Towards population estimates for birds of central Africa's Albertine Rift

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Abstract

Globally, biodiversity faces severe pressures, which are likely to increase with ongoing climate change and a growing human population. Despite birds being one of the world's best-monitored taxa, data on population sizes, distributions and demography remain patchy, rendering threat evaluation and mitigation planning difficult. Few studies comparing impacts of data collection methods on population estimation exist. Accurate population data are fundamental for conservation applications. In this thesis, I first use distance sampling, a method of density estimation accounting for individuals' detectability, to compare the efficacy of two widely-used data collection methods, line transects and point counts. I demonstrate point counts obtain systematically higher density estimates, and show there are marked differences in estimates between methods related to species behavioural and morphological traits. The results demonstrate that survey method should be evaluated case-by-case, considering issues such as target species and landscape characteristics. Following this, I apply distance sampling to estimate population sizes of birds across regions of central Africa's Albertine Rift, a global biodiversity hotspot lacking baseline data. This region harbours the continent's highest levels of vertebrate species richness and endemism but faces major threats from climate and land-use change. This work reveals non-uniform patterns of species richness and densities, helping identify priority regions and habitats to protect individual endemic and threatened species. Finally, I investigate the effects of competitor abundance and habitat on abundance of the endemic and threatened bird species in the region. These analyses indicate little effect of competitor abundance, with habitat being a more important determinant of population sizes. In fact, species identified as competitors largely occur at higher abundances when co-occurring, something possibly attributable to habitat quality effects dominating over competitive interactions in driving density patterns. These findings suggest that translocation of species between mountain peaks in the Albertine Rift, a possible solution to extinction risk in this region where many populations occur on isolated high elevation sites, is unlikely to be detrimental to potential competitor species already present at recipient sites.

Towards population estimates for birds of central Africa's Albertine Rift

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Declaration

The material contained within this thesis has not been previously 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.

Oscar Dewhurst

March 2019

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1

General Introduction

1.1 Introduction

Species are currently experiencing significant and rapid population declines and extinctions on a global scale. Anthropogenic influences are a significant factor in an extinction rate between 100 and 10,000 times greater than background rates (Dirzo and Raven, 2003; Brook *et al.*, 2008). This reduction in biodiversity will likely have pronounced severe effects on ecosystem function (Loreau *et al.*, 2001), lessening their resilience to environmental change (Peterson *et al.*, 1998; Chapin *et al.*, 2000) and severely influencing the provision of ecosystem services (Tilman *et al.*, 2006; Worm *et al.*, 2006; Cardinale *et al.*, 2012). The current global biodiversity crisis can be attributed to a range of causes operating on both local and larger scales. The former includes habitat loss and degradation, invasive species and overexploitation, whereas the latter comprises processes such as climate and land-use change. Whilst traditionally, local scale processes were regarded as the main cause of population declines (Diamond, 1989, Pearce-Higgins and Green, 2014), today it is arguably the processes operating on a larger scale that pose a more significant threat, due to ongoing climate change and a rapidly rising global human population (Bellard *et al.*, 2012). There is evidence that, in the next few decades, climate change may overtake habitat destruction to become the most significant global threat to biodiversity (Leadley *et al.*, 2010). Between 1880 and 2012, global temperatures have risen on average by 0.85°C (IPCC, 2014), and there is significant evidence that these recent climatic changes have led to responses in many species, including changes in phenology (Crick *et al*, 1997; Warren *et al.*, 2001; Fitter and Fitter, 2002; Root *et al.*, 2003; Menzel *et al.*, 2006; Yang and Rudolf, 2010), species range and distribution (Parmesan *et al.*, 1999; Beaugrand *et al.*, 2002; Walther *et al.*, 2002; Zuckerberg *et al.*, 2009), community composition and dynamics (Pounds *et al.*, 1999; Menéndez *et al.*, 2006; Both *et al.*, 2009; Yang and Rudolf, 2010), ecosystem structure and dynamics (Polovina, 1996; Visser *et al.*, 1998; Pounds *et al.*, 1999; Both and Visser, 2001), and life-history parameters (Smith *et al.*, 1998; Catchpole *et al.*, 2000; Møller and Szép, 2005; Yom-Tov *et al.*, 2006; Twiss *et al.*, 2007).

Today, birds are one of the most highly monitored taxa in the world, resulting in large datasets spanning considerable time periods. From these, we have gained important insight into ecological aspects such as community composition, species abundance and migration, and understanding into applied processes such as the effects of climate and land-use change over time (e.g. Boren *et al.*, 1999; Jenni and Kéry, 2003; Shoo *et al.*, 2005; Huntley *et al.*, 2006; Lemoine *et al.*, 2007; Huntley *et al.*, 2008; Devictor *et al.*, 2012; Lindström *et al.*, 2012; Stephens *et al.*, 2016). Essential but basic information on birds that allows this sort of work includes baseline data on their abundances. These are crucial to be able to prioritise locations and habitat types for conservation (Gregory and Baillie, 1998; Pérez-Arteaga *et al.*, 2005), given the future pressures likely to be imposed by increasing global human population and climate change. Baseline data that allow for the calculation of population densities are also vital to determine which species should be listed as being of conservation concern, and therefore where conservation efforts and funding should be targeted, in a world where resources for conservation are severely limited (IUCN, 2004).

Despite the evident importance of baseline data on bird densities and the widespread monitoring of birds that occurs, such population density data are often lacking, particularly in tropical areas, which often harbour the highest levels of species richness and endemism, and which face significant threats from climate change and an expanding human population (Laurance and Peres, 2006; Bradshaw *et al*., 2009). Developing countries, which hold a large extent of tropical areas, are experiencing greater rates of population increase than the global average, placing severe threats on biodiversity (Roland Berger, 2011). The importance of, and relative paucity of, baseline biodiversity data means the efficacy of the methods used to collect raw data, which often form the basis of population estimations, must be considered. Several methods currently exist to estimate bird abundance, though there is little information on whether there exist systematic differences between them, and whether there are situations in which one should be preferred over another.

In the following section I first provide an overview of the survey methods currently used in studies of bird abundance, and their associated benefits and pitfalls. Following this, I briefly cover the effects of climate change on biota, before focusing on threats facing tropical regions, specifically climate and land-use change. Next, I introduce the Albertine Rift, and the pressures it is facing. I then look at possible implications the results may have, Finally, I outline the specific aims of this project.

1.2 Methods for estimating bird abundances

There are several options for estimating abundance of bird species, ranging from relatively time- and labour-intensive methods such as territory mapping (involving repeat surveys of nesting territories), through to very simple species lists. The latter are most frequently used in speciose and infrequently visited parts of the tropics due to their relative simplicity and speed. Unfortunately, species lists provide very little information other than simply species presence/absence, and so are little help in deeper investigation of any changes that may be occurring. Timed species lists and McKinnon lists (MacKinnon and Phillipps, 1993; Poulson *et* *al*., 1997) provide slightly more information on relative abundances but they are incapable of generating data for, for example, population estimates.

Today, one of the most widely applied methods to estimate densities, an approach increasingly recognised as the 'industry standard', is distance sampling (Buckland *et al*., 2001), which takes account of the fact that bird detectability declines with distance from the observer. However, the shape of this detectability function is not constant; it differs depending on factors such as species, time and habitat. Distance sampling allows for this (Buckland *et al*., 2001; Rosenstock *et al*., 2002), and estimates densities incorporating both observed and unobserved birds via modelling the distance function (Gregory *et al*., 2004). However, there are several assumptions associated with the method that must be considered and their effects minimised in the field, such as the fact that all species located on the transect line/point count station are recorded (this may not be the case for particularly cryptic or shy species) (Buckland *et al*., 2001).

1.2.1 Line transects and point counts

Raw data collection tends to use one of two main methods: point counts, whereby birds are recorded at regular intervals along the route for a set duration, and line transects, whereby recording is continual along the pre-defined route. These two survey methodologies are preferred as they are flexible and adaptable to a wide range of situations, such as calculating relative and absolute measures of bird abundance and investigating bird-habitat relationships, and can be used in terrestrial and aquatic systems. However, so far there has been little study considering the differences in results obtained by each method in the same area, yet this surely has significant implications for future study, if systematic differences between the two methodologies exist. Both methods require significant levels of observer skill to be able to correctly identify birds by both sight and sound. Recording the distance at which each observation was made (for line transects, perpendicular distance from the transect line is used) provides a detectability measure and allows calculation of population density estimates. These distances can either be exact or placed into categorical distance bands.

Line transects are carried out by recording birds either side of a predetermined route, as the observer walks along the transect. The perpendicular distance to a bird seen/heard from the transect line is also recorded, either exact (in practice, to the nearest metre) or in distance bins. The arrangement of the transects can be random, such as using random selection of start and end points, or regular and systematic, such as parallel transects running from east to west, or a series of transects all positioned along an axis of the study area. Alternatively, a stratified random approach can be used, ensuring that each transect is located within a different habitat stratum, but within which transect start points and direction are selected randomly. In practice, flexibility is likely to be required, and there will likely be discrepancies between actual and ideal routes due to obstacles such as permissions, topography, land uses, roads, and waterbodies, which all have the potential to restrict access.

Point counts are carried out by stopping at intervals along the transect, allowing the birds a short time to settle (normally approximately 1 minute), and recording all species seen or heard for a set period (extremes of 2-20 minutes, but normally 5-10) and the distance from the observer (again, exact or in distance bins). There are the same choices of how to determine point count location, and there is significant variation on survey site selection, as there is no requirement for counting locations to follow a set route. Obstacles such as those mentioned for line transects above can still pose problems, however. Despite the adaptability to species and habitats of both line transects and point counts, different situations suit different methods (Table 1.1).

Table 1.1: A comparison of line transects and point counts (from Gregory *et al*., 2004).

Line transects	**Point counts**
Suit large, open and uniform habitats	Suit dense habitats, e.g. forest
Suit mobile, large or conspicuous species, and those prone to flushing	Suit shy, cryptic and skulking species
Suit species poor areas with lower population densities.	Suit species rich areas with higher population densities.
Efficient – cover ground quickly, and so may record more birds	Lose time moving between counting stations, but counts give time to observe shy species
Double counting is a small issue, as the observer is always moving onwards	Double counting is more of a concern within the count period, particularly when carrying out longer counts
Birds unlikely to be attracted to the observer	Observer presence at count location may attract birds
Suited to locations with good access	Suited to locations with restricted access
Possible to use for bird-habitat studies	Ideal for bird-habitat studies
Errors in distance estimation have a lesser effect on density estimates (as sampled area increases linearly from the transect line)	Errors in distance estimation can have a greater effect on density estimates (as sampled area increases geometrically from the count point)

So far, few studies have carried out comparisons of line transects and point counts for studying birds, and the results obtained have been varied. Work comparing their efficacy in forested wetlands of the Mississippi Alluvial Valley recommended that line transects be used over point counts (Wilson *et al*., 2000). However, studies in riparian habitats of the Great Basin found no differences between point counts and line transects in terms of numbers of species or relative abundances (Dobkin and Rich, 1998), and Yinting *et al*. (2010) found that point counts resulted in higher density estimates than line transects, in work estimating saltmarsh bird richness and abundance in a Chinese delta, despite this being an open environment. Point counts were also recommended by Verner and Ritter (1985) after work carried out in California's oak-pine woodlands.

1.3 The effects of climate change on ecosystems

Significant increases to the level of anthropogenic greenhouse gas (GHG) emissions since the industrial era have led to a dramatic rise in atmospheric levels of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (IPCC, 2004). Of the last 1400 years, between 1983 and 2012 was likely the warmest 30-year period, and between 1880 and 2012, the globally averaged combined land and ocean surface temperature rose by 0.85°C (IPCC, 2014). Approximately half of the total anthropogenic CO_2 emissions between 1750 and 2011 were from just the most recent 40 years (IPCC, 2014). Climate change is predicted to have significant effects on a range of factors associated with biodiversity such as species distributions and ecological communities.

Climate change has had widespread and significant effects on species distributions, leading to range shifts along both latitudinal and altitudinal gradients. General warming trends are shifting climate envelopes polewards to higher latitudes or upslope to higher elevations (Walther *et al*., 2002), moving the area of suitable climatic conditions for species. Many species are unable to track climate at the required speed, however (Parmesan *et al*., 2013), or their distributions may be limited by other factors, such as light (Hoegh-Guldberg, 1999). Range shifts occur when the ratio of colonisations to extinctions at the range boundaries changes (Parmesan *et al*., 1999), and there are many studies across a wide range of taxa that have showed the existence of consistent trends in species' range shifts and demonstrated strong links between these shifts and recent warming (e.g. Chen *et al*., 2011; Gottfried *et al*., 2012; Poloczanska *et al*., 2013; Burrows *et al*., 2014).

Climate change also has significant effects on ecological communities, as species respond individualistically to climate change. There are many examples of changes to community composition because of climate change. In the Sonoran Desert in the southwestern United States, regional climatic shifts have led to an increase in the density of woody shrubs, extinction of previously common species, and population increases of species that were previously rare (Brown *et al*., 1997). Another mechanism by which communities are often affected is asymmetrical range shifts. The rate at which new species invade from lower latitudes or elevations is often slower than resident species are retreating polewards or upslope (Pounds *et al*., 1999; Sagarin *et al*., 1999; Thomas *et al*., 2004). Habitat specialists often fare worse than habitat generalists, which can sometimes even benefit from habitat disturbance (Warren *et al*., 2001). This can lead to 'biotic homogenisation', where differences between ecological communities become diminished (Devictor *et al*., 2008; Le Viol *et al*., 2012). This has been observed in avian communities in both Britain (Davey *et al*., 2012) and France (Devictor *et al*., 2008). Changes in community composition will lead to changes in community dynamics. As there is great variation among and within species of dispersal ability, climate change may mean interacting species that previously overlapped (in distribution) may no longer do so in the future, affecting the balance of interactions, whereby some interactions no longer occur and novel ones will emerge (Walther *et al*., 2002). In order to be able to measure the impacts of climate change, baseline data are essential, and provide a gauge against which future population changes can be compared.

1.4 Threats to biodiversity in tropical regions

The tropics cover 36% of the Earth's landmass (Bridgman and Oliver, 2006), and harbour a significant proportion of its biodiversity. Indeed, tropical rainforests, which cover less than 7% of the Earth's landmass (Bradshaw *et al*., 2009), harbour over 60% of all known species (Laurance, 1999; Dirzo and Raven, 2003), and this figure could be even higher. Several studies have suggested that the current extinction crisis will have the most severe effect in the tropics (e.g. Brook *et al*., 2003; Brook *et al*., 2006; Malcolm *et al*., 2006; Corlett, 2007).

Tropical regions also hold 40% of the world's human population, a figure which is predicted to rise to 50% by 2050 (State of the Tropics leadership group *et al*., 2014), resulting in significant pressures being placed on the land and its biodiversity. The greatest threats to tropical forest biodiversity are likely to be land-use and climate change. Despite the difficulty associated with accurately calculating both the number of species found in tropical regions, and the number that are at risk, it is clear that both threats present a significant danger to the biodiversity of these regions.

1.4.1 Land-use change

Between 1830 and 1984, approximately half of the world's rainforests were lost to deforestation (Hambler and Canney, 2013), and from 1990 to 1997, an average of 0.73% (8.5 million hectares) of tropical rainforest was cleared or degraded per year (Achard *et al*., 2002; Achard *et al*., 2004). The UN Food and Agriculture Organisation reported a significantly higher annual figure of over 1% (14.2 million hectares) annually over the 1990s (FAO, 2001). One explanation for the discrepancy is the omission of the 1997-1998 fires during the El Niño southern oscillation (ENSO) event from the studies by Achard *et al*. (2002, 2004). Fire is becoming an increasingly significant threat in tropical forests, due to its use in rapid forest clearance, and as a by-product of careless land management (Barlow and Peres, 2004; Barlow and Peres, 2008; Gardner *et al*., 2010).

Despite the volume of work that suggests we are heading for a tropical biodiversity disaster, an analysis by Wright and Muller-Landau (2006) argued that we may avoid a tropical extinction crisis due to the rate of secondary re-growth being sufficient to at least compensate for deforestation, as a result of the migration of rural human populations to urban environments. According to the authors, this is because rural slash-and-burn farming is the main cause of forest loss (Wright and Muller-Landau, 2006). There has been much criticism of this analysis, however, specifically relating to the assumptions made (see Laurance, 2007; Bradshaw *et al*., 2009). Perhaps most significant is the omission of the expected extinctions in endemism hotspots, and the effects of global climate change, as well as the authors' prediction that degraded and secondary habitats will still allow populations of tropical species to persist, despite evidence that suggests otherwise (e.g. Barlow *et al*., 2007; Gardner *et al*., 2007). In addition, despite the well-known links between human population size and environmental decay (Tilman *et al*., 2001; Laurance and Peres, 2006), the rising economic globalisation, industrialisation and consumption occurring in developing countries is likely to affect the impact of local populations on forest cover (Laurance, 2007). Both papers concluded that the migration of humans from rural to urban areas was unlikely to have the effect suggested by Wright and Muller Landau (2006) (Laurance, 2007; Bradshaw *et al*., 2009). Rather, the presiding view is that we are in a tropical biodiversity tragedy and heading towards disaster.

