, and therefore if conservation actions will be necessary under these scenarios to stop population sizes becoming too small and thus extinct.

To further aid conservation efforts, we can also use these individual population estimates in population viability analysis (PVA) models to calculate the extinction risks of species. Research has shown that population sizes are highly correlated to extinction risk, and are therefore one of the most useful parameters to include in PVA models (O’Grady *et al.* 2004). This means the population sizes calculated in this chapter have the potential to be extremely useful as they bring us one-step closer to being able to calculate extinction probabilities for all these species. Ultimately, this will help to inform conservation practices and policy decisions (see Chapter 5).

Concluding thought

Overall, we have shown that this method does provide a good starting framework to estimate population sizes of bird species. However, it will be necessary for any future research to improve this method to ensure population estimates are as accurate as possible. First and foremost, future research should focus on using multiple density estimates for each species so population sizes can be estimated with greater precision across distribution ranges. Secondly, any subsequent research should attempt to clip distribution areas by future habitat change scenarios, so the impacts of climate change on population sizes can begin to be understood. Research should also consider clipping range areas by climatic suitability and altitudinal suitability, as this will better represent the actual area of occupancy. Ultimately, we hope that by demonstrating here that it is possible and extremely useful to calculate population sizes, that this will stimulate more research to gather more data and to ultimately provide more reliable population size estimates.

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Chapter four: Estimating survival rates for the world’s birds

Abstract

Survival estimates are a vital demographic parameter to include in population viability analysis (PVA) models to calculate extinction risks. Typically, they are estimated through field methods such as mark-recapture of live or dead recoveries. However, these methods are expensive, resource intensive and time consuming. They are also highly likely to underestimate survival rates and are difficult to apply to rare species - arguably the most important species to study in terms of conservation. Following this reasoning, Collingham *et al.* (2014) proposed a new model for calculating survival estimates of species using just their body mass and clutch size data. In this chapter, we review this method and attempt to calculate survival estimates for all birds across the globe. We calculate 5,291 survival estimates and compare these to 184 survival estimates collated from literature sources. We find that the model performs marginally better for South African species, but that more survival estimates must be collected from the literature before any definitive conclusions can be drawn about the model.

Introduction

One goal of biodiversity conservation is to maintain or improve a species conservation status to prevent them becoming extinct. Population viability analysis (PVA) is a powerful tool that helps to tackle this issue by estimating individual species extinction risks, therefore identifying the species most vulnerable and in need of priority conservation. Furthermore, PVA models can be run under current and future anthropogenic and climatic change scenarios (for example see, Maschinski *et al.* 2006 and Pe'er *et al.* 2013) making them extremely useful in predicting which species will be more at risk under certain conditions, again allowing conservation efforts to be prioritised (Morris and Doak 2002). However, despite the potential utility of PVA models, their use has been limited due to the paucity of reliable demographic data (Stephens 2016).

The previous two chapters discussed the importance of population estimates in PVA models, and another vital demographic parameter for such models is survival (Neil & Lebreton 2005) which shall be discussed here.

Survival rates can be defined as the proportion of individuals at a given age or life stage in a population that survive from one breeding season to the next, or from one life stage to the next (Saether 1989). If the data are available, juvenile, immature and adult survival rates can be calculated. These are useful as they allow comparisons to be made between age classes; this can help highlight the demographic mechanisms of population growth or decline within the species. Survival is not constant during a bird's life, and generally adult survival rates are higher than juvenile or immature survival rates (Saether 1988). Survival is typically lowest just after hatching: a study on Song Thrushes found that only 20% of birds survived after hatching (Robinson *et al.* 2004). Often only the mean adult survival rate can be calculated due to limited data availability and resources (Saether 1988), however these estimates are still useful as they allow comparisons to be made between species. Amongst species, survival rates vary enormously; for example, Northern Fulmars (*Fulmarus glacialis*) can live up to 55 years whilst some Warblers, such as the Red-faced Warbler (*Cardellina rubrifrons*), are only expected to survive up to 4 years (Tacutu *et al.* 2003).

Estimating survival rates

Survival rates of birds may be estimated in a number of ways. One method of calculation is to record the number of recaptures or re-sightings of individually marked birds. This is achieved in the field by either the regular recapture of ringed birds, or by identifying ringed birds using binoculars (Piper 2002). However, this method can underestimate survival rates as the permanent presence of researchers can cause emigration from the area, which can lead to the assumption that these birds have died. An alternative method, which is less sensitive to emigration, is to record the number of ringed birds that are recovered dead (Saether 1989). However, this method typically relies on members of the public reporting the deaths of ringed individuals which biases recoveries towards large conspicuous species, birds that are hunted, or species associated with areas frequented by people (Piper 2002; Green 2004). In contrast, the deaths of small inconspicuous species or migrants that spend a large part of the year in regions with low human populations are less likely to be reported, and consequently survival rates of these species cannot be calculated using this method. Furthermore, both these mark-recapture techniques are underpinned by several assumptions, which cannot always be met. For example, they assume that marked birds are a random subset of the population and all individuals have an equal chance of being caught. However, typically the probability of capture can vary with age and individuals on the edge of a study area are less likely to be caught (Buckland 1982). Furthermore, common species are more likely to be ringed than rarer species (Piper 2002). Another assumption is that no marks are lost over the course of the study, but this is often unpredictable. Lost tags can cause a loss in precision of estimates, which can only be corrected if an estimate of tag-loss rate can be calculated (Anderson & Millis 1981), but this isn't always possible. Finally, these methods must assume that the populations being studied are closed, i.e. there are no births, emigration or immigration. However, all these factors are likely to be prevalent in a real population. Furthermore, the simple act of marking an individual could make it more conspicuous and vulnerable to predation, therefore causing more marked individuals to die than unmarked individuals, and thus skewing the results (Saether 1989). As all these assumptions are very difficult to meet any survival estimates calculated through these mark-recapture techniques must be treated with caution.

An alternative method of estimating survival rates could be through the use of other ecological variables. Much research has shown that life history traits and ecological variables are correlated to survival rates (for example, see Sæther & Bakke 2000 and Collingham *et al.* 2014). This is most likely due to the evolution of optimal life history traits (Collingham *et al.* 2014). For example, it has been shown that species with a higher clutch size have lower survival rates because reproduction is energetically expensive and it also increases competition for resources (Saether 1988). In contrast, body mass has been shown to be positively correlated to survival rates: species with larger bodies have higher fat reserves which better equips them to survive harsh conditions (Monticelli *et al.* 2013). Both of these ecological traits contribute to a fundamental life history strategy for a species and help to classify the species as an R or K strategist, which can tell researchers a lot about the expected survival of a species (Pianka 1970). For example, species with small body masses and high clutch sizes are likely to be R-selected species. These species invest most of their energy in producing numerous offspring rather than in maturation. They typically have short gestation periods and reach maturity quickly, which results in lower expected survival probabilities (Type III survivorship) (Deevey 1947). In contrast, species with large body masses and small clutch sizes are more likely to be K-selected species. These species produce few offspring so they can invest more energy in maturation, which contributes to their higher expected survival probabilities (Type I or II survivorship) (Deevey 1947).

Diet also correlates with survival, with some research demonstrating that, at least in southern Africa, insectivores and nectivores have a higher survival rate than granivores (Peach *et al.* 2001).

Survival rates amongst species have also been shown to differ across latitudes. For example, the survival rates of passerines have been shown to increase as latitude decreases (Skutch 1985, Piper 2002). This is likely driven by the relationship between clutch size and latitude. For example, it is known that clutch sizes are smaller in the tropics, therefore contributing to higher survival rates (Skutch 1985). This highlights that there are potentially many interacting influences which effect the survival rates of birds, and so these must be considered when trying to understand the differences in survival amongst species.

Due to the strong evidence that demographic and ecological co-variates are correlated to survival, Collingham *et al.* (2014) postulated that it should be possible to calculate survival rates using just these variables. They estimated

survival for 67 South African birds using dead recovery methods and then predicted these survival values using five covariates: body mass, clutch size, age at first breeding, diet and migratory tendency. These covariates were used in regression models with and without phylogenetic information.
They found that both models performed equally well with and without phylogenetic relatedness. A leave-one-out cross validation test also indicated good predictive power of their model, and they were able to predict survival rates of 38 southern African species (which had independent mark-recapture survival estimates) with a 48% accuracy (Collingham *et al.* 2014). Of the five covariates used in their models, they concluded that clutch size and body mass were the most influential and proposed that survival rates could be accurately predicted, for at least southern African species, from just these variables.