As such a large proportion of the world's species inhabits tropical forests, deforestation in these regions is likely to cause significant population declines for many species, including extinctions. Using a species-area model and extrapolations from observed and inferred local extinction data in Singapore since 1819 (during which time the country has suffered over 95% habitat loss (Corlett, 1992; Turner *et al*., 1994)), Southeast Asia's current rate of habitat destruction has been estimated to result in the regional loss of 13-42% of populations in the next 100 years; of this, over half will be global species extinctions (Brook *et al*., 2003). Given the uncertainty over the number of species that exist in tropical forests, and the difficulty associated with knowing when a species can be designated as no longer present, it is extremely hard to determine accurately the number of species becoming extinct annually in tropical forests due to deforestation. However, if the tropics harbour two-thirds of species (Groombridge and Jenkins, 2002), it is currently estimated that 3.3-20 million species may be found there, most of them in tropical forests (Lewis, 2006). It has been estimated that each decade, between 10,000 and 10 million species become extinct, and that 40% of species found in the 25 biodiversity 'hotspots' listed by Myers *et al.* (2000) may become extinct from deforestation alone (Pimm and Raven, 2000). These 'hotspots' contain 40% of all vascular plant, mammal, bird, amphibian and reptile species (Myers *et al.*, 2000). Of the 25, 17 are in tropical forests, and on average harbour only 12% of their original primary forest, compared to the tropical forest average of at least 50% (Lewis, 2006). If the lowest extreme of the estimate for species found in tropical forests by Groombridge and Jenkins (2002) is correct, at least 40% of 3.3 million species occur in the 'hotspots'. Using the finding that a 90% area reduction leads to 50% of species being lost (MacArthur and Wilson, 1967), approximately 50% of the species found in, and 15% of those outside, these 'hotspots' are committed to extinction via land-use change alone (Lewis, 2006). This results in a total estimate of 1 million species, which rises to a staggering 5.8 million if the total number of species in the tropics is 20 million (Lewis, 2006). Log-linear species area curves have also been applied; using an estimate of annual loss of global forests of 0.8%, 14,000-40,000 species (0.1-0.3% of tropical forest species) are predicted to become extinct each year (Hughes *et al.*, 2007). However, these species area curves ignore feedbacks that may affect the accuracy of the resulting extinction rate predictions.

Deforestation is also contributing to the role of tropical forests as carbon stores. Evidence currently suggests that the tropics act as more of a carbon source than a sink. While the occurring forests are a sink of approximately 1 PgC a^{-1}, deforestation will add carbon to the atmosphere at the higher end of recent estimates (1-2 PgC a^{-1}). Burning forest as part of the deforestation process also contributes trace gases to the atmosphere such as nitrous oxides and methane, which can increase radiative forcing by 6-25% (Fearnside, 2000). Aerosols are also produced, which have the opposite effect of providing negative radiative forcing (Ramanathan *et al.*, 2001).

1.4.2 Climate change

Climate change affects species in several ways, as mentioned earlier, and is currently occurring at great speed in landscapes already heavily modified by humans, resulting in more severe implications than there would be otherwise (Brook *et al.*, 2008). Despite the precise nature of climate change effects depending on precipitation changes (Prentice *et al.*, 2007), it is generally acknowledged that the effects will be negative as scenarios of both increased and reduced precipitation have been predicted to have severe effects. Forest dieback caused by droughts and rising evapotranspiration (due to higher temperatures) (Phillips *et al.*, 2009) has been forecast under most climate projections for the Amazon (Malhi *et al.*, 2009). However, scenarios of increased precipitation are also likely to have negative effects as tropical forests are already located in some of the warmest and wettest parts of the world.

Tropical species are particularly at risk from climate change as they are often specialised to narrower climate ranges than temperate species (Tewksbury *et al*., 2008; Wright *et al*., 2009). These specific microclimates are likely to face disruption from climate change (Bradshaw *et al*., 2009). In Australia's Wet Tropics, the fauna is particularly vulnerable to climate change as species are adapted to a cool, wet environment, and impacts of warming will likely be most obvious along altitudinal gradients, which dominate the region's biogeography (Nix and Switzer, 1991; Williams *et al*., 1995; Williams *et al*., 2003). Tropical montane systems are also particularly vulnerable to climate change as they are often adapted to cooler conditions, but will likely face inhospitable conditions under warming associated with climate change (Shoo *et al*., 2005). The reasons behind mountains being hotspots of biodiversity and endemism (the compression of climatic zones over the altitudinal gradient) also mean they are especially vulnerable to climate change (Körner, 2002).

There is widespread evidence that latitudinal and altitudinal shifts to species distributions will be a large component of responses to climate change (Parmesan, 1996; Hill *et al*., 2002; Peterson *et al*., 2002; Walther *et al*., 2002; Parmesan and Yohe, 2003; Root *et al*., 2003). While the dispersal distances required to track the climate up-slope may be small in most montane systems, some environmental types are predicted to completely disappear, such as in the Australian Wet Tropics (Williams *et al*., 2003), and many species that inhabit tropical forests are poor dispersers (Van Houtan *et al*., 2007). In other areas, the dispersal distances required for some tropical forest species to track the changing climate are significant, and may be too great for some species to achieve (Wright *et al*., 2009; Loarie *et al*., 2009). Studies in Australia's Wet Tropics suggest we are facing an unprecedented montane biodiversity loss; using a conservative value for temperature increase of just 1°C, one species lost the entirety of its core environment, and the vast majority experienced severe reductions in distribution (Williams *et al*., 2003). This study only considered the effects of increasing temperature, whereas the impacts of climate change are likely to be greater due to other factors such as reduced nutritional value, and increased toughness and concentration of defence compounds in foliage because of increased CO_2 levels (Lawler *et al*., 1997; Kanowski, 2001). The cloud bank is also likely to lift, causing reduced inputs of mist and water at high altitude and so diminished cloud contact, leading to increased rates of evapotranspiration (Still *et al*., 1999). In Costa Rica's Monteverde cloud forests, this has been linked with simultaneous amphibian population declines and altitudinal shifts in bird distributions, where in most cases new range areas were restricted and fragmented, leading to lower population sizes and a higher risk of extinction (Pounds *et al*., 1999). Temperature increases may also result in an influx from lower elevations of invasive species. Severe disease outbreaks may occur if previously geographically-separated species end up overlapping due to climate change (Bradshaw *et al*., 2009). The distribution for mosquitos is shifting upwards due to global warming; this will reduce available habitat to endemic birds, and has severe implications with regards to the persistence of less adaptable species (Harvell *et al*., 2002).

An increase in net primary productivity (NPP) across South American tropical forests has resulted from long-term increases to resource availability (Lewis *et al*., 2004a; Lewis *et al*., 2004b). This increase to NPP has led to structural changes in Amazonian forests, most likely via increased stem growth rates and increased competition for limited resources. Baker *et al*. (2004) have shown increases to above-ground biomass of $0.50 \pm 0.17\% a^{-1}$ via analysis of 59 plots over 20 years. As well as this, forests have become faster growing, more productive and more dynamic (increases to both tree recruitment and mortality) (Lewis *et al*., 2004a). Changes are also occurring in other parts of the tropics; across the paleotropics, forest dynamism has increased over the last 50 years (Phillips and Gentry, 1994), and there is evidence that forests in Africa and Australia are showing similar structure changes to forests in South America (Lewis *et al*., 2009). It is hypothesised that the cause of the increase in resource availability observed during the 1980s and 1990s in South America was due to rising atmospheric CO_2 and incoming solar radiation (Lewis *et al*., 2004a), although there is debate on the matter as no studies have investigated the response of mature tropical forest to increasing CO_2 (see Chambers and Silver, 2004; Clark, 2004; Lewis *et al*., 2004b).

Changes to the physical, chemical and biological environments over recent decades have led to the remaining intact tropical forests experiencing significant shifts in structure, dynamics, productivity and function (e.g. Lewis *et al*., 2004a, 2004b). As well as long-term monitoring of tropical trees in permanent sample plots, as carried out by Lewis *et al*. (2004a, 2004b), there is also evidence from alternate studies, such as micrometeorological (Grace *et al*., 1996) and satellite data (Weishampel *et al*., 2001), and atmospheric carbon dioxide concentrations and transport model data (Rödenbeck *et al*., 2003). Changes to tropical forest structure and dynamics will likely result in changes to species composition and the interactive balance between species. This has already been observed; Laurance *et al*. (2004) found evidence of changes in tree species composition in central Amazonian forest plots, and in western Amazonia, Phillips *et al*. (2002) found that lianas are becoming more dominant due to increases to their density, size and basal area. These changes are likely to benefit disturbance-adapted taxa as many are faster growing and will therefore do better under increasing resource supply rates (Coomes and Grubb, 2000; Lewis *et al*., 2004b). Tree mortality rates are also increasing, leading to more openings in the forest and greater resource supply rates (Körner, 2004; Lewis *et al*., 2004a, 2004b).

1.5 The Albertine Rift and threats facing it

The Albertine Rift covers over 313,000km^2 of central Africa. Covering parts of six countries (Zambia, Tanzania, Uganda, the Democratic Republic of the Congo (DRC), Rwanda and Burundi), it spans an elevational range of 600-5109m and encompasses a broad range of habitats (Plumptre *et al*., 2007). The region holds Africa's highest levels of vertebrate species richness and endemism, as well as many threatened species (Vulnerable, Endangered or Critically Endangered, as listed by the IUCN). Endemism occurs at all altitudes (Brooks *et al*., 2001; Plumptre *et al*., 2003; Burgess *et al*., 2004). Due to these factors, the Albertine Rift is included in Conservation International's Eastern Afromontane Hotspot (Brooks *et al*., 2004), and the region has been designated as an Endemic Bird and Biodiversity Area by Bird Life International (Stattersfield *et al*., 1998) and a 'Global-200' priority ecoregion by the World Wildlife Fund (WWF) (Olson and Dinerstein, 1998; Burgess *et al*., 2004). Despite its biodiversity, the region has received relatively little study attention, an issue made more concerning by the severity of threats facing the Albertine Rift.

1.5.1 Land-use change

40-50 million people inhabit the Albertine Rift, and human population densities exceed 1000 people km^{-2} in some areas (Seimon and Plumptre, 2012). The juxtaposition of high population densities and biodiversity levels makes the Albertine Rift one of the world's most threatened conservation-poverty hotspots (Fisher and Christopher, 2007). Most human inhabitants are dependent on resources from the region for their livelihoods, as many are subsistence farmers and hunters. In surveyed areas by Bush *et al*. (2004), 8-30% of annual household income was obtained via forest products. The Albertine Rift has already suffered significant land conversion to agriculture, from small-scale multi-cropping subsistence agriculture to larger-scale farming for tea (Hartter and Southworth, 2009), resulting in lasting conversion of the landscape. The percentage of the population relying on fuelwood for heating and cooking in the immediate region of the central Albertine Rift is at least 90% in Rwanda, Burundi, Tanzania and Uganda (United Nations Development Programme – UNDP, 2007; African Studies Center – ASC, 2010).

The area's human population is also growing, which will likely lead to greater habitat clearance. A population doubling at a national level is predicted to cause 2.06% annual forest cover loss (Ryan *et al*., 2017). Should Uganda's current annual population growth rate of 3.24% (Central Intelligence Agency, 2007) continue, population doubling would occur after just 20 years. This population rise would be likely to lead to increased demand for meat and tea, resulting in greater land clearance and hunting respectively (Ryan *et al*., 2017). The increasingly affluent and urban population of Africa is also likely to lead to increased meat consumption (Ryan *et al*., 2017). Doubling tea and meat production was responsible for a 1.90% loss of annual forest cover, and 0.71% reduction in annual cover gain, respectively (Ryan *et al*., 2017). The heavy fertilisation required by tea (contrasting with most other agriculture occurring in the region, which has a lesser requirement) may have additional impacts on landscape health via ecotoxic effects (Ryan *et al*., 2017). Wetlands in the AR are also suffering via exploitation for irrigation and drinking water and loss of vegetation for thatching (MacLean *et al*., 2003; Hartter and Southworth, 2009).

Another consequence of the rising human population is increased isolation of protected areas (PAs) (Olupot *et al*., 2009; Akinyemi, 2013; Ryan *et al*., 2017). Some protected areas, such as Kibale National Park, have become islands of the natural habitat, surrounded by a matrix of intensive agriculture (Hartter *et al*., 2011). Fragmentation is primarily caused by deforestation for resources and conversion to arable land and pasture (Hartter and Southworth, 2009; Hartter *et al*., 2011; Akinyemi, 2013). There is strong evidence for a local household zone effect on fragmentation patterns in part of the Albertine Rift; fragmentation in both forest and wetland patches has been shown to occur more in the immediate surroundings of households (Ryan *et al*., 2015), and direct linkages have been found in other areas between household location, resource use and fragmentation (Munroe *et al*., 2004; Nagendra, 2008; Nagendra *et al*., 2008; Southworth *et al*., 2012). Landscapes immediately surrounding PAs are important as they act as buffers (Schonewald-Cox and Bayless, 1986) or stepping stones, increasing connectivity within the larger landscape (Dobson *et al*., 1999; Rudnick *et al*., 2012). However, fragments of suitable habitat left unconverted pose a threat to local farmers as they are sources of primates, elephants and birds, all of which are responsible for consumption of or damage to crop plants (Ryan *et al*., 2015). To replace the habitat for potential crop raiders, and increase the available land area for agriculture, these fragments are increasingly converted (Ryan *et al*., 2015). Fragmentation of the surrounding areas to patches may also cause edge effects, including understorey encroachment, reduced seedling recruitment to the forest, and less effective buffering of climate impacts (Hartter *et al*., 2011). This was suggested to be a reason behind the reduction in forest productivity inside Kibale National Park between 1984 and 2003 (Hartter *et al*., 2011). The increased pressures suffered by areas outside PAs also make establishing protected corridors of land difficult (Seimon and Plumptre, 2012). These corridors aid conservation and reduce habitat fragmentation (Beier and Noss, 1998; Gilbert-Norton *et al*., 2010; Christie and Knowles, 2015), a problem that affects biodiversity across the world (Brashares *et al*., 2001; Wade *et al*., 2003; Hanski, 2005). The establishment of land corridors ensures that populations of species remain well connected.

1.5.2 Climate change

The Albertine Rift is predicted to be especially vulnerable to climate change-related stresses due to its limited adaptive capacity, its geographical location and the projected temperature and precipitation increases (IPCC, 2007). Many of the region's seven main ecosystems are at risk from climate change, particularly those at higher altitudes such as montane, bamboo and alpine forests (Ponce-Reyes *et al*., 2017). All seven ecosystems are projected to shift in altitude, with suitable environmental conditions for six forecast to decrease. 44% of the Albertine Rift is projected to become unsuitable for current ecosystems by 2070 (Ponce-Reyes *et al*., 2017). Similarly, the region's endemic bird species are forecast to alter their range extent in future, with some projected to lose up to 100% of their current range by 2080 (Ayebare *et al*., 2013). The bamboo ecosystem, which harbours endemic birds such as the red-faced woodland warbler (*Phylloscopus laetus*) and Archer's ground robin (*Cossypha archeri*) is the most threatened, with suitable conditions for this ecosystem being projected to disappear by 2070 (Ponce-Reyes *et al*., 2017). Species dependent on this ecosystem will therefore be under severe threat of extinction. Many of the endemic and threatened species of the Albertine Rift are now concentrated in montane habitats, which are often separated from similar areas by lowland areas comprising different ecosystems, or by land that has been converted to agriculture. This acts as a significant barrier to dispersal, reducing the likelihood that species will be able to shift their ranges to new areas of suitable habitat and environmental conditions (Seimon *et al*., 2011; Seimon and Plumptre, 2012; Ayebare *et al*., 2013). If species' climate envelopes ascend an altitudinal gradient in response to climate change, as has been projected in several studies (e.g. Shoo *et al*., 2005), the extent of suitable conditions will likely be reduced, simply as a result of the smaller extent of high elevation habitat, resulting in declining populations.