For birds, body mass and clutch size data are more readily available than survival data, and can often be easily found within species monographs and anthologies. This is because the data required to calculate these traits are relatively easy to collect in the field. In contrast, collecting survival rate data for species can require lengthy fieldwork and often there is inherent uncertainty in the estimates they produce (Gregory *et al.* 2004). As such, survival data is often not available, and even when it is available the reliability of the data must often be questioned. In this chapter, we will use available body mass and clutch size data to calculate survival rates of birds using the equation given in Collingham *et al.* (2014). This will be carried out for birds across the world, not just South African birds, to see if this method is viable at a global scale.

Methods

Following the BirdLife Taxonomic Checklist v7.0 (BirdLife International 2014) an initial database was created with 10,455 accepted bird species (as in Chapter 2). Both body mass data and clutch size data were collated for these species from available life history databases. In total, we collected body mass estimates for 8,547 species (1,157 from the AnAge database (Tacutu *et al.* 2013) and 8,542 from BirdLife International’s World Bird Database) Clutch size estimates were collected for 6,346 species (540 from the AnAge database (Tacutu *et al.* 2013) and 6,327 from personal communication with Stuart Butchart at Birdlife International). For species that had multiple body mass or clutch size estimates, the mean values were calculated, along with the associated standard error. In total, there were 5,291 species which had both body mass and clutch size data. It is these species for which we calculated survival estimates.

The logit of annual adult survival, ϕ_A, was calculated for each species using the model of Collingham *et al.* (2014),

$$Logit\ (\emptyset_A) = 0.5419 + 0.1595 \times Log_e\ (body\ mass) - 0.7246 \times Log_e\ (clutch\ size).$$

From this, ϕ_A was then calculated by using,

$$\emptyset_A = \frac{e^{logit(\emptyset A)}}{1 + e^{logit(\emptyset A)}} \qquad (1)$$

To summarise the results, modelled annual adult survival estimates were binned into the following categories: 0.2-0.29, 0.3-0.39, 0.4-0.49, 0.5-0.59, 0.6-0.69, 0.7-0.79 and 0.8-0.89. Mean survival estimates and their associated standard error were also calculated and plotted for each taxonomic order, feeding guild and IUCN conservation category (the sources of these are described in the previous chapters). Mean body mass and clutch size were also calculated for each of these groups and plotted as the normalised mean body mass or clutch size, so they could be easily visualised. Normalised values were calculated by dividing all values by the largest value, therefore giving the largest value a number of one and all smaller values a number under one. This allows data which are on different scales to be plotted on the same axis.

To explore the spatial variation in the modelled survival estimates, the following maps were produced: the total percentage of species in each 0.5-degree terrestrial grid cell with a survival estimate and the mean survival estimate for all birds in each 0.5-degree terrestrial grid cell (based on range polygon data from BirdLife). These maps were produced using the methods as outlined in Chapter

2. Species were also grouped into southern and northern hemisphere species, and their modelled survival estimates compared to the latitude of the center of their breeding range.

The modelled survival rates were compared to survival estimates available in the published scientific literature. In total 184 survival estimates were collected from the following sources: Sæther (1989), Karr *et al.* (1990), Faaborg & Arendt (1995), Johnston *et al.* (1997), Jullien & Clobert (2000), de Swardt & Peach (2001), Peach *et al.* (2001), Piper (2002), Altwegg & Underhill (2006), McGregor *et al.* (2007), Blake & Loiselle (2008), Altwegg & Anderson (2009) and Altwegg *et al.* (2014). These literature estimates were correlated to the modelled survival estimates for the same group of species to determine the accuracy of the model, and thus the level of confidence we could have in our modelled data.

The absolute difference between the modelled and literature estimates was also calculated and plotted against the $\log_{10}$ clutch size and body mass to see if these variables were contributing to the differences between the estimates.

Results

Annual survival estimates were modelled for 5,291 species globally (Figure 1). Estimates ranged from 0.29 (Goldcrest, *Regulus regulus*) to 0.88 (Daurian Partridge, *Perdix daurica*); most species had an estimate between 0.50 and 0.69 (Figure 2). The order with the highest modelled mean survival probability was the Catharitformes (New World vultures) (0.85). Other orders with high survival probabilities were the Otidiformes (Bustards) (0.79) and the Cariamiformes (Seriemas) (0.75). Conversely, the order with the lowest modelled mean survival was the Anseriformes (Waterfowl) (0.54). As predicted, Passeriformes also had a low average survival probability (0.58) (Figure 3).

Mean survival probabilities across the IUCN Red List classification categories did not follow the expected pattern outlined in the introduction. The group of species with the lowest mean modelled survival were those in the Least

Concern category (0.59), whilst species in the Critically Endangered category had an average modelled survival of 0.66 (Figure 4). However, the large standard error bars for this category suggest that there is considerable variation amongst these estimates.

Across feeding guilds, frugivorous species had the highest average modelled survival probability (0.69), whilst species classified as nectivorous, granivorous and insectivorous had the lowest (all under 0.58) (Figure 5). Furthermore, in contrast to the research by Peach *et al.* 2001, we found that granivores did not have a significantly lower survival rate than nectivores or insectivores; we found all three to have survival probabilities between 0.57 to 0.58.

Global patterns of modelled survival probabilities highlight that survival is lowest in the northern hemisphere and highest in the tropical southern hemisphere (Figure 6), which is in line with the predictions outlined in the introduction (Skutch 1985). As latitude increases, modelled survival estimates decrease more sharply for northern hemisphere species than for species in the southern hemisphere (Figure 7). Survival probabilities tend to peak around the equator, with Indonesia, Papua New Guinea and parts of the Saharan belt in Africa having the highest mean survival rates of birds (Figure 6).

To gauge the accuracy of the modelled survival results they were compared to survival estimates collected from the literature. In total, survival estimates were found for 184 species from across 13 sources of primary literature. These estimates varied from 0.31 (Little Owl, *Athene noctua*) to 0.90 (Hen Harrier, *Circus cyaneus*). Over half of the species had a survival estimate between 0.50 and 0.69, a similar range to our modelled estimates. We found a positive correlation between the modelled and literature derived estimates (R^2= 0.36) (Figure 8). Model performance was not dependent on clutch size or body mass (Figure 9), but did vary depending on the region the species was from (Figure 8); African species showed the strongest correlation between literature and modelled estimates (R^2= 0.47), whilst species from the Americas showed the weakest correlation (R^2=0.34).

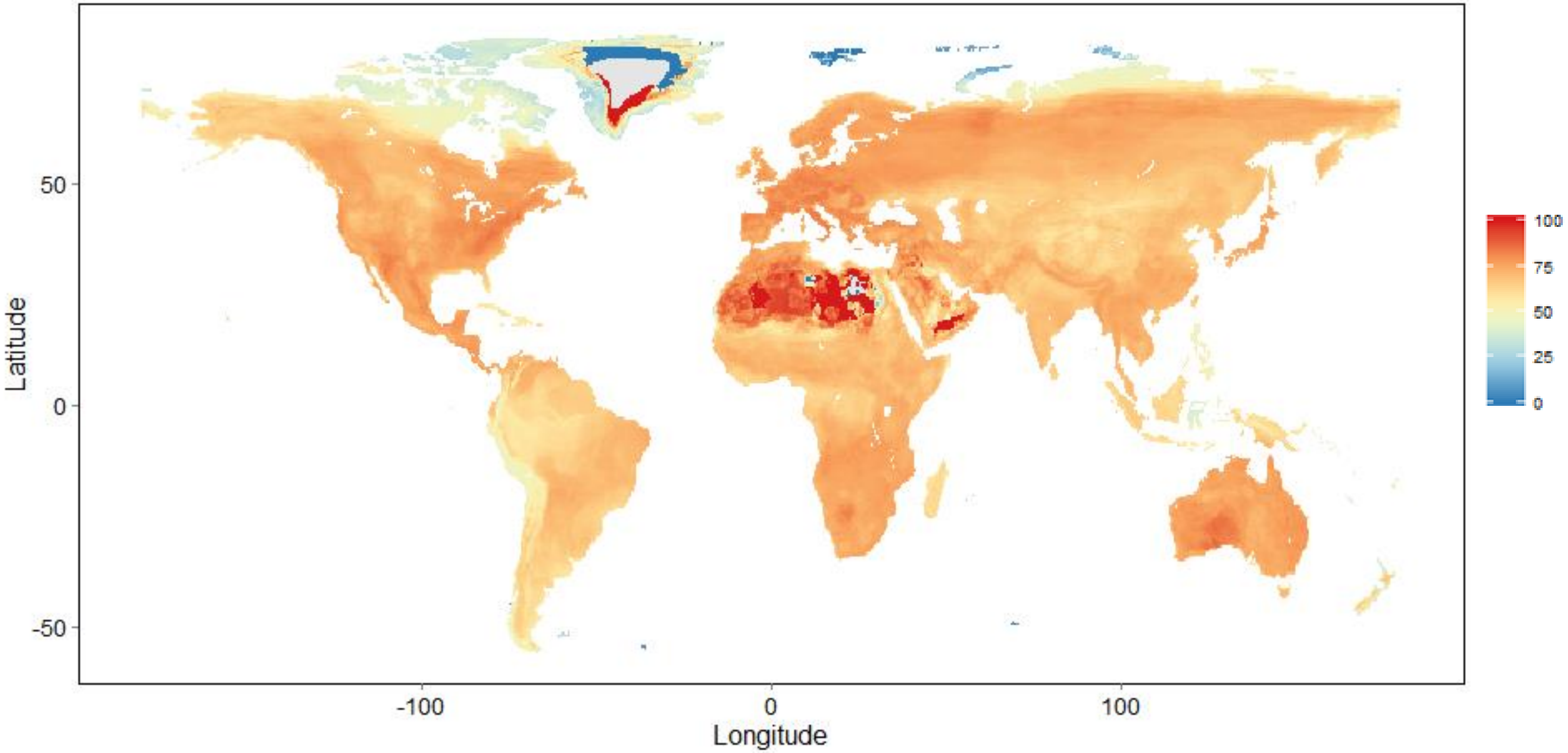

Figure 1: The percentage of species in each 0.5-degree terrestrial cell with at least one modelled survival estimate. The red colours represent a high percentage of species in that area with modelled survival estimates, whereas the blue colours indicate that few species in that area have modelled survival estimates. The grey areas indicate no species were present in these areas.

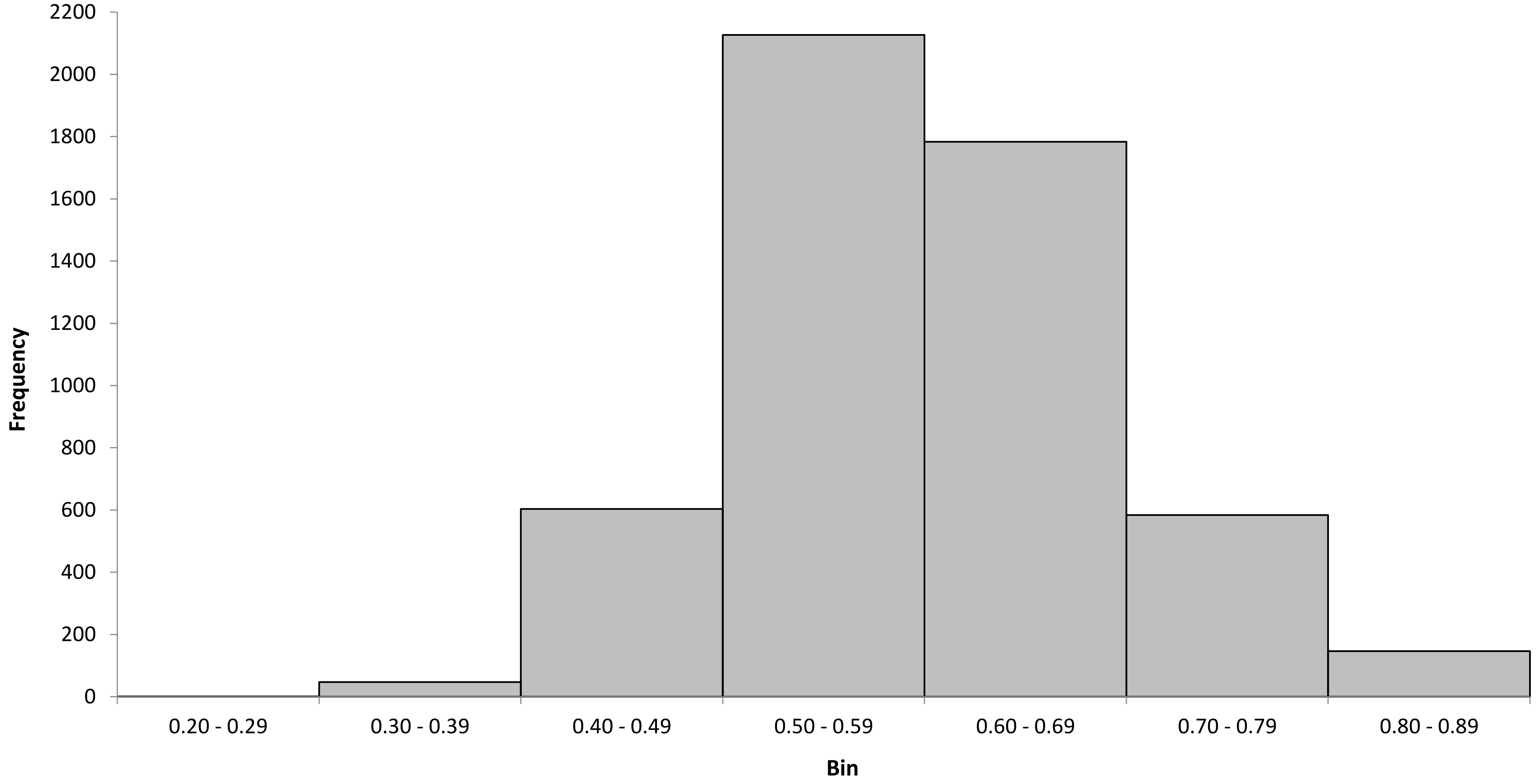

Figure 2: The frequency of annual mean adult survival probabilities, grouped into bins of 0.9