1.6 Implications of results for conservation and management

Human alteration and exploitation of the natural environment is driving rapid significant losses of biodiversity over recent decades (Vitousek *et al*., 1997; Butchart *et al*., 2010; Cardinale *et al*., 2012). In addition, extinction rates are consistent with former mass extinction events, currently at levels between 1000 and 10,000 times greater than background rates (Leakey and Lewin, 1992; Barnosky *et al*., 2011). This, in combination with the limited funds available to conservation, means that efforts need to be efficiently prioritised and targeted to achieve best effect. Despite the significant amount of study that birds have been the subject of, there are still areas that have received very little survey attention. While it may be expected that this would only apply to relatively species-poor areas, that is not the case, with some tropical areas of high biodiversity lacking attention, such as Africa's Albertine Rift (Plumptre *et al*., 2007). This region comprises the highest vertebrate species richness and endemism in Africa (Brooks *et al*., 2001; Plumptre *et al*., 2003; Burgess *et al*., 2004), yet at the same time holds extremely high human population densities (Seimon and Plumptre, 2012). Effective conservation measures require at the very least baseline data, such as population densities, to prioritise locations. These results show the population densities for many of the birds found in the Albertine Rift, as well as their densities in the different regions that comprise the area, allowing possible prioritisation of locations for conservation. Population size and trend are the best correlates of extinction risk (O'Grady *et al*., 2004), so these results that provide data on species' spatially variable patterns of abundance will facilitate work into effects of climate change. With the predicted future impacts of climate change and rapidly-rising human population, forecasting which areas are likely to become more or less important is crucial in mitigating the effects of climate change and ensuring continued persistence of species and populations.

Many of the endemic and threatened bird species of the Albertine Rift are found in montane habitats. One widespread response to increasing temperatures, as are predicted to occur in the Albertine Rift due to climate change, is shifting along (often up) altitudinal gradients (Shoo *et al*., 2005). However, this leads to a decrease in the area of suitable conditions, and therefore populations will likely reduce. The montane areas that harbour many of the Albertine Rift endemics are often separated from each other by large expanses of unsuitable habitat, be it different natural habitats, or agriculture or settlement due to anthropogenic conversion. This poses significant barriers for species shifting their range to new areas of suitable conditions (Seimon *et al*., 2011; Seimon and Plumptre, 2012; Ayebare *et al*., 2013). Assistance, in the form of translocation, may be required to aid species persistence in these habitats. However, the impacts of biotic factors (e.g. interspecific competition) must be included, as they are a significant determinant of species distributions and range boundaries (Wiens, 2011; Wisz *et al*., 2013; Godsoe *et al*., 2015). Therefore, investigating the effects of interspecific competitor species abundance and habitat on densities of endemic and threatened species will help suggest whether translocation of endemic and threatened species may have detrimental effects on competitor species already present at the recipient sites.

Comparisons of line transects and point counts carried out in the same location simultaneously will help to reveal where one should be preferred over the other, therefore increasing the accuracy of future studies that use distance sampling to estimate bird population densities. Currently these methods are often used interchangeably, and the data that are obtained from them are crucial in calculating population densities, which are in turn used to prioritise locations. Therefore, estimating densities accurately is extremely important, and using the right methodology will improve the accuracy of estimations.

1.7 Project aims

1. **To assess how survey methodology affects density estimation in birds**

   Firstly, I will investigate differences in density estimates obtained from distance sampling when using point counts and line transects in an area of Outback Australia, taking advantage of an extensive dataset in which point and line transect data were collected concurrently. There have been few studies that have compared these two methodologies in the same habitat simultaneously, and compared discrepancies in the resulting density estimates.

2. **To calculate populations for birds in six core conservation areas of central Africa's Albertine Rift.**

   Currently, there are very limited baseline data of the bird species of the Albertine Rift other than from a small number of studies. Here, I will use distance sampling to calculate bird densities for 239 bird species from a set of point count data collected over 16 years throughout the Albertine Rift. This area is forecast to be particularly vulnerable to climate change, due to its geographic location and low adaptive capacity. Consequently, baseline population data are vital to understand population changes due to the various ongoing and future threats to this system.

3. **To investigate the effects of habitat and competitor abundance on abundance of endemic and threatened species in the Albertine Rift**

   The Albertine Rift holds the highest levels of species endemism in Africa, with 41 endemic bird species. Here, I will compare densities of competitor species with endemic and threatened species of the Albertine Rift. Many of these species are restricted to montane habitats separated from similar areas by large lowland areas comprising unsuitable habitat. Work on the drivers of endemic and threatened population densities has conservation implications relating to issues such as potential for translocating endemic species to aid persistence, and prioritising of sites for conservation.

2

Using distance sampling to compare density estimates from line transects and point counts for Australian arid-zone birds

2.1 Abstract

Despite the critical importance of baseline data on abundances, comparisons of the efficacy and relative merits of data collection methods are rare. Two of the most widely used approaches for birds are line transects and point counts. Here, I use distance sampling to estimate population densities of birds, using data from line transect and point counts that were conducted in parallel across large regions of Australia's arid zone. Overall, density estimates varied from 0.07 to 20.9 individuals km^{-2} for line transects, and 0.05 to 29.4 individuals km^{-2} for point counts. There was high correlation between the two methods, but density estimates from point counts were, on average, higher than those from line transects, though line transects consistently resulted in more observations and higher species richness as a consequence of their larger survey area. In addition, marked differences in density estimates between methods were observed between species and groups of species with similar behavioural or morphological traits. Density estimates for ground-dwelling species were generally higher from line transects, whereas for foliage-dwelling insectivores point counts gave higher estimates. Determining the preferred method to use is best evaluated on a case-by-case basis, taking account of factors such as the focal species and landscape characteristics such as habitat and topography.

2.2 Introduction

Biodiversity around the world is currently undergoing a crisis, with extinction levels between 100 and 10,000 times higher than the background rates that naturally result from slow environmental change, novel competitive interactions and occasional stochastic events (Dirzo and Raven, 2003; Brook *et al*., 2008). Pressures on biodiversity are likely to increase in future, due to ongoing climatic change and a rapidly rising human population. Despite the wealth of studies on birds, which have significantly increased our understanding of ecological processes and of the effects of e.g. climate change (discussed in section 1), relatively little attention has been paid to comparisons of the survey methods used to collect raw data. Choosing the appropriate method for data collection is crucial to obtain accurate data, which is essential if the data are to have conservation applications. Baseline survey data are required to estimate population densities, and hence populations, the latter being the cornerstone of conservation management and status designation. Baseline data obtained from surveys such as line transects and point counts are widely used in conservation, from prioritising locations and habitat types for conservation (Gregory and Baillie, 1998; Pérez-Arteaga *et al*., 2005), to designating species of conservation concern, and overall help conservationists to determine how to target and allocate the limited funds and resources available to conservation efforts (IUCN, 2004). Methodological studies that increase our understanding of when one survey type might be preferred over others will only increase the precision of future studies.

Several methods can be used to estimate bird abundances, from the time- and labour-intensive territory mapping to markedly more simple species lists. Distance sampling (Buckland *et al*., 2001) is increasingly recognised as the 'industry standard' for accurate estimation of species densities in a timely fashion. Despite the widespread acknowledgement of the benefits of this method (Barraclough, 2000; Buckland *et al*., 2001; Thomas *et al*., 2010), the underlying methods used to collect the raw data from which densities are derived can vary. The two methods most frequently used in distance sampling are line transects and point counts. The former involves recording carried out by an observer(s) moving continually along a predetermined route or set length; point counts necessitate a stationary observer(s), and all observations from that point for a set time period are recorded. What little work has been undertaken to compare methodologies has produced mixed conclusions. Dobkin and Rich (1998) found no differences in numbers of species or relative abundances between the two methods in riparian habitats of the Great Basin, USA, although comparisons in forested wetlands of the Mississippi Alluvial Valley suggested that line transects were preferable to point counts (Wilson *et al*., 2000). By contrast, point counts undertaken in a Chinese saltmarsh gave higher density estimates than line transects for bird populations (Yinting *et al*., 2010).

Verner and Ritter (1985) also expressed a preference for point counts over line transects following work in oak-pine woodlands of California.

In this chapter I aim to compare densities estimated from these two survey methods and to explore whether there are systematic differences in density estimates that can be related to species traits. I used distance sampling, based on a dataset of point count and line transect surveys carried out simultaneously in the same area of arid-zone Australia, to estimate species densities. The two estimates were compared to investigate whether systematic differences between the two methodologies exist, and whether body mass and bird behaviour-type affected densities generated by each method. It was expected that differences would exist due to detectability of species differing between the two methods. For example, line transects might be expected to result in more observations of skulking ground-dwelling species such as Galliformes that prefer to walk rather than fly. Similarly, the stationary nature of point counts could be better suited to observing cryptic species such as small insectivores that spend time in foliage.

2.3 Methods

2.3.1 Study site

The data were collected by several observers (myself not included) as part of a project run by the Conservation Ecology Group, Durham University and the Fuller Lab, University of Queensland. Surveys were conducted in South Australia and Queensland, within the greater Lake Eyre basin (Figure 2.1). The predominant vegetation types are chenopod and samphire shrublands, and forblands, which between them occurred at 47% of sites (National Vegetation Information System (NVIS) – Major Vegetation Groups version 4.2; Table S2). Other vegetation types that make up the area can be found in Table 2.1.

Table 2.1: vegetation types making up the study area, and the percentage of sites at which they occurred (from Gibson, 2018).

Vegetation type	**Sites at which vegetation type occurs (%)**
Tussock grassland	29
Eucalypt and acacia woodland	10 (combined)
Hummock grassland	6
Acacia shrubland	5
Aquatic, naturally bare, and other shrublands and grassland	3 (combined)

The study area is mostly desert and semi-desert habitat and has the highest precipitation variability of any arid region (McMahon *et al*., 2008; Morton *et al*., 2011). Short irregular bouts of rainfall break up extended drought periods. Mean annual rainfall is 186mm, with average intra- and inter-annual rainfall coefficients of variation of 1.5 and 0.56, respectively. Average annual temperatures range from a minimum of 14.5°C to a maximum of 29.5°C (Gibson, 2018 – calculated by averaging conditions from three representative weather stations from the 1961-1990 reference period used by the Australian Bureau of Meteorology (www.bom.gov.au/climate/data).

2.3.2 Study design

Surveys were carried out along three long-distance transects in South Australia and Queensland, each approximately 800km in length. They were located along the Birdsville, Strzelecki and Oodnadatta tracks (Figure 2.1). Surveying occurred over approximately a 10-day period each winter (June – September) from 2011 until 2016. Surveys took the form of standardised line transects and point counts carried out by experienced ornithologists. Census stops were located at 16km-intervals along the three transects and formed a focal point from which surveys were conducted in the surrounding habitat. At each census stop, a standardised set of surveys was performed, comprising eight 400m line transects and seven 5-minute point counts, in a figure-of-eight pattern that sampled the surrounding 1x1km cell. At each stop, weather, and the presence of livestock (cattle) or potential avian predators (such as dingo (*Canis lupus dingo*) or feral cat) were recorded. Transects and point counts were conducted as described in *Section 2.3.3* below. Attempts were made to visit all census stops each year, though in some years some locations were inaccessible, typically due to access roads being closed by floods.

2.3.3 Line transect and point count method

Surveys were carried out between 06.00 and 20.30, avoiding hot periods in the day when bird activity declined. For line transects, surveyors walked along the transect line at a slow even pace for the duration of the survey. Point counts comprised observers recording birds for a 5-minute period. For both survey types, and for all observations and sound detections, the following were recorded: (1) species, (2) the number of individuals comprising the group, (3) the perpendicular distance of the bird from the transect line/point count location (measured using a laser rangefinder, where possible; otherwise estimated), (4) whether visual or aural observations were used, and (5) whether observations were flying or perched. All birds seen within the transect bounds or point count were recorded.

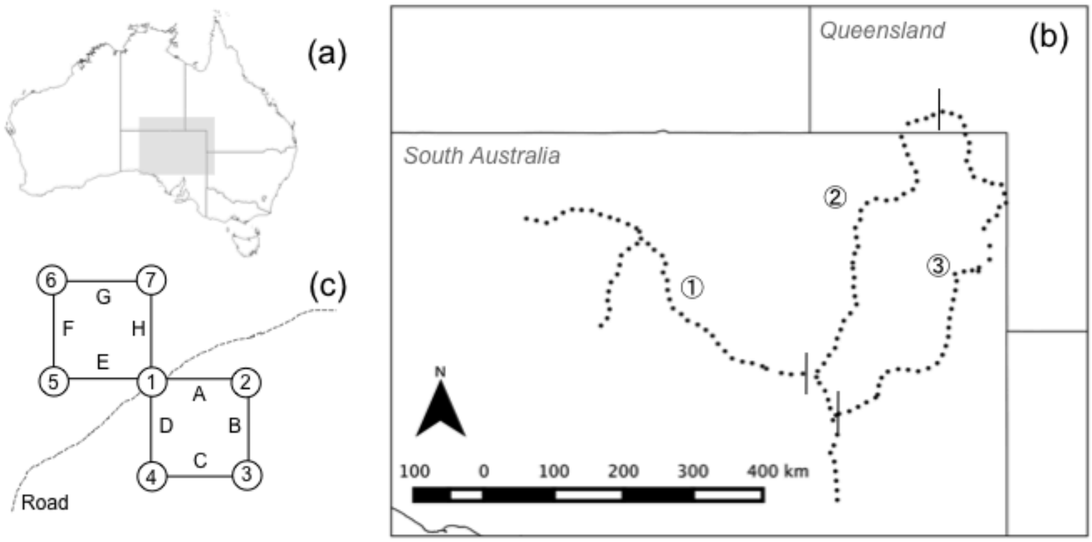


Figure 2.1: (a) Study area is shown by the shaded rectangle. (b) Dots represent each census stop along the three driveable mega-transects ([1] Oodnadatta track; [2] Birdsville track; [3] Strzelecki track). The start/end of tracks are shown by vertical lines, if ambiguous. (c) Survey design showing the pattern of line transect (letters) and point count (numbers) surveys carried out at each census stop. From Gibson (2018).

2.3.4 Density estimation

1258 line transect and 1101 point count surveys were carried out. Each line transect or point count was considered to be independent and observer bias was assumed to be constant between methods. Line transects and point counts were undertaken by the same observers at any site in any year. I used the function ‘ds()’ within package ‘distance’ (Miller, 2016) in R v. 3.3.3 (R Core Team, 2017) to estimate densities. Buckland *et al.* (2001) recommend 40 as the minimum number of observations for a species’ density to be estimated. Two different approaches were used depending on whether a species received the threshold of 40 observations in both line transect and point count surveys, although even this falls short of the preferred threshold of 60 (Buckland *et al*., 2001). Densities for species were calculated if they met the required number of observations for both survey methodologies. Species that did not meet this were excluded as their data were considered insufficient to accurately estimate density. Also included were a further three species groups by pooling approach, whereby observation data for two or more similar species were combined. Without amalgamating these species, observations for each species alone were insufficient to estimate densities. Species were only pooled if they were considered to have similar detectabilities and behaviour. The three groups were (1) parrot species (comprising observations from eastern bluebonnet (*Northiella haematogaster*), Bourke’s parrot (*Neopsephotus bourkii*), Australian ringneck (*Barnardius zonarius*), elegant parrot (*Neophema elegans*) and mulga parrot (*Psephotellus varius*)); (2) wader species (comprising observations from inland dotterel (*Peltohyas australis*), Australian pratincole (*Stiltia isabella*) and masked lapwing (*Vanellus miles*)); and (3) ground flusher species (comprising observations from little button-quail (*Turnix velox*), stubble quail (*Coturnix pectoralis*), red-chested button-quail (*Turnix pyrrhothorax*) and unidentified quail species, as well as sight observations of cinnamon quail-thrush (*Cinclosoma cinnamomeum*)).

Before density calculations, data were formatted. For each table of species observations, new rows were added corresponding to survey locations where the species was not observed to ensure the avoidance of artificially high estimates. The following rows were removed as very large flocks observed close to the survey location would skew the density estimations: a budgerigar (*Melopsittacus undulatus*) flock of 1000 birds at a distance of 100m; two little corella (*Cacatua sanguinea*) flocks of 2000 birds each at distances of 300m and one flock of 2000 at 500m; a zebra finch (*Taeniopygia guttata*) flock of 1000 birds at a distance of 0m. Observations were truncated to remove the most distant records (as recommended by Buckland *et al*. (1993)). The threshold I used for truncation differed for small versus large species, as larger species could be more readily detected at greater distance. Consequently, for species with body mass < 300g I excluded records beyond 145m from the transect line or point and 505m for species with body mass > 300g as probability of detection at these distances was often below the suggested 15% detectability threshold (Buckland *et al*., 2001). Two types of function were fitted to describe the decay in detectability with distance for each species: hazard-rate (HR) and half-normal (HN). Cosine adjustments were also added sequentially. Each model fitting produced an Akaike information criterion (AIC) score for model fit and a density estimate with associated standard error and confidence limits. I visually assessed plots of cluster size against distances of observation for individual species to determine whether there was evidence of bias in detectability related to group size large flocks. For species where this was evident, cluster size was included as an additional covariate in estimating densities (Table 2.2). Model goodness of fit was evaluated using the Cramér-von Mises test, which assesses the compatibility between data and the chosen probability distribution. If the test result was significant, the detectability function and corresponding estimate was discarded. The density estimate with the corresponding lower AIC value was selected, assuming it passed goodness of fit tests. There was one exception to this protocol for model selection and elimination. The ground flusher species group was one of particular interest, due to the expectation that the secretive and ground-dwelling behaviour of the comprising species might result in higher density estimates from line transects than point counts. The paucity of observations for species in this dataset meant that the resultant models for line transect data did not pass goodness of fit tests. Nonetheless, due to our particular interest in this group, I retained density estimates from the best model, as model fit was parsimonious with the data.