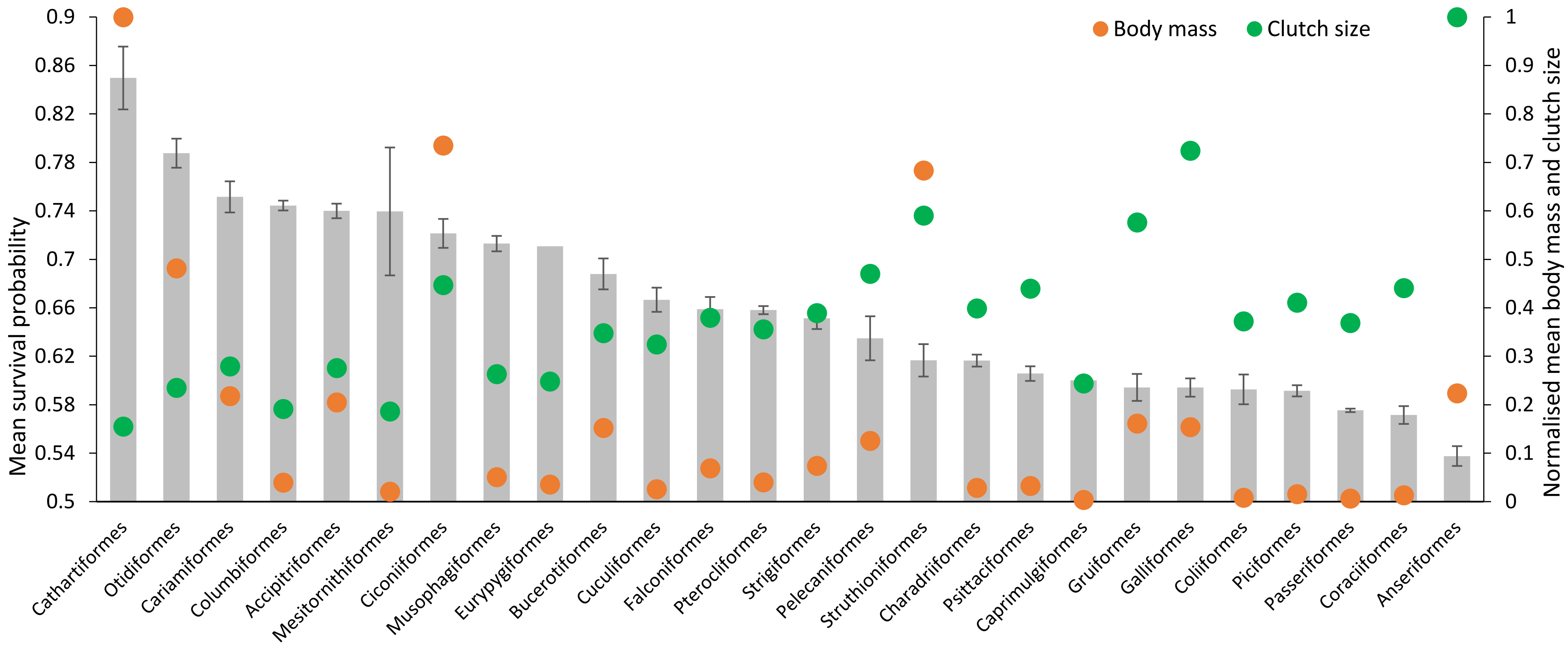

Figure 3: The modelled annual mean adult survival probabilities grouped by taxonomic order. The error bars show the SEM. The orange dots represent the normalised mean body mass of each order. The green dots represent the normalised mean clutch size of each order. The number of species with data in each order are as follows: Cathartiformes, 4; Otidiformes, 23; Cariamiformes, 2; Columbiformes, 185; Accipitriformes, 172; Mesitornithiformes, 2; Ciconiiformes, 5; Musophagiformes, 21; Eurypygiformes, 1; Bucerotiformes, 50; Cuculiformes, 64; Falconiformes, 43; Pterocliformes, 15; Strigiformes, 96; Pelecaniformes, 19; Struthioniformes, 31; Charadriiformes, 164; Psittaciformes, 187; Caprimulgiformes, 307; Gruiformes, 111; Galliformes, 206; Coliiformes, 6; Piciformes, 210; Passeriformes, 2847; Coraciiformes, 86; Anseriformes, 84.

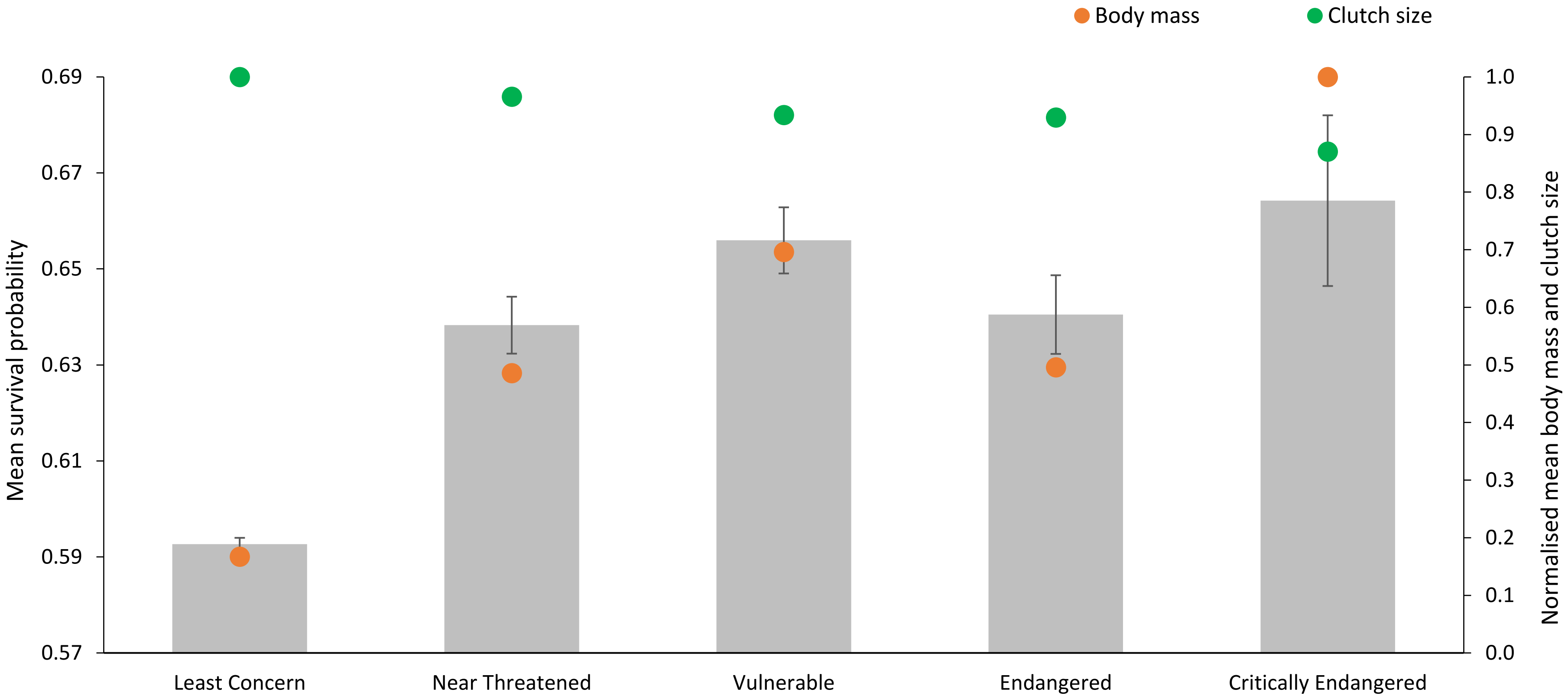

Figure 4: The modelled annual mean adult survival probabilities grouped by IUCN status. The error bars show the SEM. The orange dots represent the normalised mean body mass of each order. The green dots represent the normalised mean clutch size of each order. The number of species with data in each category are as follows: Least Concern, 4255; Near Threatened, 308; Vulnerable, 217; Endangered, 115; Critically Endangered, 42.

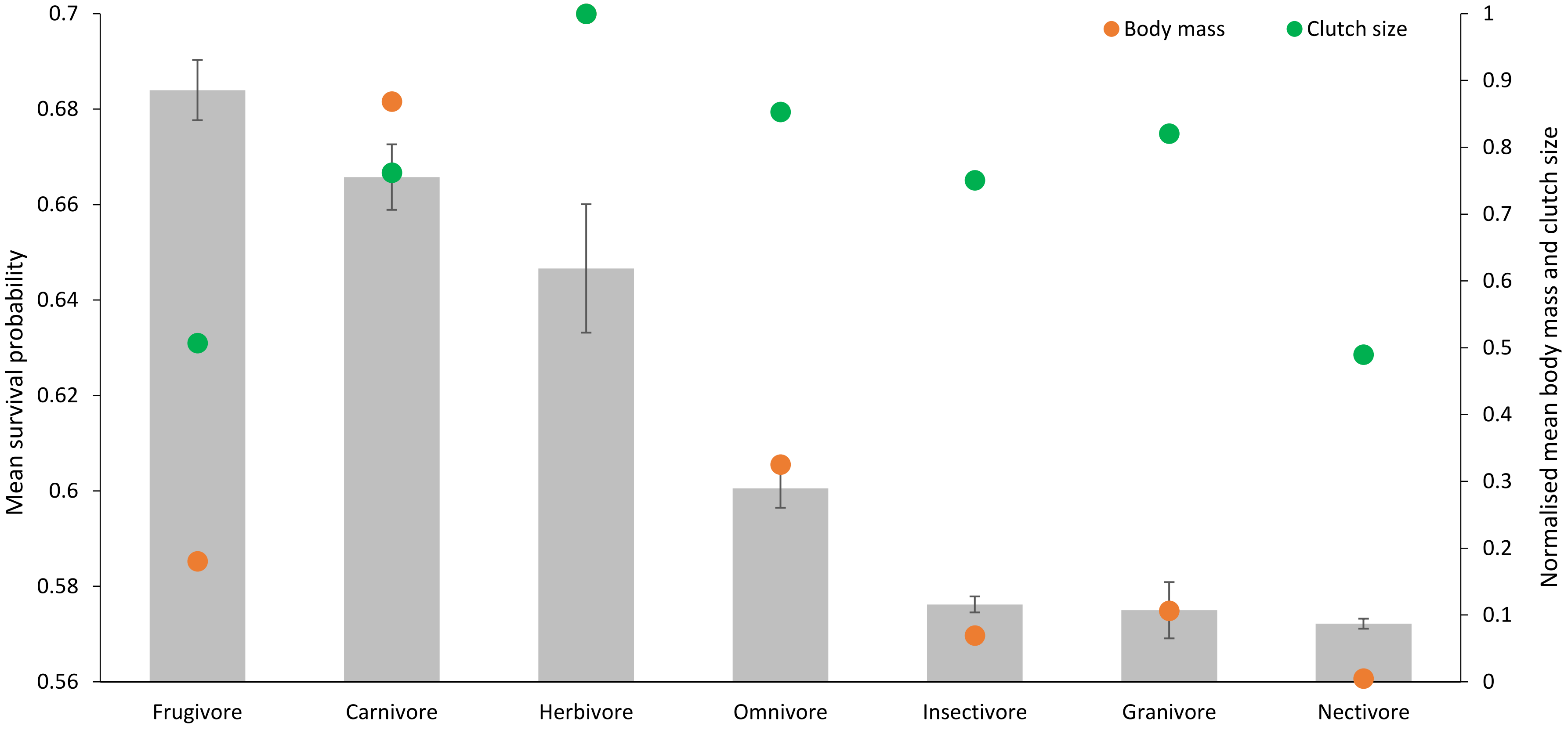

Figure 5: The modelled annual mean adult survival probabilities grouped by feeding guild. The error bars show the SEM. The orange dots represent the normalised mean body mass of each order. The green dots represent the normalised mean clutch size of each order. The number of species with data in each feeding guild are as follows: Frugivore, 198; Carnivore, 210; Herbivore, 79; Omnivore, 485; Insectivore, 2194; Granivore, 311; Nectivore, 205.

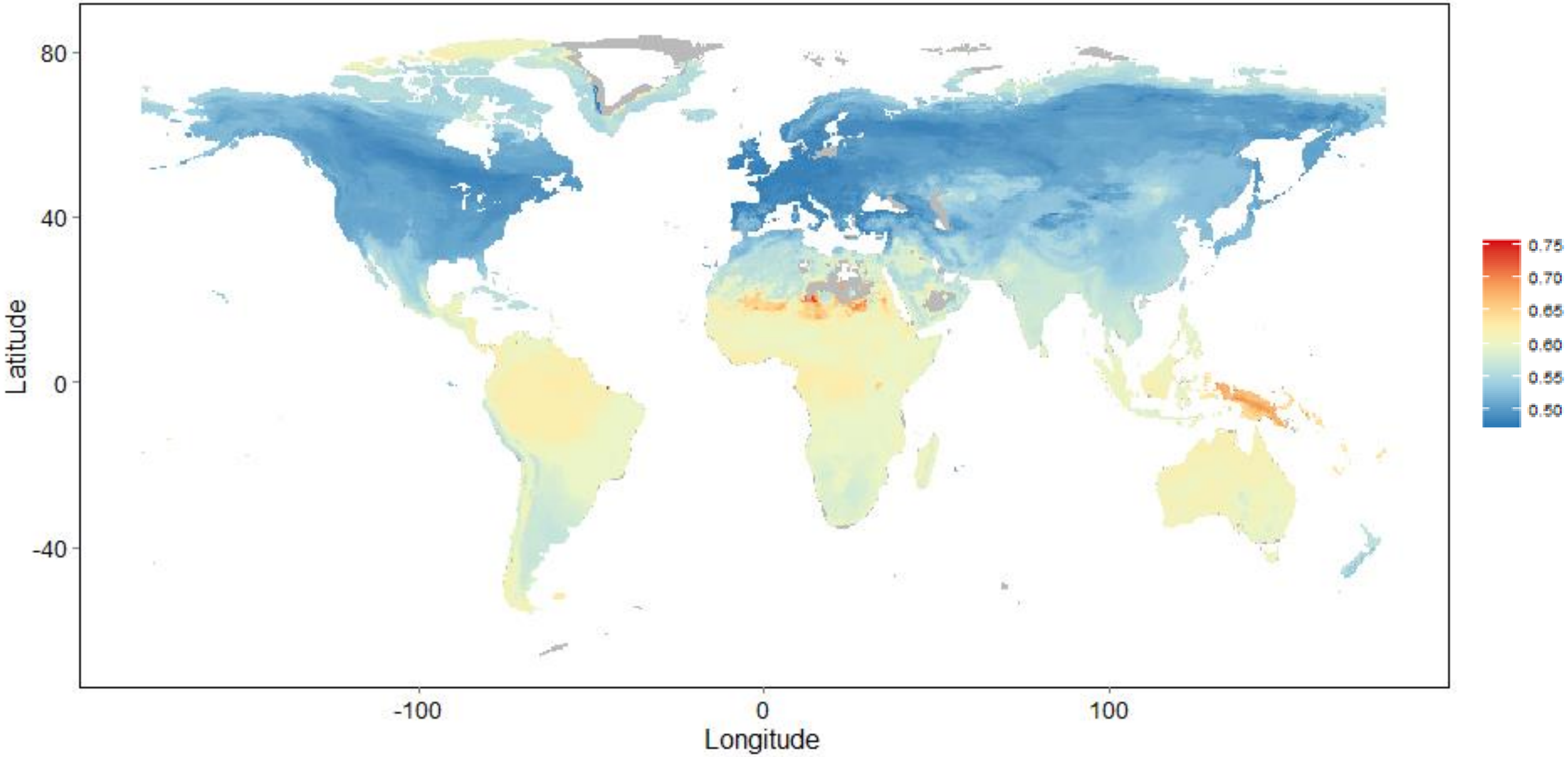

Figure 6: The modelled mean adult survival probability for each 0.5-degree cell across the globe. The red colours indicate a high survival probability for that area, whereas blue areas indicate a low survival probability for that area. The grey areas highlight areas that are data deficient in terms of survival probabilities.

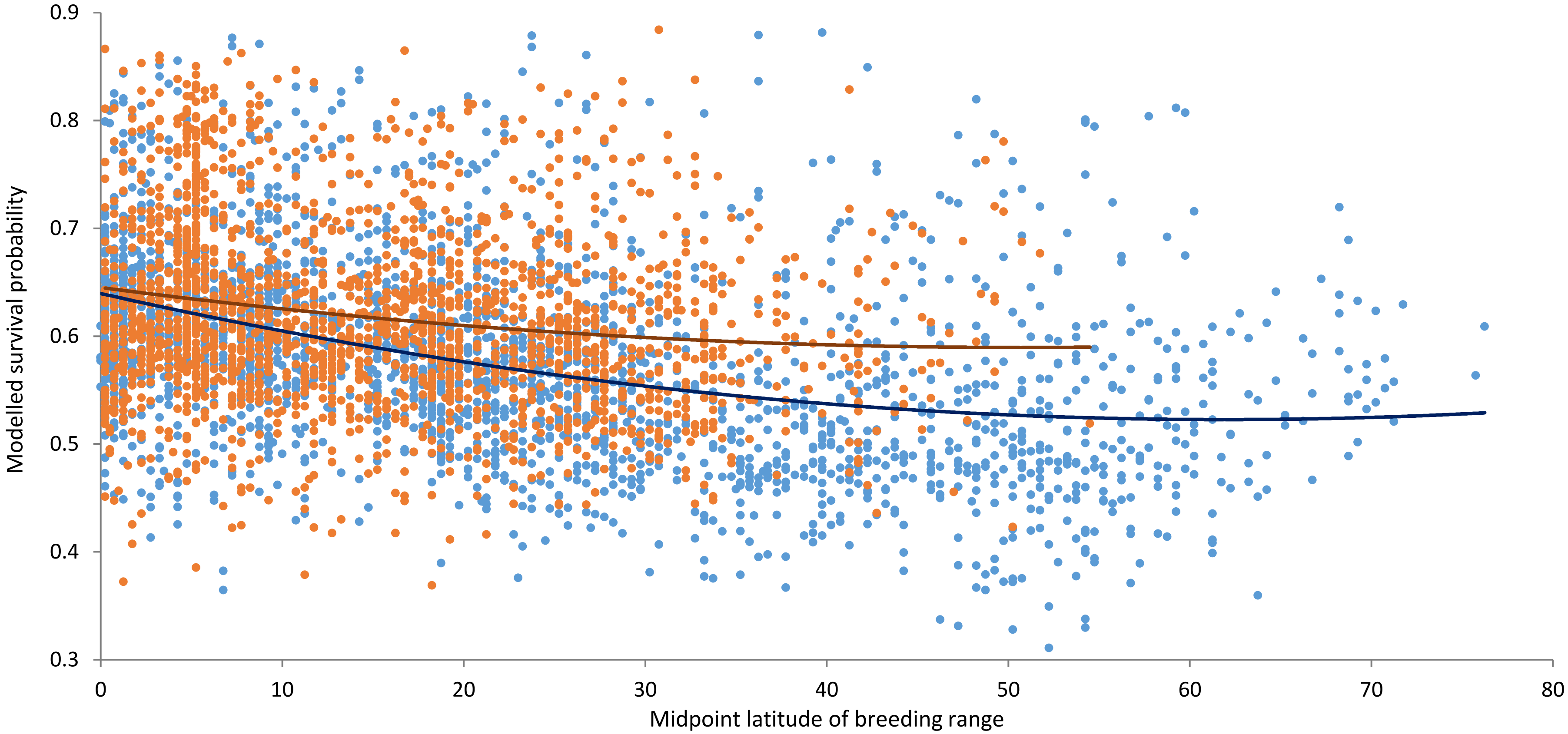

Figure 7: The modelled mean adult survival probability for each species against their midpoint latitude of their breeding range. The blue points indicate species with a breeding range latitude in the northern hemisphere; a quadratic curve of best fit in blue (R^2=0.17). The orange points represent species with a breeding range latitude in the southern hemisphere, quadratic curve of best fit in orange (R^2 = 0.03).