Table 2.2: species for which size was included as a covariate in density calculations.

Species	**Size as a covariate for line transects?**	**Size as a covariate for point counts?**
Budgerigar	Y	Y
Crested Pigeon	Y	Y
Fairy Martin	Y	Y
Emu	Y	Y
Little Corella	Y	Y
Little Crow	Y	Y
Masked Woodswallow	N	Y
Galah	N	Y

Density estimates for the study region from line transects and point counts were log-transformed and plotted against each other for each species. A generalised linear model was used to compare density estimates for each species from the two survey methodologies, with two covariates: (1) logged body mass and (2) whether a species was an arboreal or ground forager.

2.4 Results

Observation data were collected for 164 species, of which 160 were recorded during line transect surveys, and 136 during point counts. After excluding species with fewer than 40 observations in either line transect or point count surveys, and including the three species amalgamated groups (ground flusher species, wader species and parrot species), this resulted in 50 species/species groups for further analyses. From these, densities were calculated for 31 (Table 2.3). Densities could not be calculated for other species because either: models could not be fitted, the resultant models did not pass goodness of fit tests, or densities could only be estimated for one of the two survey datasets, prohibiting comparisons. For line transects, estimated densities ranged from 0.07 (crested bellbird, *Oreoica gutturalis*) to 20.9 individuals km^{-2} (white-winged fairy-wren, *Malurus leucopterus*), and for point counts from 0.05 (whistling kite, *Haliastur sphenurus*) to 29.4 individuals km^{-2} (white-winged fairy-wren, *Malurus leucopterus*). Line transects consistently recorded more observations and higher species richness, although point counts tended to result in higher density estimates (Table 2.3).

Table 2.3: density estimates for Australian arid bird species from line transect and point count methods, plus/minus one standard error. For species labelled with an asterisk, models did not pass goodness of fit tests, but estimates were retained anyway (see note at the end of section *2.3.4*).

Species	**Density from line transects (km^{-2})**	**Density from point counts (km^{-2})**
Australian Magpie	0.44 ± 0.05	0.49 ± 0.11
Banded Lapwing	0.24 ± 0.07	0.16 ± 0.05
Black-faced Woodswallow	5.19 ± 0.66	6.19 ± 1.06
Black-shouldered Kite	0.12 ± 0.03	0.11 ± 0.03
Brown Songlark	1.14 ± 0.11	1.92 ± 0.21
Chirruping Wedgebill	1.18 ± 0.08	1.84 ± 0.2
Cinnamon Quail-thrush	1.84 ± 0.11	2.41 ± 0.24
Crested Bellbird	0.07 ± 0.02	0.37 ± 0.16
Crimson Chat	2.83 ± 0.4	6.81 ± 2.17
Diamond Dove	2.77 ± 0.59	4.11 ± 1.41
Gibberbird	0.31 ± 0.05	0.34 ± 0.09
Ground Flusher spp.*	18.22 ± 2.93	9.03 ± 23.34
Horsfield's Bronze-cuckoo	0.22 ± 0.05	0.21 ± 0.05
Mistletoebird	0.33 ± 0.07	0.7 ± 0.25
Pied Honeyeater	0.93 ± 0.21	1.62 ± 0.44
Red-backed Kingfisher	0.16 ± 0.03	0.24 ± 0.13
Red-capped Robin	0.84 ± 0.12	1.02 ± 0.23
Rufous Fieldwren	0.8 ± 0.14	0.98 ± 0.2
Rufous Songlark	0.61 ± 0.11	0.99 ± 0.18
Singing Honeyeater	4.78 ± 0.36	8.42 ± 0.85
Spiny-cheeked Honeyeater	1.19 ± 0.18	3.74 ± 1.13
Striated Pardalote	0.19 ± 0.04	0.25 ± 0.09
Wader spp.	0.80 ± 0.17	2.30 ± 4.12
White-plumed Honeyeater	3.42 ± 0.39	6.55 ± 1.21
White-winged Fairy-wren	20.9 ± 0.92	29.4 ± 3.6
Willie Wagtail	1.91 ± 0.14	3.31 ± 0.52
Yellow-throated Miner	1.56 ± 0.24	3.96 ± 0.91
Crested Pigeon	3.83 ± 0.42	5.08 ± 1.5
Wedge-tailed Eagle	0.09 ± 0.01	0.08 ± 0.04
Whistling Kite	0.10 ± 0.02	0.05 ± 0.02
Little Crow	1.64 ± 0.61	1.42 ±. 0.44

Detection functions varied widely between species, as would be expected due to morphological and behavioural differences (see Figure 2.2 for examples).

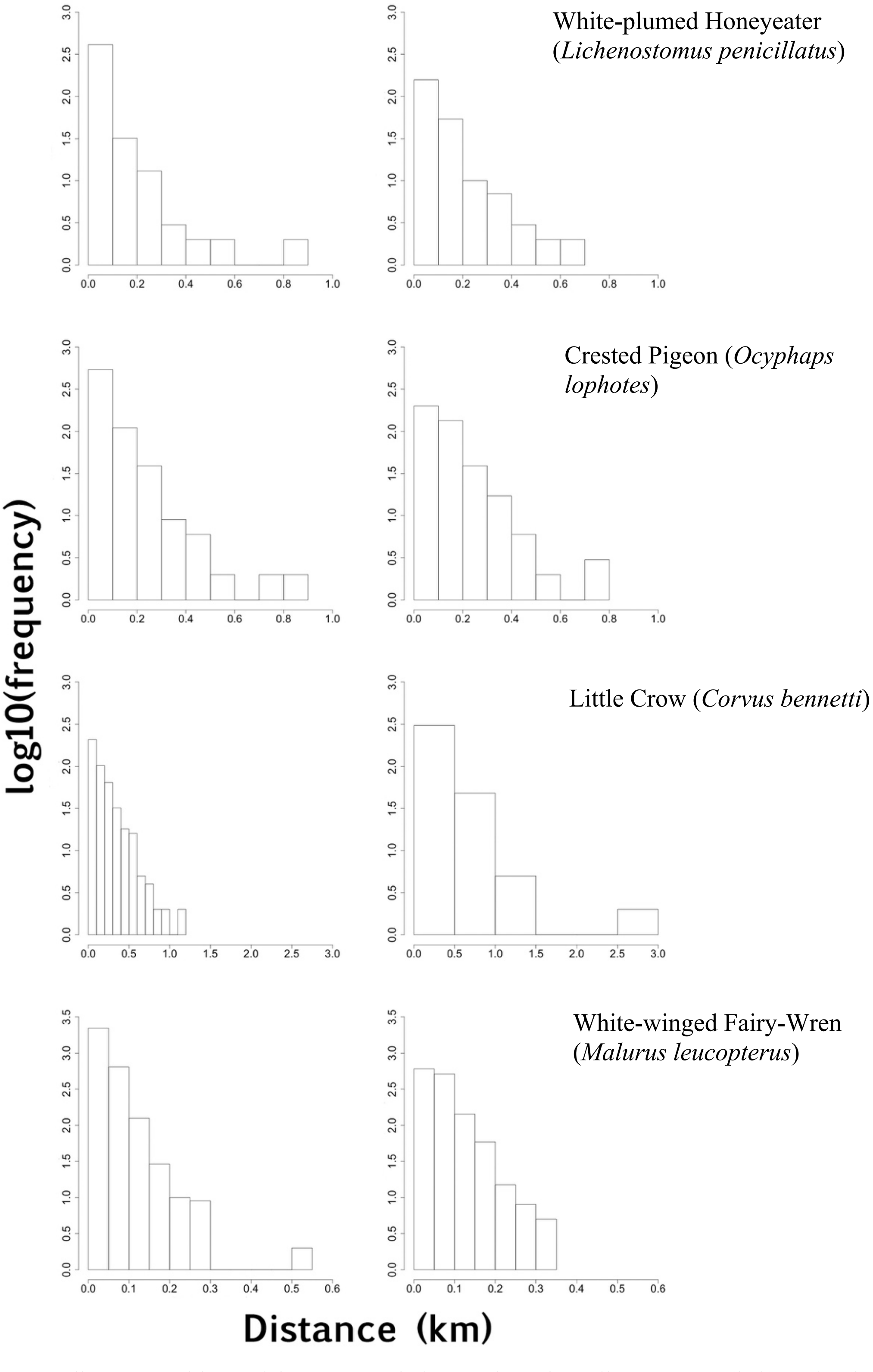


Figure 2.2: distance and logged frequency of observations from line transect (left) and point count (right) surveys for four species: (A) a common species with typical detection function (white-plumed honeyeater, *Lichenostomus penicillatus*); (B) a flocking species where cluster size was included in the subsequent distance analysis (crested pigeon, *Ocyphaps lophotes*); (C) a large widespread species (little crow, *Corvus bennetti*); (D) a widespread species with an atypical detection function (white-winged fairy-wren, *Malurus leucopterus*). NB: to avoid problems arising from logging zero values, 1 was added to frequency counts before logging.

Over the 31 species, density estimates obtained from point counts were higher than those from line transects (t = 16.4, $P < 0.001$), and 24 species had higher estimates from the former method. There was correlation between the corresponding density estimates for each species (correlation coefficient = 0.95) (Figure 2.3). Logged body mass did not have a significant effect on density estimates according to survey type (t = 0.457, $P = 0.651$), but foraging strategy did (t = -2.45, $P = 0.021$). The latter suggests that arboreal foragers may be better detected by point counts, and ground foragers by line transects.

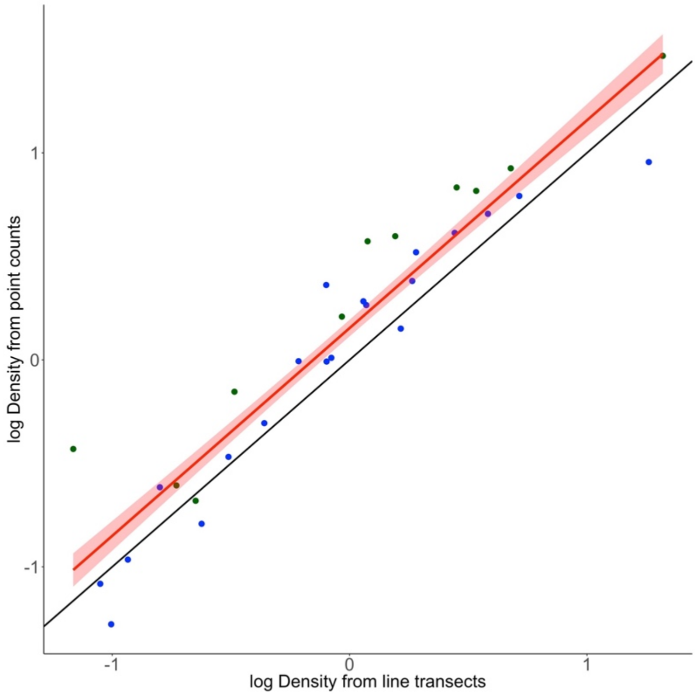


Figure 2.3: logged density estimates from each method. Each point represents one species. The red line is the fitted estimate of the effect and the shaded red region represents ± standard error. The colours of the points represent whether a species is an arboreal or ground forager: green points indicate arboreal foraging; blue points indicate ground foraging. The black line represents y=x.

2.5 Discussion

Density estimates derived from points counts were significantly higher than those from line transects for birds in the Australian Outback: 24 out of 31 species had higher density estimates from point counts. Looking at species with certain traits showed more marked differences. This was expected as differences in methodologies between the two methods seem likely to lead to each one being advantageous for observations of certain species. This showed when incorporating foraging type (ground or arboreal) as a covariate; the former received higher density estimates (on average 102% higher) from line transects, and the latter from point counts. As well as the higher estimates, line transects gave nearly five times as many observations of ground flushers. Although line transects often received more observations than point counts, due to a larger area being surveyed, this ratio was the highest of all the species/species groups with over 40 observations from both survey types. This is likely because ground flusher species are skulking and secretive birds that are difficult to observe, and are often seen only when disturbed. Point count methodology does not lend itself to observations of such species. Line transects would be expected to result in more observations due to birds being disturbed and flushed. Similarly, density estimates for insectivorous passerines, such as white-winged fairy-wren (*Malurus leucopterus*) were, for the most part, higher from point counts than line transects. This may be because these species could be missed if the observer(s) is walking through a landscape, due to their small size and propensity for dwelling in foliage, and a stationary observer would have a higher chance of observing inconspicuous species like this.

Differences in methodology may be responsible for the higher density estimates obtained from point counts. Reynolds *et al*. (1980) found that stationary observers spent more time searching for birds and less time looking at the route ahead. The stationary nature of point counts means the observer can remain focused on observing and identifying birds (assuming the presence of a scribe who records observations, as occurred for this dataset). However, line transects involve continual moving along the transect line, so an observer(s) must pay some attention to the route to follow it accurately and ensure care when walking through what can be rough ground with obstructions. This is expected to result in fewer observations and smaller density estimates and could be particularly likely to affect observations of inconspicuous species such as small foliage-dwelling insectivores. If these birds are not disturbed by the presence of an observer(s) moving through the habitat, they may go unrecorded. Contrastingly, if they are disturbed, they may become less mobile while an observer(s) walks past, reducing likelihood of detection. Birds may behave more naturally after the observer(s) has remained stationary for a period in a point count.

Despite the finding that line transects are better suited to open habitats than point counts (Bibby *et al*., 1992a), and although more species and individuals were detected with line transects in this study, the density estimates were higher from point counts. The increased number of species and individuals from line transects is likely because line transects sample a greater area. As surveys were paired, and corresponding line transects and point counts were carried out in the same location, using the same observer(s) and at very similar times, observer bias was not thought to be an influence on relative comparisons between the two survey methods. The spacing of point count locations at least 400m apart also minimised the risk of the same birds being counted at more than one location (Hamel *et al*., 1996). The higher densities from point counts may be due to other factors. Wilson *et al*. (2000) suggest that spending more time at a single point, and the resulting increased identification of birds nearby, may cause higher density estimates. Spending more time at a single point may also mean transient birds moving into and out of the point count area are recorded, inflating density estimates. Distance sampling assumes an instantaneous sample of subjects, but a point count cannot guarantee this as observations are recorded over a period of time. Therefore, one could argue that the non-instantaneous nature of point counts will result in artificially inflated density estimates.

The data used in this analysis were the result of consistent monitoring over 6 years. However, the lack of an absolute standard of densities that we know to be correct limits our ability to make comparisons between the two methods. Although vast number of surveys were carried out, there still exist only relatively small sample sizes for many species. Of the 164 species in the dataset, over 70% had fewer than 40 observations in either line transects or point counts, so had to be excluded. Buckland *et al.* (2001) suggested a preferred requirement of at least 60-80 observations for accurate estimates, with accuracy increasing with more observations. Given the frequency of encounter of animals in the arid landscapes of the current study, a significant increase in monitoring would be required to obtain sufficient records to estimate densities for the majority of species; at the current rate, even continuing monitoring for a further 24 years results in just over half the species having at least 40 observations from both survey methods (Figure 2.4). More years of censusing is required for many species before the number of observations reaches this level. This would also reduce the need to pool species in order to calculate densities. Another limitation with the dataset is the absence of recording sex of observations. Differences in detectability between males and females of the same species may lead to biases in population density estimates (Newson *et al.*, 2008), but this would be extremely difficult, if not impossible, to record in most species. Time of year was also not controlled for. Censusing occurred from July until mid-September, over which period bird behaviour will change (e.g. birds have a higher probability of detection when they are vocalising more, such as occurs during the breeding season). Presence of observer(s) is likely to affect bird behaviour, likely causing a reduction in detectability, for both point and line transects. For the latter, birds further along the transect line may move before being recorded. Movement of birds during a count, but prior to detection, violates one of the assumptions of distance sampling (Buckland *et al.*, 1993). The most critical assumption that must be met if the resulting density estimates are to be considered accurate is that all birds either on the transect line or point count location are recorded. Small errors in bird detections close to the transect line or point count location can have significant effects on density estimates. Observer presence is likely to have more of an effect on birds nearer the transect line or count location, and even if it does not cause birds to move further away from the observer(s), it may reduce detectability if they become more skulking. This is of particular importance for point counts, as with increasing distance from the count location, the sample area increases geometrically. One other factor that must be considered is the location of the point count survey being at the end of transect lines. This introduces the potential of bias to detections, as observers may have prior knowledge of the identification and location of species (Wilson *et al*., 2000). The survey design may also result in birds being flushed during one survey (probably more likely to be line transects due to observer movement) that would have been recorded in subsequent point counts. Therefore, densities resulting from point counts may be an underestimate.