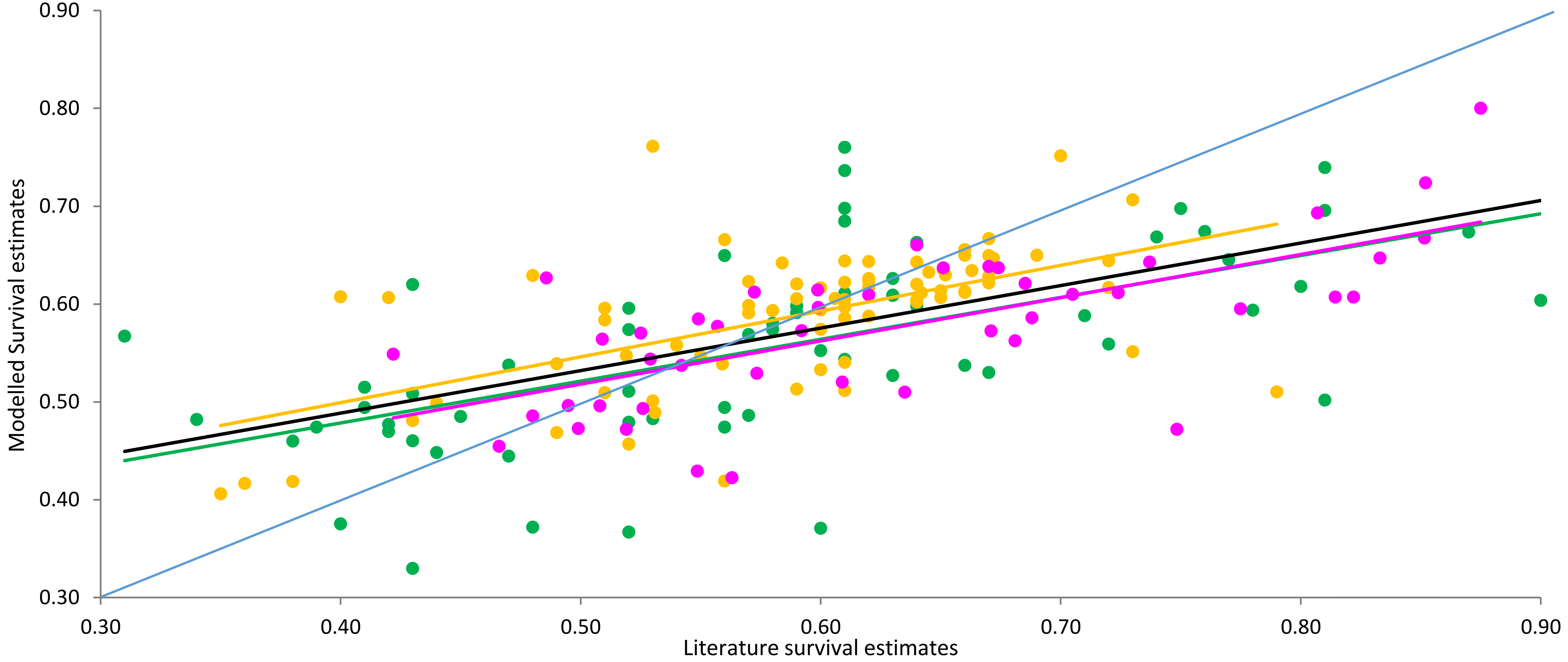

Figure 8: Species modelled survival estimates plotted against their mean survival estimate from the literature. The best fit line of all the data is represented by a black line and the R^2 value is 0.37. A Line of modelled survival estimate to literature survival estimate is shown in blue. The yellow points and line of best fit represent species just from the Americas, $R^2 = 0.33$ (n=75). The green points and line of best fit represent just European species, $R^2 = 0.36$ (n=62). The pink points and line of best fit represent just African species, $R^2 = 0.47$ (n=47).

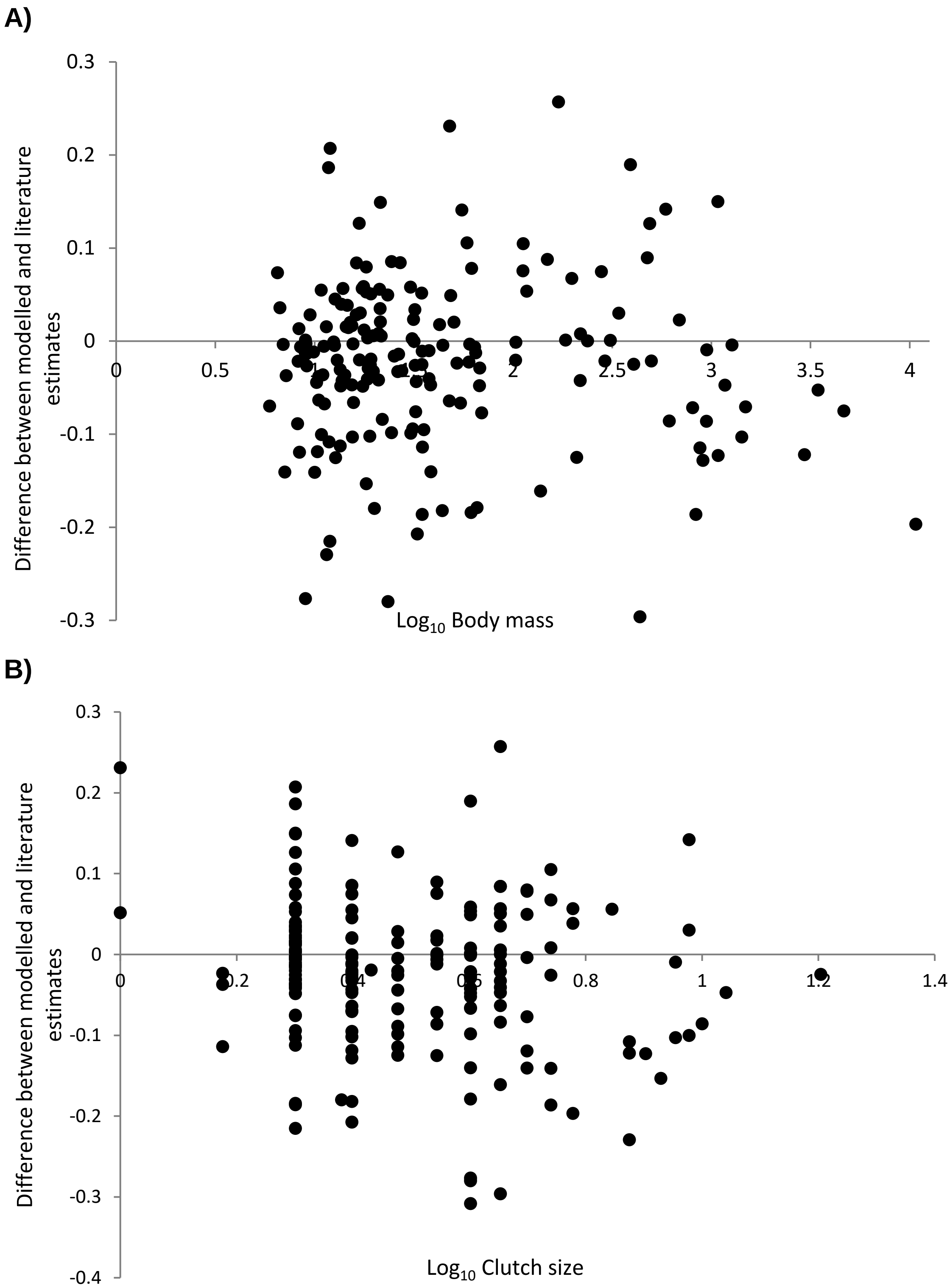

Figure 9: The absolute difference between species modelled and literature estimates against their respective body mass or clutch size. **A)** Body mass **B)** Clutch size. Neither relationship was significant.