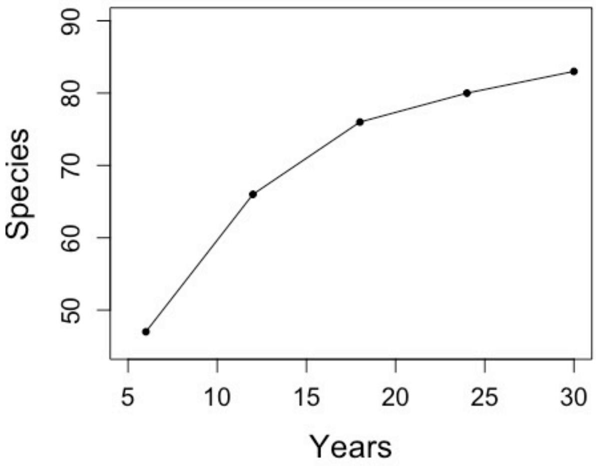


Figure 2.4: future projections of the number of species with over 40 observations from both line transects and point counts following continued monitoring. NB: first point is current survey effort (6 years).

Investigating the effect of survey methodology choice on the resulting abundance data has significant implications. Conservation relies on baseline data such as population densities for uses such as indicating whether species should be listed as of conservation concern (IUCN, 2004) and prioritising locations and habitat types for conservation (Gregory and Beillie, 1998; Pérez-Arteaga *et al*., 2005). With the limited funds and resources available for conservation, and increasing pressures faced by birds by factors such as ongoing climatic change and a rapidly rising population, it is imperative that conservation work that is carried out is made as effective and efficient as possible. Therefore, it is crucial that baseline data are accurate and can then be used in a wide range of studies, such as looking at population trends in response to drivers of change (e.g. climatic and land-use change). The two different methodologies each suit observations of certain species, and in certain habitats, more than others. Sampling design must therefore be considered case-by-case, factoring in the study species and habitat (i.e. topography, vegetation, etc.). Efficiency of the method will also likely affect the decision; point counts often require more time due to the travelling non-counting time between count locations, but have the advantage that duration of counting can be controlled, whereas line transects involve a fixed length of transect, and so the counting period is determined by how long it takes to walk the route. Line transects often sample a greater area but take longer (Raman (2003). More work on the merits of these two methods, as well as research into the application of multiple methods over prolonged periods, will help to clarify in which situation one method might be preferred over the other, and increase accuracy of resulting data that form the basis for a huge range of conservation and ecology work.

3

Estimating populations for birds of the Albertine Rift

3.1 Abstract

The Albertine Rift harbours the Africa's highest vertebrate species richness and endemism. However, it faces severe ongoing and future pressures from climate change and a rapidly-rising human population. Given the high topographic diversity of the region, and the large number of endemic and near-endemic species that are confined to relatively few areas, it is imperative to understand the current locations and population sizes of such species, to ensure their conservation and to plan effectively for future changes. Here, I use distance sampling with point count surveys for bird species, carried out over 16 years during extensive field campaigns across the Albertine Rift to estimate bird populations for 239 species. Overall species richness was highest in the Murchison-Semliki and Greater Virunga regions, and woodland-grassland, shrubland and tropical forest habitats. Endemic and threatened species richness was highest in the Greater Virunga and Maiko-Itombwe regions, and montane tropical forest and woodland-grassland habitats. Species densities varied significantly in the same habitat across regions, as well as by feeding guild. This work provides essential baseline data on bird populations in a biodiversity hotspot that has so far been relatively poorly studied and provides insight into the relative value of six core conservation sites in terms of species richness and abundances.

3.2 Introduction

Baseline population data for species are the cornerstone of conservation management and status designation; this is particularly true in the case of population size (see section 2.2). Huge numbers of studies have utilised estimates of population data or size across a broad spectrum of taxa, geographic location and scale. Such data help determine the most efficient way of targeting and allocating the limited funds and resources available to conservation (IUCN, 2004), via a wide range of applications, from prioritising locations and habitat types for conservation (Gregory and Baillie, 1998; Pérez-Arteaga *et al.*, 2005), to designating species of conservation concern. They are also essential in evaluating the effectiveness of conservation interventions (Bull *et al*, 2014). Despite the acknowledged importance of population estimates, such baseline data are still lacking across many parts of the world. Indeed, even in very well monitored regions of the developed world, populations estimates are often little more than extrapolation from simple surveys, which take little account of detectability among species. Population estimates are even more crucial for evaluating the conservation status and threat to restricted range and endemic species in the world's biodiversity hotspots; central Africa's Albertine Rift (AR) being one such hotspot.

The AR covers over 300,000 km^2 and spans parts of Zambia, Tanzania, Uganda, the Democratic Republic of the Congo (DRC), Rwanda and Burundi. Due to its position across the equator and significant elevational range (600-5100m), it harbours tremendous biodiversity; indeed, Africa's highest levels of vertebrate species richness and endemism are found in the AR, with endemics occurring at all altitudes (Brooks *et al.*, 2001; Plumptre *et al.*, 2003; Burgess *et al.*, 2004). The area also holds many threatened species (Vulnerable, Endangered or Critically Endangered, as listed by the IUCN) (Table 3.1) (Plumptre *et al.*, 2003), and these biodiversity levels have been used in several priority-setting studies. The AR is included in Conservation International's Eastern Afromontane Hotspot (Brooks *et al.*, 2004), and the region has been designated as an Endemic Bird and Biodiversity Area by Bird Life International (Stattersfield *et al.*, 1998) and a 'Global-200' priority ecoregion by the World Wildlife Fund (WWF) (Olson and Dinerstein, 1998; Burgess *et al.*, 2004). Despite these high levels of biodiversity, the region remains little studied from a biodiversity perspective, with scant information on avian diversity beyond basic metrics such as species richness (e.g. Plumptre *et al.*, 2007). Some areas of the region have received little survey attention, examples include Kahuzi Biega National Park and the Itombwe Massif (Plumptre *et al.*, 2004). Consequently, many areas remain unprotected, including the Itombwe Massif, despite its holding 34 bird species that occur only in the AR region (Plumptre *et al.*, 2007). This lack of data is particularly concerning given the significant pressures facing the Albertine Rift such as land-use and climate change, as discussed previously in this thesis. Data that facilitate prioritisation of sites for conservation are therefore essential, especially due to the lack of financial resources available for conservation in the area (Owiunji and Plumptre, 2011).

Table 3.1: Species data from the Albertine Rift (from Plumptre *et al*., 2003, 2007 2016).

	Species recorded in AR	**AR endemic species**	**Threatened species (CR, EN, VU)**
Mammals	420	42	35
Birds	1063	42	33
Reptiles	185	21	1
Amphibians	165	57	13
Butterflies	581+	117	-
Plants	6569	350	66

In this chapter, I aim to estimate baseline populations for birds in the AR. I use distance sampling, based on a dataset of point counts carried out between 2001 and 2016 across the region to estimate species densities. Distance sampling allows density estimates to be calculated under moderate assumptions (Buckland *et al*., 2001). I calculate different detectability functions (and therefore densities) for the same species in different habitat types. I then produce abundance estimates for species for six core conservation regions of the AR and their comprising habitats, and use these data to assess the relative importance of different areas for the endemic and threatened bird species.

3.3 Methods

3.3.1 Study site

Central Africa's Albertine Rift straddles the equator and covers an area of 313,000km^2, comprising the rift valley, its escarpment and freshwater lakes, and surrounding mountains that run from Lake Tanganyika's southern tip in Zambia to 30km north of Lake Albert in the Democratic Republic of the Congo (DRC)/Uganda. It spans parts of Zambia, Tanzania, Uganda, the DRC, Rwanda and Burundi (Figure 3.1) **(**Plumptre *et al*., 2003, 2007). Over its significant elevational range of 600-5109m it harbours a broad range of habitats (Table 3.2). In addition to these, it accommodates other specialised habitats such as papyrus and *Carex* wetlands, and the ongoing volcanic activity in Virunga National Park means the area holds hot springs and lava flows, with associated vegetation (Plumptre *et al*., 2007).

Table 3.2: Habitat types of the AR and the elevation ranges over which they occur (data from Plumptre *et al*., 2007).

Habitat type	**Elevation range (m)**
Lowland forest	600-1400
Savannah woodland and grassland	600-2500
Montane forest	1400-2500
Bamboo forest	2500-3000
Giant heather	3000-3500
Raised bogs	3000-4000
Giant *Senecio* and *Lobelia* vegetation	3100-3600
Alpine moorland	3400-4500
Glaciers and rocks	4500-5100

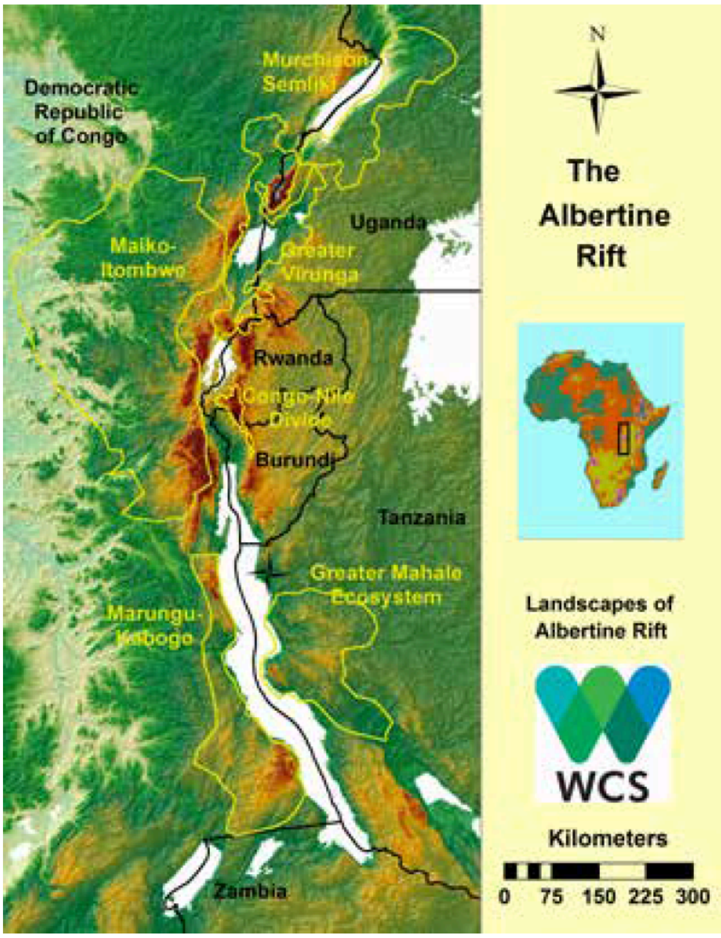


Figure 3.1: The six core conservation areas of the Albertine Rift, as were used in this analysis (from Plumptre *et al*. (2016)), the boundaries and names of which are in yellow. Country boundaries and names are in black.

3.3.2 Study design

Bird surveys were carried out throughout the Albertine Rift region between 2001 and 2016 by several observers (myself not included) as part of a project run by the Wildlife Conservation Society. 18,379 surveys were undertaken across 7,875 survey locations, covering an elevational range of 600-4150m. Each was visited between one and 77 times (mean 2.37, standard deviation 8.82). Survey locations were distributed along transects and were located to ensure good coverage of different regions, habitats and altitudes across the Albertine Rift, albeit with a focus on tropical forest, alpine and savannah grassland habitats. Surveys were conducted throughout the day between 05.35AM and 19.52PM. At each survey the date, time, transect and unique survey location, elevation, observer initials and other factors that could affect the survey results, were recorded. For each bird survey, two minutes settling time was followed by a five-minute survey using both visual and aural records. For each record (1) the species, (2) the number of individuals in the group, and (3) the distance from the observer (allocated to categorical bins of 0-10, 10-20, 20-50, 50-100, 100-200 and 200-500m) were recorded. Surveys were not carried out in severe weather such as heavy rain, as this would reduce detectability.

3.3.3 Population estimation

The method of density estimation largely followed Chapter 2 (see *2.3.4* for more details), with minor modifications due to the differences in datasets. The function ‘ds()’ within package ‘distance’ (Miller, 2016) in R v. 3.5.1 (R Core Team, 2018) was used to estimate densities. The function ‘ds()’ automatically conducts a binned analysis based on the recorded distance categories. Densities were calculated for all species with at least 30 observations. This threshold falls below the minimum of 40 observations recommended by Buckland *et al*. (2001), but was selected as a pragmatic balance to permit densities estimations for rare species with low recording rates, which included several species endemics and threatened species. In all cases, goodness of fit tests were carried out to ensure that functions fitted the data adequately (discussed later in this section). Densities were estimated, where possible for species in all of the habitat types given in Table 3.3. Observations for each species were split according to these habitat groups, as it was assumed detection curves would vary between them. The alternative approach of including habitat as a covariate in distance analyses was not adopted due to the limited degrees of freedom in resultant models.

Observations were truncated to remove the most distant records (as recommended by Buckland *et al*., 2001). Observations were excluded from analyses if detections occurred in the furthest two distance bins (100-200m and 200-500m) as the surveyed habitats have very limited visibility at these distances. This removed approximately 15% of observations. Two functions were fitted to describe the decay in detectability with distance for each species, a hazard-rate (HR) and a half-normal (HN) function. For the half-normal function, cosine adjustments were also added sequentially, up to cosine(2) adjustments (limited degrees of freedom for subsequent goodness of fit tests precluded the addition of more). Cosine adjustments were not added to the hazard-rate function due to limited degrees of freedom. Each model fitting produced an Akaike information criterion (AIC) score for model fit and a density estimate with associated standard error and confidence limits. Detectability model goodness of fit was assessed by chi-square test between data and the chosen probability distribution. If a species model passed the goodness of fit test in at least one habitat, density estimates were retained for all habitats. This approach was adopted as in some habitats the number of observations were too sparse to pass habitat-specific goodness-of-fit tests. Retaining densities estimated across all habitats resulted in more realistic population total estimates. If the goodness of fit test result was significant for detectability models for a species in all habitats, density estimation was run again, but observations in the first two distance bins (0-10m and 10-20m) were combined into one bin, as several species showed significant skew in observations towards 0-10m, and visual inspection of observation data suggested this may improve fitting. After this, if the goodness of fit test result was still significant for all habitats (i.e. the detectability models failed in all habitats for a species), the detectability functions and corresponding estimates for that species were discarded. For species being retained, the density estimate with the corresponding lower AIC value was selected.

Population estimates for individual species in a habitat were produced by multiplying the mean density of the species in a habitat by the habitat extent, with the latter determined from vegetation maps of the study area (Table 3.3) (Wildlife Conservation Society, unpublished data). The combined area of these natural habitats was 147,319km^2, approximately 50% of the total area of the Albertine Rift (313,000km^2), with much of the remainder being agricultural land. Additionally, in some areas of the Democratic Republic of the Congo the natural habitat was outside the area in which the study was operating. The populations of individual species estimated across all habitats in a region were combined, to give an overall population for each species in each region. The regions used to split up the study area were identified between 2001 and 2004 as part of a process involving NGOs, universities, local communities and Protected Area authorities to identify six core areas for conservation that would result in many endemic and threatened species being protected (Plumptre *et al.*, 2016).

Table 3.3: Extent of different key habitats in different surveyed regions of the AR (from Wildlife Conservation Society, unpublished data). * denotes that in Maiko-Itombwe, the low-resolution imagery used to map habitats meant that shrubland could not be separated from tropical forest (≤ 1400m), so these areas are combined.

Region	**Habitat Area (km^2)**						
	Bamboo	**Woodland-Grassland**	**Tropical Forest (≤ 1400m)**	**Shrubland**	**Miombo Woodland**	**High Elevation-Alpine**	**Tropical Forest (> 1400m)**
Congo-Nile Divide	15	48	976	78	0	106	160
Greater Mahale Ecosystem	0	194	228	12	10,264	0	65
Greater Virunga	786	4,754	6,072	873	0	496	1,334
Kabobo-Marungu	20	3,096	956	11	1,867	0	54
Maiko-Itombwe	307	4,308	*94,287		1,367	0	1,920
Murchison-Semliki	0	4,307	2,462	458	5,437	0	1

3.4 Results

Across all surveys, 694 species were recorded in the key habitats (Table 3.3). Of these, I was able to estimate densities and populations for 239 (Table A1 and A2, respectively). Populations could not be calculated for the remainder for a number of reasons. The majority had insufficient observations to be able to calculate densities (n = 397), and for others detectability models could not be fitted (n = 8), or species failed goodness of fit tests in all habitats (n= 39). Finally, 11 migratory species that do not spend all year in the Albertine Rift were also removed.

The Murchison-Semliki region held the highest species richness (508 species), although this was not represented in endemic and threatened species (Table 3.4). If prioritising richness of these species, the Greater Virunga region may be more valuable; as well as harbouring the second highest species richness, 36 endemic and threatened species were observed here, the most endemic and threatened species in any of the six core conservation areas of the Albertine Rift used in this analysis (Table 3.4).

Table 3.4: Number of bird species recorded from surveys in each region (only including habitats in Table 3.3).

Region	Number of species observed	Number of endemic/threatened species observed
Congo-Nile Divide	127	24
Greater Mahale Ecosystem	193	5
Greater Virunga	463	36
Kabobo-Marungu	168	21
Maiko-Itombwe	179	25
Murchison-Semliki	508	16

Even in the same habitat type, some regions hold, on average, significantly greater densities of species than others (Table 3.5). The average species density in shrubland, for example, is 25 times greater in the Maiko-Itombwe region than in the same habitat in the Murchison-Semliki region. Similarly, average species densities in tropical forest are highest in the Greater Mahale Ecosystem, for both low and higher altitudes (Table 3.5).

Table 3.5: Mean species population densities in habitats across different regions. '-' indicates that no densities were estimated in this region-habitat combination.

Habitat	Average Species Density (km^{-2})					
	Congo-Nile Divide	Greater Mahale Ecosystem	Greater Virunga	Kabobo-Marungu	Maiko-Itombwe	Murchison-Semliki
Bamboo	83.5	241.1	126	214.6	157.9	-
Woodland-Grassland	17.2	62.1	31.3	22.6	123.6	14.6
Tropical Forest (≤ 1400m)	-	130.1	36.5	63.3	31.7	41.8
Tropical Forest (> 1400m)	45	135.1	58.5	71.2	53.8	-
Shrubland	140.2	172.4	38.8	193.2	435.7	16.9
Miombo Woodland	-	46	-	-	-	-
High Elevation-Alpine	-	-	425.5	-	-	-

The habitats which hold the greatest species richness are woodland-grassland, shrubland and tropical forest (Table 3.6). However, many species were observed extremely infrequently; looking at just species for which densities were estimated (i.e. species that received at least 30 observations in key habitats, minus a small number of those for which densities could not be calculated, due to reasons stated previously), shows a significant drop-off in richness, but woodland-grassland still harbours the greatest species richness, with montane and lower altitude tropical forest next highest. Despite showing the highest species richness, species density in woodland-grassland habitats are low (9.10 individuals km^{-2}). Bamboo, which harbours significantly less species richness, exhibits the second highest average density (90.7) (and the average density in high elevation-alpine habitats comprises results from just two species).

Table 3.6: number of species observed, number of species with density estimated, and average density of species in each habitat.

Habitat	Number of species observed	Number of species with density estimated	Mean density (km^{-2})
Bamboo	173	24	90.7
Woodland-Grassland	535	133	9.10
Tropical Forest (≤ 1400m)	366	83	31.3
Tropical Forest (> 1400m)	307	100	42.0
Shrubland	392	64	15.1
Miombo Woodland	149	8	46.0
High Elevation-Alpine	40	2	213

Whilst bamboo, woodland-grassland and tropical forest habitats show little difference in number of species observed, this is largely due to many being observed at very low frequencies. Of the endemic and threatened species for which densities were estimated, montane tropical forest harbours the majority (15 out of 18 in total), and has a high average species density (84.7 individuals km^{-2}) (Table 3.7).

Table 3.7: endemic and threatened species observed, for which densities could be estimated, and the average density of endemic and threatened species in each habitat.

Habitat	Number of species observed	Number of species with density estimated	Mean density (km^{-2})
Bamboo	25	7	135
Woodland-Grassland	31	1	0.01
Tropical Forest (≤ 1400m)	20	3	7.05
Shrubland	25	0	-
Miombo Woodland	4	0	-
High Elevation-Alpine	9	1	142
Tropical Forest (> 1400m)	34	15	84.7

Total populations summed across the entire study region surveyed ranged from 409 (African black-headed oriole, *Oriolus larvatus*) to 60 million (olive sunbird, *Cyanomitra olivacea*). Populations were estimated for 18 of the 57 endemic and threatened species in the observation data, for which total populations ranged from 217 (white-headed vulture, *Trigonoceps occipitalis*) to 5.5 million (red-throated alethe, *Chamaetylas poliophrys*) (Table 3.8).

Different feeding guilds of species appear to exist at different densities (Figure 3.2). Birds of prey have the lowest average population density (1.72 individuals km^{-2}) by some distance, and nectarivores exist at the highest average density (169 individuals km^{-2}).

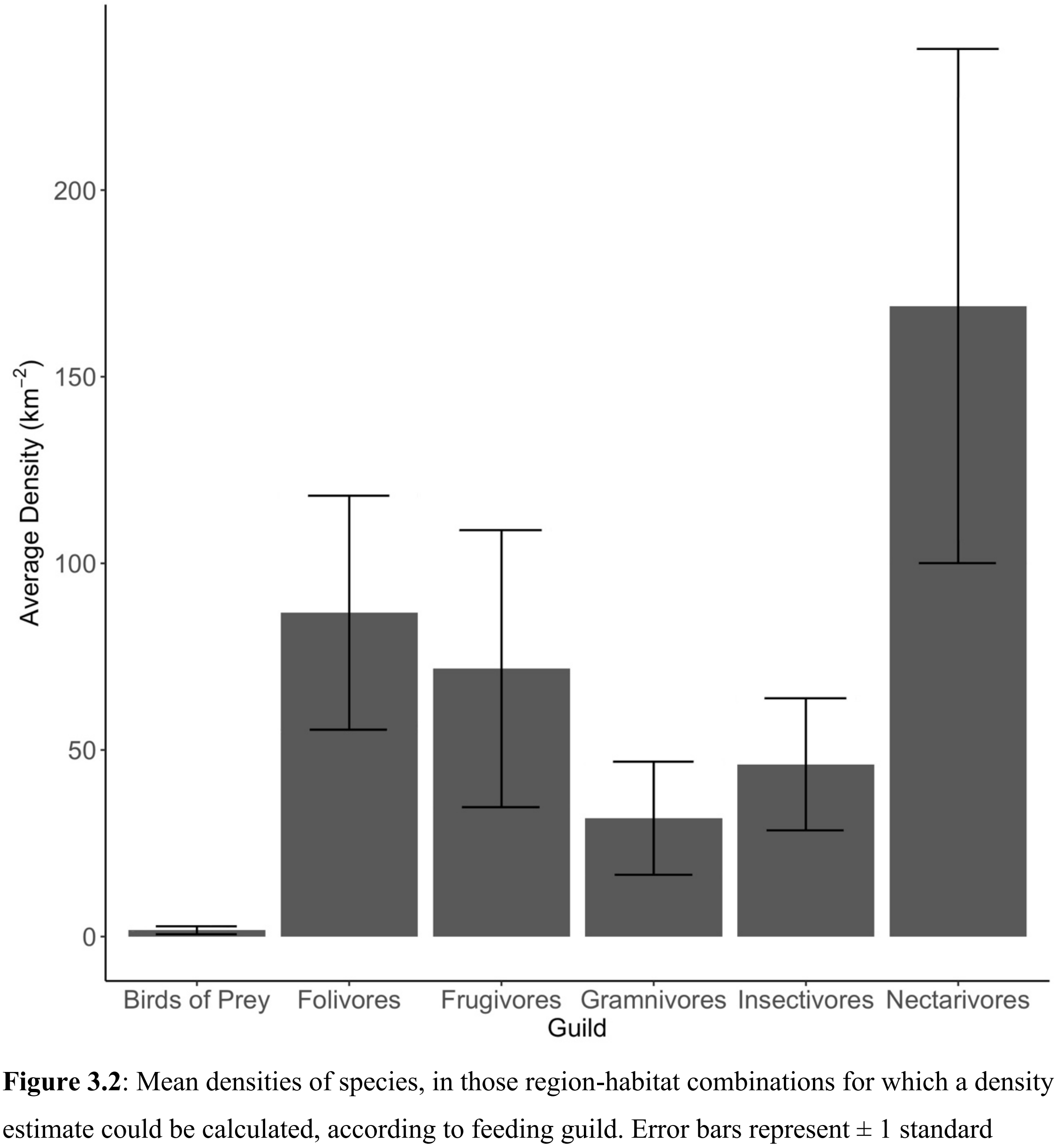


Figure 3.2: Mean densities of species, in those region-habitat combinations for which a density estimate could be calculated, according to feeding guild. Error bars represent ± 1 standard error.

Table 3.8: Regional populations estimates of endemic and threatened bird species across the study area. * denotes a species for which estimates failed goodness of fit tests in some, but not all, habitats. '–' denotes that a density, and therefore population, could not be calculated due to insufficient observations, or failure of detectability models to fit observation data, or goodness of fit tests in all habitats.

Species	**Population**						
	Congo-Nile Divide	**Greater Mahale Ecosystem**	**Greater Virunga**	**Kabobo-Marungu**	**Maiko-Itombwe**	**Murchison-Semliki**	**TOTAL**
Archer's Ground Robin	7,824	0	343,649	1,734	34,576	-	387,783
Blue-headed Sunbird	19,669	0	135,599	10,249	427,818	-	593,335
Collared Apalis	19,341	0	335,787	9,135	217,816	-	582,079
Grauer's Warbler	536	0	6,986	277	10,965	-	18,764
Grey Parrot	-	0	200,463	0	53,077	21601	275,141
Kabobo Apalis	0	0	0	4,130	0	-	4,130
Montane Masked Apalis	28,491	0	254,166	15,747	430,669	-	729,073
Nahan's Francolin	-	0	2,824	0	0	16219	19,043
Purple-breasted Sunbird	17,509	0	217,915	11,363	443,010	-	689,797
Red-faced Woodland Warbler	24,226	0	592,558	31,786	564,165	-	1,212,735
Red-throated Alethe	6,595	0	27,090	3,636	5,375,965	0	5,413,286
Regal Sunbird	50,776	7,305	622,842	49,911	786,554	-	1,517,388
Ruwenzori Double-collared Sunbird	19,847	0	218,227	749	150,727	-	389,550
Rwenzori Batis	6,632	0	129,908	2,941	89,151	-	228,632
Rwenzori Turaco*	3,922	0	21,821	1,466	41,101	-	68,310
Strange Weaver	2,621	0	41,259	387	34,107	-	78,374
Stripe-breasted Tit	5,826	0	36,302	3,595	22,604	-	68,327
White-headed Vulture*	0	0	0	0	0	217	217

Of species for which densities could be calculated in montane (> 1400m) and lower (≤ 1400m) elevation tropical forest, there was high correlation (correlation coefficient = 0.803). Linear regression showed montane forest density to be a significant predictor of medium altitude forest density (t = 9.92, *P* < 0.001). Overall, densities were greater in medium elevation forest in 34 out of 56 species (t-test: t = 2.05, *P* < 0.0449) (Figure 3.3).

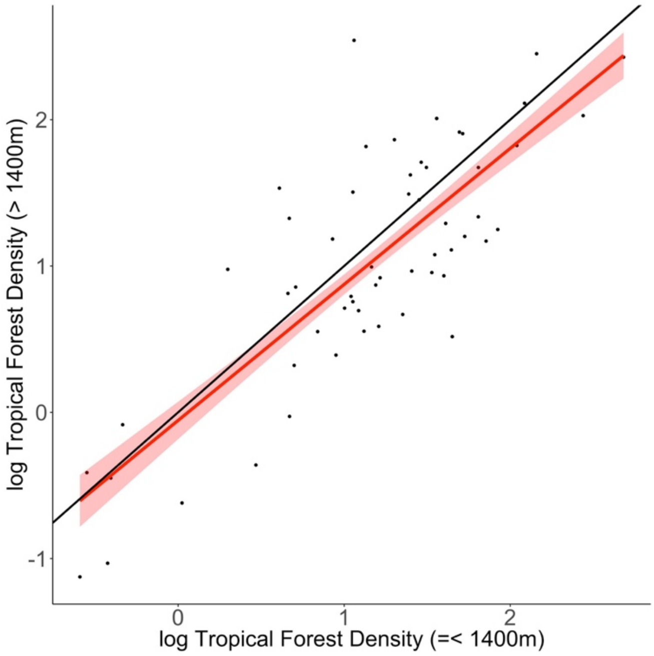


Figure 3.3: Density estimates from the montane and medium elevation tropical forest. Points represent the overall density for an individual species in the habitat. The red line is the fitted estimate of the effect and the shaded red region represents ± standard error. The black line is y=x.

3.5 Discussion

These results present population densities and sizes for 239 bird species across six core conservation areas of central Africa's Albertine Rift which provide insight into relative species richness and abundance measures of these six regions and their constituent habitats. The most important habitats, in terms of species richness for avifauna as a whole, and just those species considered endemic to the Albertine Rift or threatened, are bamboo and tropical forest. Certain regions appear to be more important to ensure protection of, although the choice of which ones is heavily dependent on the best or most suitable measure of conservation value, whether it be species richness, measures applying to all avian species.

When considering richness and densities of all species observed, the Murchison-Semliki area harbours greatest species richness, with 508 species observed in this region. The Greater Mahale Ecosystem holds the highest average species density in both lower elevation (≤ 1400m) and montane (> 1400m) tropical forest, suggesting it may be a high priority region to conserve, given the importance of preserving this specialist habitat. However, it should be noted that the calculations of average population density, across species, in different region-habitat combinations may be inherently biased as the number of species for which I was able to estimate densities was different across the six areas. Woodland-grassland, tropical forest (≤ and > 1400m) and shrubland were the habitats with the greatest species richness. Several species existed in both tropical forest habitats, and for these, densities tended to be greater at lower altitudes. However, montane (> 1400m) tropical forest held, on average, higher densities of all species than did the lower elevation tropical forest ≤ 1400m). The greater densities in lower elevation tropical forest for species that exist at all altitudes may be because these are more generalist species that show preference for lower elevations, but can tolerate a wider elevational range than strictly montane species, and so are found at higher elevations, albeit at lower densities. The higher average densities shown in montane tropical suggest a similar pattern to one of the most common patterns of diversity along elevation gradients seen, which is a hump-shape, with a peak in species density at mid-elevations (McCain, 2009). This has also been reported in the Himalayas (Acharya *et al*., 2011). As expected, birds of prey existed, on average, at the lowest population densities. This is not surprising, due to their large territories and higher energy requirements than species at lower trophic levels. Nectarivores had a significantly greater population density than other feeding guilds. This may be because for the comparison of densities according to feeding guilds, region-habitat combinations with densities of zero were excluded. They may be very abundant in areas where their food source is found, so by excluding areas where they were not seen, it appears they exist at very high densities.

When considering just the endemic and threatened species, different regions appear more important. The Murchison-Semliki region, for example, despite harbouring greatest overall species richness, showed observations of just 16 endemic and threatened species. Similarly, while the Greater Mahale Ecosystem holds the highest average species density in both lower elevation and montane tropical forest, only five endemic and threatened species were observed here, and only one of the 18 endemic and threatened species with populations calculated existed in this region. The Greater Virunga area, however, shows the highest species richness for these key species, as well as harbouring the second highest species richness overall, and therefore may be a higher priority. Woodland-grassland and tropical forest are the most important in terms of endemic and threatened species richness, along with bamboo and shrubland. However, of the 31 endemic and threatened species observed in woodland-grassland, and 25 in shrubland, habitats, densities could be estimated for just one and zero of these, respectively, largely due to insufficient observations for the remainder. This suggests that these habitats are not as important for endemic and threatened species; the high number of these species observed here may be species that are more often found in other habitats, but occasionally can be found in woodland-grassland and shrubland. Similarly, lower elevation tropical forest (≤ 1400m) had the second highest endemic and threatened species richness (in terms of species observed), but densities could only be calculated for 3. The large number of species observed in this habitat may be again due to occasional visits from species more often found in other habitats, such as montane (> 1400m) tropical forest. Some of the endemic species have very low populations across the study area, particularly the white-headed vulture (*Trigonoceps occipitalis*; 217 individuals), Kabobo apalis (*Apalis kaboboensis*; 4,130 individuals), Grauer's warbler (*Graueria vittata*; 18,764 individuals) and Nahan's francolin (*Ptilopachus nahani*; 19,043 individuals). The two regions that appear most important for the conservation of endemic and threatened species for which populations could be calculated are the Greater Virunga and Maiko-Itombwe regions, which harbour the greatest richness and density of these species.