Discussion

Model reliability and accuracy

Overall, we found a moderate correlation between the modelled survival estimates and the survival estimates collected from the literature (Figure 8). However, limited data availability meant we were only able to collect 184 survival estimates from the literature. This does not allow for many comparisons to be made between the estimates, and consequently this gives us less certainty in any conclusions we draw about the similarities and differences between our model and previous research. Furthermore, nearly all the literature estimates collected were calculated through mark-recapture methods. As described earlier, this method has limitations, which can reduce the accuracy of the data. We therefore suggest that future research attempts to gather more survival estimates, and if possible more than one estimate per species, so any comparisons that are made are more robust and reliable.

Regardless of the above limitations, this work has found a moderate correlation between the modelled and literature estimates. The correlation was not dependent on body mass or clutch size (Figure 9) but did improve when modelling just African species, as opposed to just European or American species (Figure 8). This is expected since the model used was developed using data from southern African species (Collingham *et al.* 2014). However, even Collingham *et al.* (2014) noted that there was variation between the survival rates they calculated through their model and the observed survival rates. This suggests that other variables, which were not included in the model, could be influencing the survival of birds. For example, environmental conditions such as extreme weather or changes in resource availability will impact the survival of most species (Bocci *et al.* 2010 and Sandvick *et al.* 2005). Survival is also likely to be influenced by density dependent processes such as competition and predation (Saether *et al.* 2002), and the survival of some species such as waterfowl and game birds is also heavily influenced by hunting. However, although these variables are likely to affect the survival of birds to at least some extent, it is difficult to quantify these factors for each species and thus the availability of data for these variables is very limited. Furthermore, even when the data is available it can often not be verified or checked for accuracy, and therefore it could be argued that this data shouldn't be included in models. Consequently, at this present time, we believe this model is the best method available for estimating adult survival probabilities for a large number of avian species.

Observations from the model

In total, we calculated mean annual adult survival rates for approximately 53% of avian species. The majority of these species had a modelled survival probability of over 0.5 (Figure 2). However, approximately 650 species had survival rates under 0.5. The species with the lowest survival rates tended to be those within the Passeriformes, Coraciiformes or Anseriformes orders (Figure 3), species that had diets of insects, seeds or nectar (Figure 5) and species in the northern hemisphere (Figure 6 and Figure 7).

The taxonomic order with the highest mean annual adult survival (of 0.85) was the Cathartiformes order (New World Vultures). These vultures are expected to have a high survival rate because they have the highest average body mass and lowest average clutch size among all other orders (Figure 3). It has also been suggested that vultures have high survival rates because they have evolved to resist bacterial toxins (Roggenbuck *et al.* 2014). However, they are increasingly at risk of persecution from humans, which could lower their future survival chances (Ogada *et al.* 2011). Conversely, the order with the lowest survival probability (0.54) was the Anseriformes (Waterfowl). This taxonomic order has a high clutch size; on average over 8 eggs per clutch (Figure 3). Large clutch sizes such as these are thought to decrease adult survival due to the energy expended on brooding and caring for the young (Saether 1988). A recent study on Eider ducks (*Somateria mollissima*) found that, under heightened exposure to avian cholera, the reduced fitness caused by large clutch sizes made them more susceptible to the disease, and reduced their survival (Descamps *et al.* 2009). Thus, in species where a high clutch size is thought to be the main cause of low adult survival rates, conservation efforts should focus on ensuring adult birds have sufficient resources to keep their energy reserves high. If possible, the breeding environment should also be well conserved to ensure any environmental stresses are mitigated, otherwise the effects of these stresses could be magnified in birds with reduced fitness, which would further decrease their survival.

Amongst the IUCN Red List conservation categories, all species classified as Near Threatened or Threatened (Vulnerable, Endangered and Critically Endangered) have a higher predicted mean adult survival rate than those classified as Least Concern. However, the differences in survival between these groups is small and the variation in the estimates within each of these groups is large (Figure 4). This suggests that the difference in the survival rates between these categories is very minimal and potentially not robust enough to draw meaningful and valid conclusions from. As no real differences are apparent across the categories, this perhaps suggests that these calculated survival rates are not a good measure of threat status, which is not surprising given that this relies on a number of other key metrics including population sizes and range sizes, which these survival estimates do not (IUCN 2001). However, they could perhaps be used side-by-side to provide greater insight into prioritising the conservation of birds.

Survival probabilities amongst feeding guilds vary less than amongst taxonomic orders; the lowest average survival probability across all seven feeding guilds is 0.57 but the highest is just 0.68 (Figure 5). This could explain why we do not see the same trend as seen in the paper by Peach *et al.* (2001). Our model predicts that Frugivorous species have the highest mean adult survival probability. Research has shown that fruits are more abundant and easier to obtain than other food items such as insects (Martin 2015). This, in turn with their comparatively low clutch size, makes it easy for frugivorous adults to get the food they require and provide for their young (Jetz *et al.* 2008): their fitness remains high giving them a higher chance of survival.

Across latitudes our model predicts that survival probabilities are marginally higher in the southern hemisphere than in the northern hemisphere (Figure 6 and Figure 7) and this trend has also been found in research, for example see Piper (2002) and Skutch (1985). This is most likely driven by the strong correlation between clutch size and latitude (Ghalambor *et al.* 2001 and Biancucci *et al.* 2010). For example, in the northern hemisphere there is very strong seasonality which can result in very harsh winters. This can reduce the survival of species especially if they're small bodied (Saether 1989), and therefore there is selection for fast maturation and reproduction. In contrast, the tropical parts of southern hemisphere have limited seasonality and so have fewer fluctuations in the abundance and availability of food resources (Karr 1976), allowing for higher survival chances. Therefore, to ensure adult bird populations in the northern hemisphere stay viable, conservation efforts may want to focus on ensuring food resources are available and abundant throughout the year.

Concluding thought

In conclusion, although Collingham *et al.* (2014) were cautious about applying this model to birds outside of southern Africa. We have been able to demonstrate that it is possible to use this method to calculate survival rates of birds across the world with some degree of feasibility. Overall, this method is an easy and useful approach for quickly estimating mean annual adult survival probabilities. Traditional field methods, such as mark-recapture of live or dead recoveries, are expensive, resource intensive and time consuming. They are also highly likely to underestimate survival rates and are difficult to apply to rare species, which are arguably the most important species to study in terms of conservation. In contrast, this method can be applied systematically to all avian species that have available body mass and clutch size data. We have been able to apply this method relatively easily to over 50% of all avian species, and to the best of our knowledge this is largest number of survival estimates that has ever been calculated. These estimates now give a good framework to work with and highlight species and groups of species that perhaps need more investigation and attention in terms of conservation. They could also be used in PVA models to calculate extinction risks of birds. Extinction risks are perhaps even more useful than survival probabilities alone as they can inform us how likely the extinction of a species is based on a number of key parameters. In contrast, the survival estimates presented here are just for a given year and are independent of factors such as climate change, and should therefore be used in initial estimates only.

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Chapter five: Synopsis

The need to calculate extinction risks

Many scientists believe we are now experiencing the ‘sixth mass extinction event’ (Cellabos *et al.* 2015). Since the 1500s there have been over 800 species extinctions (Proença and Pereira 2013), of which over 200 have been avian and mammalian species (Baillie and Cokeliss 2004 and Butchart *et al.* 2010). And since the twentieth century, there have been over 100 documented extinctions of amphibians, birds and mammals (Mace *et al.*, 2005), which is 30-120 times greater than the background extinction rate (Proença and Pereira 2013). This doesn’t include extinctions of undescribed species, so the actual number of extinctions may be much larger (Scheffers *et al.* 2012 and Costello *et al.* 2013), and perhaps more than double the recorded value for some taxa (Tedesco *et al.* 2014). On top of this, current climate change is expected to increase the extinction probability of many species (Araújo *et al.* 2006 and Barnosky *et al.* 2011), and Thomas *et al.* (2004) predict that under intermediate climate warming scenarios 15-37% of species will be committed to extinction by 2050. Despite the best efforts of conservationists worldwide, species extinction risks continue to rise (Butchart *et al.* 2010 and Pimm *et al.* 2014), and coupled with limited funding and resources, this means conservation management must be prioritised (Bottrill *et al.* 2009 and Arponen 2012).

Population viability analysis (PVA) models can help prioritisation by providing empirical estimates of extinction risks for individual species (Beissinger 2002 and Reed *et al.* 2002). PVA models differ in complexity, and as computational power improves and modelling techniques advance, increasingly complex scenarios can be modelled using PVA. However, parameterising such models with sufficient data remains a challenge. For example, VORTEX (a computer simulation model for PVA) has 65 input criteria, 11 of which are essential (Morrison *et al.* 2016). Morrison *et al.* (2016) found that, despite only studying models they believed would have the highest number of demographic parameters, up to 43 of these parameters could be missing in a single PVA model and 12% of the avian PVAs examined did not even meet the minimum data requirements. This is surprising: given that birds are some of the most well studied species in the world, we would expect a wealth of information to be readily available. Available information includes distributions and conservation statuses. However, when we consider other data, such as densities, abundances and life history traits (all of which are necessary to successfully carry out PVAs), it becomes apparent there are significant gaps in our knowledge. Even when these data are present, they are often located across numerous journals in individual species papers, and despite the best efforts of large teams of researchers producing resources like Handbook of Birds of the World Alive (del Hoyo *et al.* 2015), little headway has been made at synthesising all this information in a form that is easily accessible.

Therefore, the aims of this thesis were to estimate and model densities, population sizes and survival rates for as many birds in the world as we could, with the intention of bringing us a step closer to being able to run PVA models for a large number of species.

Estimating data parameters

Species densities underpin much of our understanding of the extinction risks birds face as they are directly linked to population sizes. We modelled densities for a total of 8,541 species with a correlation coefficient of 0.37. This low accuracy suggested other variables not included in our model were contributing to density patterns. For example, biotic interactions, nest availability and current climate and land use change are just some of the variables not included that may have an impact on density. However, we noted that these variables were difficult to quantitatively measure and no large reliable data sources were available, and therefore it was not possible to include these variables in our analyses. The low predictive ability could also be due to the amount of missing data within our model. In the dataset used, over 70% of species were missing density data, and many were also missing data for a number of explanatory variables. It has been suggested that you can only predict missing data well if fewer than 60% of the values in the dataset are missing (Penone *et al.* 2014). We therefore concluded that to improve the modelling of species densities, future research efforts should focus on gathering more data either through field methods or through robust modelling methods.

Despite the potential inaccuracies of the density data we modelled, we were able to use these values to calculate species population sizes with no effect on the accuracy of the modelled population sizes. In total, we calculated population sizes for 6,206 species with a correlation coefficient of 55%. Individual population sizes varied from under 100 individuals to over 1 billion individuals, and we estimated there to be as many as 295 billion individual birds across the globe. It is well known that population sizes are one of the most useful demographic parameters to include in PVA models due to their strong correlation with extinction risk (O'Grady *et al.* 2004). We concluded that future research could further improve the accuracy of these modelled population sizes (and thus extinction risks calculated with them) by using multiple density estimates per species and by incorporating the effects of climate change on the distribution polygons; this will again require more data collection.

The final data parameter calculated were survival estimates. These are another vital demographic parameter to include in PVA models and can also be used to infer morality rates, which can also be used in these models. In total, we calculated survival estimates for 5,291 species with a 36% accuracy. This accuracy improved to 47% when just African species were considered, mirroring the results of Collingham *et al.* (2014). However, due to the limited amount of survival data available in the literature, we concluded that more survival estimates from the field are needed before any definitive conclusions could be drawn about the accuracy of model. Only after this is achieved can we infer the reliability of the model when applied globally.

Are there enough data available for PVA models?

There are two schools of thought for PVA modelling: build the simplest model that encompasses the most important robust parameters only; or build a complex model that can be supported by available data of sufficient quality (Pe’er *et al.* 2013). Often the data available dictates which path is followed; for example, Radchuck *et al.* (2016) found that the availability and resolution of dispersal data, spatial data and demographic data had the greatest influence on what type of model was selected. For well-known keystone species or commercial species associated with tourism or hunting, complex PVA models can often be run as more resources are available for data collection (Morrison *et al.* 2016). In contrast, as we have shown in this thesis, the majority of avian species have very limited data available. This means that typically only simple PVA models can be run that have limited predictive power (Radchuck *et al.* 2016). If more complex models are run the data used are not always robust, and this can reduce the replicability of the models (Morrison *et al.* 2016).

At present, the number of published avian PVA models remains low. In this thesis, we have calculated densities, population sizes and survival rates for over half of the worlds birds. We believe this is a huge step forward in being able to calculate extinction risks for a significant number of species. However, even for the simplest PVA models, some data are still crucially missing. Perhaps most fundamentally, data on fecundity is still needed. For avian species, this can be calculated from clutch size data (which we collected in chapter 4) and data on the number of broods per year. Once this data has been collected, very simple population models could be performed using this and the rest of the data collated in this thesis.

The real utility of PVA models arises when we can model more complex and accurate scenarios by including the effects of density dependent processes, spatial processes, stochasticity, genetics and climate change. By calculating extinction risks under these scenarios the results become more realistic since they better reflect the experiences of a species. However, both Pe’er *et al.*

(2013) and Morrison *et al.* (2016) noted that most studies struggled to include these parameters in their PVA models due to limited data availability. For example, out of all of the studies Pe'er *et al.* (2013) looked at, they found only 3% included Allee effects and only 9% included spatial heterogeneity. Furthermore, when stochasticity is included in models, it often isn't separated into environmental, demographic or genetic stochasticity, and often catastrophes and disturbances are included within environmental stochasticity even though they have shown to have different effects on PVA outcomes (Morris & Doak 2002). If robust and reliable data can be collected for all these variables and included in PVA models, the results from the models would be truly informative and insightful for conservation management and prioritisation.

Concluding remarks

The aims of this thesis were to review and collate the available data on densities, population sizes and life history data for all bird species. We also aimed to estimate densities, population sizes and survival rates for the remaining birds which had no available data. Finally, we sought to make recommendations on what further data needed to be collected in order to run the best possible models for PVA. We believe this thesis has met all these aims, and there is now real scope for future research to build on this work.

The IUCN Red List currently uses PVA predictions (under Criterion E) to classify endangered species (Brook and Kikkawa 1998). To be listed as being critically endangered, quantitative analysis (such as a PVA models) must show that the species has a 50% chance of extinction within 10 years (Vié *et al.* 2009). However, of the 1,375 bird species listed on the Red List as being threatened, none have been assessed under criteria E (IUCN, 2014). Future research has the potential to change this, and this could make Red Listing more replicable (if the PVAs themselves are reliable and replicable).

However, researchers must first decide what type of models to run. On the one hand, simple PVA models would require little further data collection, so results could be generated sooner; given the state of current biodiversity this can only be a good thing. However, these models might not produce the most accurate or realistic extinction risks. In contrast, researchers could opt for producing more complex models, which are arguably more useful as they better simulate species populations. However, these models require a lot more data to be collected, especially if run on large scales. Ultimately, both these methods have their benefits and limitations. We recommend that simple models with robust data should first be run to gauge the extinction risks of many species. Results from these models should then be used to highlight those species with the highest extinction risks, and more complex models then run for just these species (after more detailed data had been collected). By not aiming to run complex models for all the bird species in the world, the amount of data collection required is dramatically reduced and is potentially much more achievable for conservationists.

In conclusion, the short term aims of any future research should be to collect more avian life history data in order so PVA models can be performed. There is great scope to involve members of the public and amateur ornithologists, as citizen science programmes have all already been shown to generate high quality avian data (Sullivan *et al.* 2009). We strongly believe that better data availability and transparency should be advocated through open source databases, as we believe this would encourage PVA research and could significantly advance the field. This will mean that, in the long-term, future research can focus on producing robust PVA models, ensuring all extinction risks calculated are as reliable, and thus useful, as possible. Finally, we believe it will also be important to find new methods of running PVAs that don’t rely on readymade software such as VORTEX or RAMAS, as this will not only allow for multiple PVAs to be run at once, but will also ensure that researchers do not rely too heavily on default values. This will ensure results are more robust (Morrison *et al.* 2016). This will improve the reporting of findings, as researchers will have a greater understanding of the underlying concepts of the model (Pe’er *et al.* 2013); this will result in more replicable PVA models and will increase the rigour of the research.

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