The threats posed by climate change mean there is likely to be significant reduction in area of some habitats in the Albertine Rift in future. Work investigating the effects of climate change on seven major ecosystems of the Albertine Rift (alpine vegetation, bamboo forest, montane forest, medium altitude semi-deciduous forest, lowland rainforest, *Combretum*-grassland/woodlands and *Acacia-Brachystegia*-grasslands/woodlands) has shown that climate envelopes associated with ecosystems currently occurring in the Albertine Rift will likely shift upslope and diminish in area within the next 100 years (Ponce-Reyes *et al*., 2017). Higher altitude species and ecosystems are often more vulnerable to climate change (Dirnboeck *et al*., 2011; Lie *et al*., 2015; Ponce-Reyes *et al*., 2012), a pattern also found in the Albertine Rift, where higher-altitude ecosystems will likely suffer significant reductions (over 80% projected loss of the climatic conditions associated with those ecosystems), or even complete destruction (Ponce-Reyes *et al*., 2017). The montane regions of the Albertine Rift harbour the most endemic species, therefore placing these under greater threat of extinction. For avian species as a whole in the Albertine Rift, medium elevation tropical forest holds higher densities of species than montane forest, but the area suitable for these species will be reduced following upslope movements of conditions. Upslope movement of species will also likely lead to populations becoming more isolated, increasing the risk of detrimental effects of genetic drift and inbreeding forces, subsequently increasing the risk of local extinctions (Templeton, 1987).

The results presented in this chapter are the product of 16 years of consistent monitoring across a significant part of the Albertine Rift. Despite this, however, there were still many species for which densities could not be calculated, most commonly because the surveys had generated insufficient observations to satisfy the recommended minimum threshold of records needed to estimate densities. Even in some cases when sufficient observations existed, detectability models could not be fitted to the observation data. Here I estimated densities for species which received at least 30 observations. This threshold falls below the minimum of 40 suggested by Buckland *et al*., (2001), and well below their preferred level of 60-80 observations (Buckland *et al*., 2001). The often local and scarce nature of endemic and threatened species makes estimating their densities more difficult, if not impossible (due to insufficient observations). In order to calculate abundances for these species, future surveying could be targeted in areas in which they have been observed, using the observation data collected so far to see if the limited records of these species are concentrated in a particular area. Placing distance recordings into bins is less desirable than using exact measurements, as the latter leads to more accurate estimates, and in this case, would have allowed the inclusion of covariates, such as minutes after sunrise and observer, in the density calculations. Surveys were carried out throughout the day, but bird activity is often greatest in the first few hours after sunrise (Pettingill, 1970; Robbins, 1981), which would likely mean greater detectability. However, in many of the landscapes of the Albertine Rift, the visibility precludes exact recording of distances, so this would have been extremely difficult. The method of estimating densities here also assumes that a species occurs at the same density in the same habitat across a region, which is unlikely to be true of all species. Ideally, each species density could be clipped to a species distribution model across the entire Albertine Rift region, but this was not possible.

Baseline data such as these, for a large region such as the Albertine Rift, have implications for conservation, as well as many opportunities for further study to aid species persistence in the Albertine Rift. Here I have just separated one habitat by elevation (tropical forest), and only crudely into two bands (split at 1400m). Including more precise elevation data with climate projections would allow predictions to be made about how species will fare under future climate change, as montane species are particularly vulnerable to these threats. In Australia, predictive models projected significant population reductions for Australian tropical montane species (Shoo *et al*., 2005). Determining abundance peaks along an altitudinal gradient for species in the Albertine Rift could help forecast the impacts of climate change by calculating the range shifts required to remain in areas of suitable climate, and the possible effects on species populations. Climate change is likely to likely to result in climatic envelopes for ecosystems to shift upslope, where area will be reduced, leading to diminished range sizes for many species. Additionally, calculating densities within narrower area bands would allow predictions to be made about possible changes in species populations given upslope movement of climate envelopes, and subsequent movement of ecosystems. Although the current distribution of protected areas in the Albertine Rift represents most ecosystems, work has shown these areas may not ensure future persistence under forecast climate change (Ponce-Reyes *et al*., 2017). In addition, the small area of the Albertine Rift that may be able to resist the forecast changes is largely unprotected (Ponce-Reyes *et al*., 2017). Given the severity of threats facing the Albertine Rift (IPCC, 2007; Seimon and Plumptre, 2012; Ryan *et al*., 2017; Ponce-Reyes *et al*., 2017), combined with the limited financial resources available to conservation there (Owiunji and Plumptre, 2011), data predicting species ranges in future is essential in prioritising site protection, maximising the biodiversity of the region and ensuring species persistence.

4

Birds of Africa's Albertine Rift: effects of competitor abundance and habitat on endemic and threatened species abundance

4.1 Abstract

It is widely-accepted that biotic factors are major drivers of species abundances, but relative importance of the different factors is unclear. Here, I use principal component analysis of bird trait data to determine the nearest likely competitor species for 17 endemic and threatened bird species of central Africa's Albertine Rift. I use generalised linear models to investigate the effects of both competitor abundance and habitat on endemic and threatened species abundance, using population densities estimated with standardised distance sampling techniques. Despite previous work suggesting the role of competition in determining species distributions and range boundaries, I found competitor abundance had a significant effect on endemic/threatened species density in just 6% of cases, and in this example the relationship was positive. Habitat was a more important determinant of endemic and threatened species abundance, leading to significant differences in density of species among occupied habitats for 33% of endemic and threatened species (which were observed in more than one habitat). Such information could be used for future conservation purposes. For example, many Albertine Rift species are limited to isolated high elevation habitat along the edges of the Rift Valley. Many such species are threatened with local extinction due to a combination of future climate change and a lack of connectivity between high elevation habitat. My findings suggest that translocations of species between different peaks in the Albertine Rift, to aid species persistence under future climate change, should have few negative effects on any competitor species already present at recipient sites. In addition, a better understanding of densities of endemic and range-restricted species among habitats can guide the conservation of sites with optimal habitat for such species.

4.2 Introduction

Knowledge of the drivers of avian occurrence and abundance is fundamental to conservation, with wide-ranging applications. These include efficient allocation of the limited resources available to conservation (Dobson *et al*., 1997), design of protected areas (Cabeza and Moilanen, 2001) and, perhaps most importantly, forecasting of species' responses to threats such as climate and land-use change (McCain and Colwell, 2011). A species' fundamental niche, the set of environmental conditions under which it can survive and reproduce, will almost always differ from its realised niche, the set of environmental conditions under which it actually exists. This can largely be explained by biotic factors, the main two factors being dispersal ability and the role of biotic (interspecific) interactions (Wiens, 2011; Wisz *et al*., 2013; Godsoe *et al*., 2015).

There is substantial evidence demonstrating the effects of abiotic factors on abundance and range patterns. Temperature, in particular, has been shown, for a wide range of taxa, to predict abundances and also the boundaries of species ranges (Root, 1988b; Rubidge *et al*., 2011; Alofs and Jackson, 2015). Abiotic factors can also explain variation in species richness and abundance patterns along altitudinal gradients (Thuiller *et al*., 2004; Boucher-Lalonde *et al*., 2014) via both direct (e.g. the correlation between large-scale climate patterns and physiological tolerances of endotherms (Root, 1988a; Khaliq *et al*., 2014)) and indirect (e.g. knock-on effects of temperature on resource availability, or effects on activity patterns (Price *et al*., 2011; Cahill *et al*., 2012)) mechanisms.

Biotic factors can affect distributions and abundances via several mechanisms, including competition, mutualism, parasitism and predator-prey dynamics (Bascompte, 2009; van Dam, 2009; Godsoe *et al*., 2015). Competition and habitat requirements are widely believed to be the primary drivers of the realised niche (Pearson and Dawson, 2003). Competitive exclusion has been shown to determine congeneric species' range boundaries in several cases (e.g. Terborgh and Weske, 1975; Jankowski *et al*., 2010; Cahill *et al*., 2014). Ecotones have been correlated with species range boundaries (Able and Noon 1976; Patterson *et al.* 1998) and specific habitats can also provide requirements for reproduction or foraging, thereby imposing habitat-related range limits (Terborgh, 1985; Price, 1991). Not incorporating the influence of these biotic interactions in predictions of species distributions could severely limit their utility (Gilman *et al*., 2010), and recognising their importance is vital to understand and predict species distributions (Wiens, 2011; Wisz *et al*., 2013). Biotic interactions have been shown to affect species distributions at all spatial scales (Wisz *et al*., 2013), and are particularly important at finer scales (Shmida and Wilson, 1985; Soberón, 2007; Peterson *et al*., 2011; Wiens, 2011; Godsoe *et al*., 2015). The accuracy of species range predictions has been shown to improve noticeably upon inclusion of biotic interactions (Araújo and Luoto, 2007; Heikkinen *et al*., 2007).

In this chapter I aim to investigate the relative effects of competition and habitat type on abundance of endemic and threatened species in central Africa's Albertine Rift, using population densities calculated in Chapter *3*. I use bill measurements and body mass data to perform a principal component analysis (PCA) to determine a species' nearest competitor, as it was assumed that bill type similarity would mean there was dietary overlap between species (Schoener, 1965; Ricklefs and Cox, 1977). Previous work looking at the effects of competition on species distributions has often used congeneric competitors (e.g. Terborgh and Weske, 1975; Jankowski *et al*., 2010; Cahill *et al*., 2014) as they tend to be ecologically very similar, and so are likely to exert intense competitive pressure (Terborgh and Weske, 1975; Jankowski *et al*., 2010; Elsen *et al*., 2017). To determine whether competition is occurring, a wide range of indicators has been used, such as song playback experiments (e.g. Robinson and Terborgh, 1995; Martin and Martin, 2001; Fletcher, 2007; Jankowski *et al*., 2010), abundance models (Elsen *et al*., 2017) and species distribution and richness patterns (Terborgh and Weske, 1975; Laube *et al*., 2013). One limitation with using congeneric species is that resource partitioning to avoid sympatry via avoidance of competition is likely (MacArthur, 1958; Price, 1991). Therefore, it was assumed that calculating a species' nearest competitor using beak traits and body mass data would be more likely to identify species that compete more for resources, particularly when foraging.

Population densities were then compared for each region, and the effect of the competitor's presence was analysed for each target species. The effect of habitat was also analysed via its inclusion as a covariate. Endemic and threatened species are often prioritised in conservation. If competitor abundance tends to drive a lower abundance of endemic and threatened species in the Albertine Rift, sites holding lower densities of competitor species could be prioritised for conservation action for focal species. If habitat is a more significant driver of focal species of conservation concern, then prioritising sites holding the best habitat quality is more appropriate. The strength of competitive effects between focal and close competitor species could also have a bearing on sites for species translocations or reintroductions. Many of the endemic and threatened species found in the Albertine Rift are restricted to montane and alpine habitats, which are often separated from areas of similar habitat by lowland areas that are cultivated or comprise different habitats, posing barriers for the possibility of range shifts to new areas of suitable habitat and environmental conditions (Seimon *et al*., 2011; Seimon and Plumptre, 2012; Ayebare *et al*., 2013). The Albertine Rift is predicted to experience temperature increases as a result of climate change (IPCC, 2007). Species often respond to such changes by shifting along altitudinal gradients (Shoo *et al*., 2005). If climate change causes species' climate envelopes to move up an altitudinal gradient, the area of suitable conditions is likely to decrease, leading to reduced population sizes. Therefore, translocating species between different peaks in the Albertine Rift would likely aid species persistence in the face of future climate change.

4.3 Methods

4.3.1 Study region

Central Africa's Albertine Rift Valley harbours the continent's highest levels of species endemism (Brooks *et al*., 2001; Plumptre *et al*., 2003; Burgess *et al*., 2004), as well as many threatened (Vulnerable, Endangered or Critically Endangered, as listed by the IUCN) species (Plumptre *et al*., 2003). Over 1061 bird species occur in the area, of which 41 are endemic and 25 threatened (Stattersfield *et al*., 1998; Plumptre *et al*., 2003, 2007). In these analyses I combine the contiguous Albertine Rift and Eastern Zairean Lowlands Endemic Bird Areas (EBAs, defined by BirdLife International) as some Albertine Rift endemic bird distributions overlap in altitude with lowland species of the Eastern Zairean Lowlands (Bober *et al*., 2001**;** Herremans *et al*., 2002). As discussed in section *3.2*, the Albertine Rift faces severe threats from climate change and a rapidly rising human population (e.g. IPCC, 2007; Fisher and Christopher, 2007; Seimon and Plumptre, 2012; Ponce-Reyes *et al*., 2017; Ryan *et al*., 2017).

4.3.2 Bird data

Bird densities used were those calculated for Chapter *3*. For this analysis, however, species were not limited to those for which goodness of fit tests suggested very robust detectability models, as this would have severely limited the species pool from which to determine nearest competitors. This does mean that density estimates for some species are less robust. I considered the trade-off between the precision of density estimates and the availability of the most relevant species pool of potential competitors to merit inclusion of species with lower fitting detectability curves here. Species models which did not pass goodness of fit tests were checked visually to ensure they remained parsimonious with the observation data. Species in this category were retained as I found no systematic biases in our results that were related to species that had detectability curves that passed or failed goodness-of-fit tests. I highlight such species in the subsequent sections. I was able to estimate densities for 17 species that are either endemic to the Albertine Rift, or listed as threatened by the IUCN (Near-Threatened, Vulnerable, Endangered or Critically Endangered in the IUCN Red List). To determine the nearest competitor, data comprising measurements for bill culmen, nares, width and depth, and body mass were used. Morphological traits have been shown to explain significant variation in species dietary and foraging niches (Pigot *et al*., 2016). The traits used in this analysis are closely related to avian resource use and foraging strategies such as niche partitioning by diet, and food item selection and manipulation (Schoener, 1965; Grant, 1968; Ricklefs and Cox, 1977; Miles and Ricklefs, 1984), and have been used in previous studies to estimate niche divergence (e.g. Pigot and Tobias, 2013; McEntee *et al*., 2018). Trait measurements were obtained from Joe Tobias and used biometric measurements obtained from skins in museum collections (primarily Natural History Museum, Tring, UK), determined using standardised protocols (see Tobias *et al*., 2014; Trisos *et al*., 2014; Bregman *et al*., 2016). For each trait, species averages were calculated using, wherever possible, a minimum sample of four individuals for each species. Large amounts of these data are presented in Ulrich *et al*. (2017).

4.3.3 Principal component analysis

Principal component analysis (PCA) was carried out using the function ‘prcomp()’ in R using standardised values (as the data comprised different units (millimetres and grams). The Euclidean distance between each species was calculated using the function ‘pca2euclid()’, and the nearest competitor for each species was selected as the species from the same feeding guild and primary habitat with the shortest Euclidean distance between it and the endemic/threatened species. The list of species pairs was then combined with their respective density estimates calculated in Chapter *3*. If one of the species was observed in a habitat but the other was not, or the model for density estimate could not be fitted, its density was assumed to be zero in this habitat. In almost all cases when models could not be fitted there were very few observation data, suggesting very low densities.

4.3.4 Generalised linear model analysis

To explore the potential effects of competitor presence on endemic/threatened species abundance, a gaussian generalised linear model was used on densities of the endemic/threatened and competitor species, using the function ‘glm()’ with competitor and endemic/threatened species density as the independent and dependent variables, respectively. In some pairings, at least one species comprising the pair was observed in more than one habitat. For such species pairs, habitat was included as a covariate. Tropical forest montane habitat was used as the reference habitat in the GLM for all species pairs, except in one case when one of the species pairs did not use this habitat. For the latter case, tropical forest medium was used as the reference habitat. In the models where habitat was included as a covariate, interactions between habitat and competitor density were not included due to the limited data available with which to explore site-species interactions.

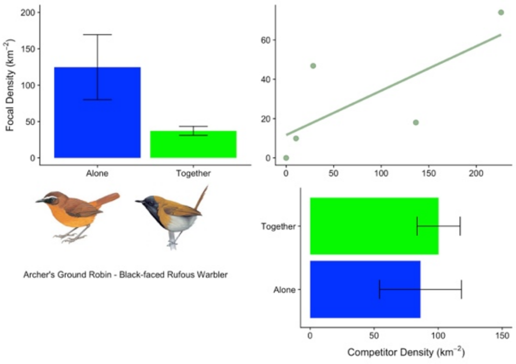
4.4 Results

Nearest competitors were determined for 17 endemic and threatened species (Table 4.1). In 16 of the 17 species pairs, competitor abundance had no effect on the abundance of the endemic/threatened species (Table 4.2). The only potentially competing pair for which a significant interaction was apparent was between blue-headed sunbird (*Cyanomitra alinae*) (endemic species) and purple-breasted sunbird (*Nectarinia purpureiventris*) (competitor species) (t = 5.31, $P = 0.013$), and this interaction was positive. In many other cases, densities of both species increased together, suggestive of a lack of competition between apparent competitors.

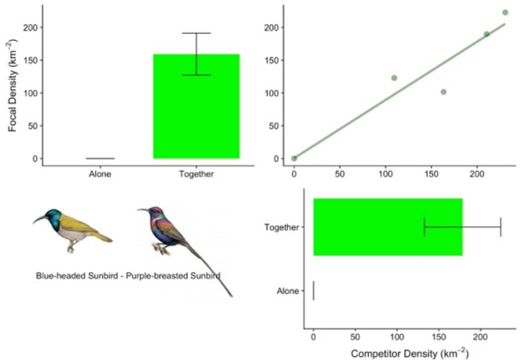
Habitat had a much more pronounced effect on the abundance of endemic and threatened species than the occurrence of an apparent competitor species. Of the 15 species pairs where at least one species was observed in more than one habitat, habitat was a significant determinant of endemic and threatened species abundance for at least one habitat in five species pairs (Figure 4.1 and Table 4.2).

Table 4.1: endemic/threatened species and nearest likely competitors. * denotes the density estimate for that species did not pass goodness of fit tests in at least one habitat. Habitat includes any habitat in which at least one of the species in the pair was observed.

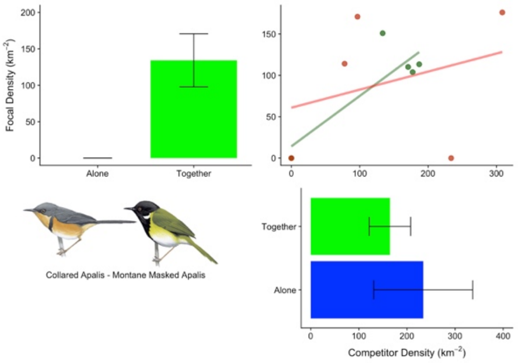
Endemic/threatened Species	**Altitude Range (m)**	**Competitor Species**	**Altitude Range (m)**	**Habitat**	**Feeding guild**
Red-throated Alethe	1067-2865	Stuhlmann's Starling	997-2699	Tropical forest (> 1400m) Tropical forest (≤ 1400m)	Terrestrial insectivore
Kabobo Apalis	1602-2691	*Chestnut-throated Apalis	1494-3317	Tropical forest (> 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Montane Masked Apalis	1091-3004	*Grey Apalis	862-2598	Tropical forest (> 1400m) Tropical forest (≤ 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Rwenzori Batis	1169-3060	Western Green Tinkerbird	1413-3026	Tropical forest (> 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Archer's Ground Robin	1106-4200	*Black-faced Rufous Warbler	675-2460	Tropical forest (> 1400m) Tropical forest (≤ 1400m) Bamboo High elevation/alpine	Gramnivore
Nahan's Francolin	692-1165	*Scaly Francolin	635-1392	Tropical forest (≤ 1400m) Woodland/grassland	Understorey gleaning insectivore
Grauer's Warbler	1091-2294	Archer's Ground Robin	1106-4200	Tropical forest (> 1400m) Bamboo Woodland/grassland	Nectarivore
Blue-headed Sunbird	1117-3110	Purple-breasted Sunbird	660-2769	Tropical forest (> 1400m)	Nectarivore
Purple-breasted Sunbird	660-2769	Regal Sunbird	1073-3242	Tropical forest (> 1400m) Bamboo	Nectarivore
Regal Sunbird	1073-3242	Purple-breasted Sunbird	660-2769	Tropical forest (> 1400m) Bamboo	Nectarivore
Ruwenzori Double-collared Sunbird	1724-3733	Olive Sunbird	608-2741	Tropical forest (> 1400m) Tropical forest (≤ 1400m)	Nectarivore
Collared Apalis	1091-3222	Montane Masked Apalis	1091-3004	Tropical forest (> 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Stripe-breasted Tit	1856-3622	Western Green Tinkerbird	1413-3026	Tropical forest (> 1400m)	Canopy/midcanopy gleaning insectivore
Red-faced Woodland Warbler	1144-3230	White-browed Crombec	943-3222	Tropical forest (> 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Strange Weaver	1774-2902	Montane Sooty Boubou	1093-3506	Tropical forest (> 1400m) Bamboo	Canopy/midcanopy gleaning insectivore
Grey Parrot	724-2470	*Blue-headed Coucal	617-2577	Tropical forest (> 1400m) Tropical forest (≤ 1400m)	Frugivore
*Rwenzori Turaco	1075-3744	*Black-billed Turaco	658-3176	Tropical forest (> 1400m) Tropical forest (≤ 1400m) Bamboo Woodland/grassland	Frugivore



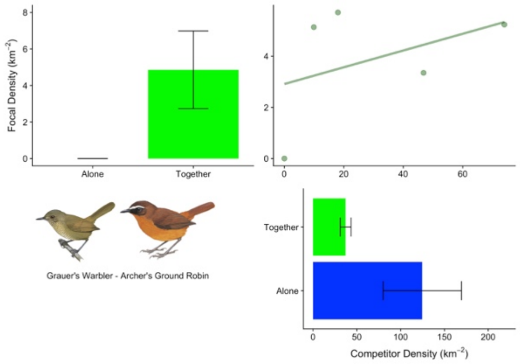
Archer's Ground Robin - Black-faced Rufous Warbler



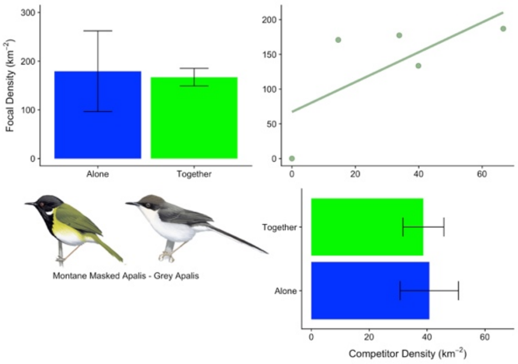
Blue-headed Sunbird - Purple-breasted Sunbird



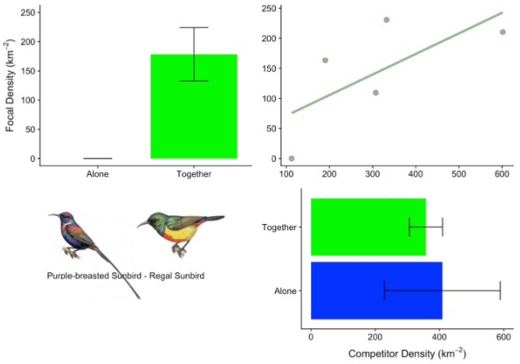
Collared Apalis - Montane Masked Apalis



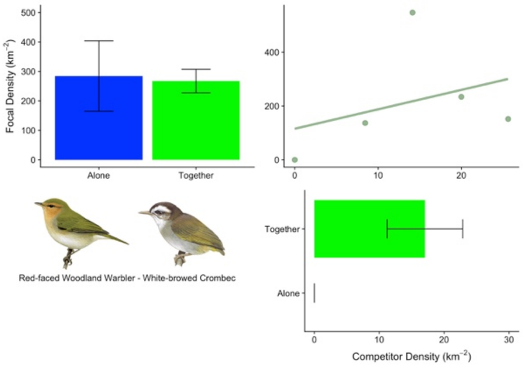
Grauer's Warbler - Archer's Ground Robin



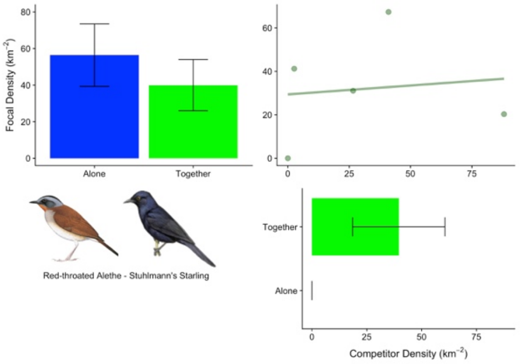
Montane Masked Apalis - Grey Apalis



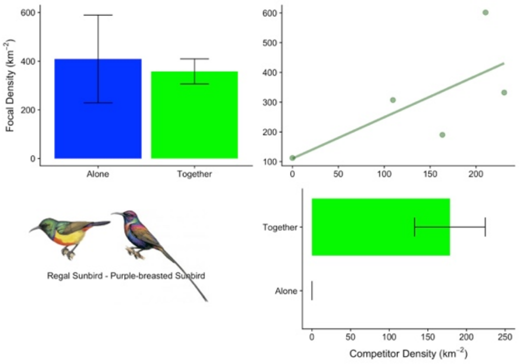
Purple-breasted Sunbird - Regal Sunbird



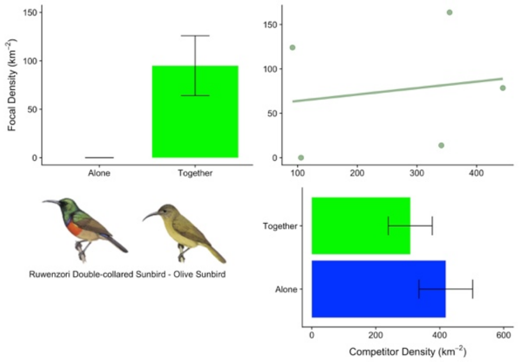
Red-faced Woodland Warbler - White-browed Crombec



Red-throated Alethe - Stuhlmann's Starling



Regal Sunbird - Purple-breasted Sunbird



Ruwenzori Double-collared Sunbird - Olive Sunbird

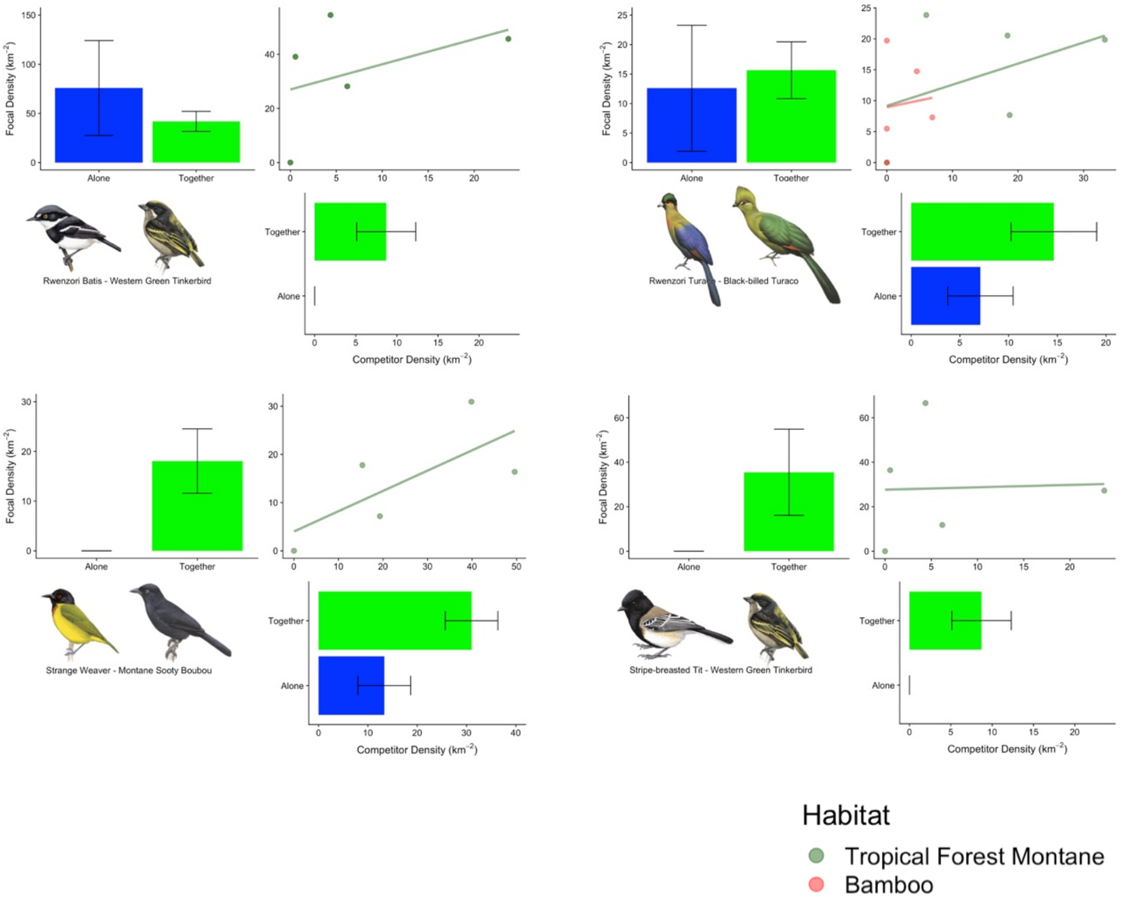


Figure 4.1 (clockwise for each plot): Mean focal (endemic and/or threatened species) density when alone and co-occurring with competitor species; regional densities of focal and competitor species in habitats where they co-occur (see legend at bottom of figure); mean competitor density when alone and co-occurring with focal species. Images obtained from Handbook of the Birds of the World Alive. Figure contains only species pairs that were observed co-occurring in the same habitat in this study. For a full figure of all species pairs and habitats, see Figure A1.

Table 4.2: GLM results for effects of habitat and competitor species density on endemic/threatened species density. Coefficient values are shown with ± one standard error. For species pairs in which habitat was included as a covariate, * indicates the reference habitat; all other habitat coefficient values are offsets to this for each species pair. Blank values indicate that a habitat did not feature in the observations for that species pair. NA values occur where each species in the pair was observed in just one, matching, habitat, so habitat was not included as a covariate.

Species Pair		Competitor		Tropical Forest (> 1400m)		Tropical Forest (≤ 1400m)		Bamboo		Woodland-Grassland	
Endemic/threatened species	**Competitor Species**	**Coefficient**	**P**	**Coefficient**	**P**	**Coefficient**	**P**	**Coefficient**	**P**	**Coefficient**	**P**
Red-throated Alethe	Stuhlmann's Starling	0.082 ± 0.373	0.832	29.391 ± 16.801*	0.124	-18.114 ± 20.621	0.41				
Kabobo Apalis	Chestnut-throated Apalis	-0.248 ± 0.177	0.204	28.715 ± 13.999*	0.079			-19.763 ± 14.796	0.223		
Montane Masked Apalis	Grey Apalis	0.978 ± 1.139	0.408	103.386 ± 52.138*	0.073	-127.318 ± 54.78	**0.04**	39.987 ± 64.739	0.549		
Rwenzori Batis	Western Green Tinkerbird	0.931 ± 2.176	0.681	26.986 ± 24.227*	0.302			18.498 ± 30.727	0.566		
Archer's Ground Robin	Black-faced Rufous Warbler	0.169 ± 0.299	0.582	16.195 ± 38.624*	0.682	-24.923 ± 43.673	0.58	26.648 ± 49.082	0.597		
Nahan's Francolin	Scaly Francolin	0 ± 2.103	1			1.411 ± 0.917*	0.16			-1.411 ± 1.297	0.309
Grauer's Warbler	Archer's Ground Robin	0.002 ± 0.007	0.768	3.824 ± 0.768*	**0.001**			-3.915 ± 1.049	**0.006**		
Blue-headed Sunbird	Purple-breasted Sunbird	0.889 ± 0.167	**0.013**	NA	NA	NA	NA	NA	NA	NA	NA
Purple-breasted Sunbird	Regal Sunbird	0.077 ± 0.084	0.391	119.045 ± 39.34*	**0.019**			-148.778 ± 42.311	**0.01**		
Regal Sunbird	Purple-breasted Sunbird	1.388 ± 1.518	0.391	110.54 ± 250.434*	0.672			276.05 ± 280.149	0.357		
Ruwenzori Double-collared Sunbird	Olive Sunbird	0.056 ± 0.144	0.71	61.072 ± 45.135*	0.218	-87.966 ± 45.316	**0.09**				
Collared Apalis	Montane Masked Apalis	0.327 ± 0.238	0.212	51.985 ± 44.647*	0.282			-6.617 ± 44.329	0.886		
Stripe-breasted Tit	Western Green Tinkerbird	0.108 ± 1.516	0.948	NA	NA	NA	NA	NA	NA	NA	NA
Red-faced Woodland Warbler	White-browed Crombec	7.226 ± 10.57	0.516	115.461 ± 172.102*	0.524			112.119 ± 196.161	0.585		
Strange Weaver	Montane Sooty Boubou	0.336 ± 0.153	0.065	6.108 ± 4.878*	0.251			-8.795 ± 5.025	0.124		
Grey Parrot	Blue-headed Coucal	0 ± 43.486	1	0 ± 5.812*	1	8.47 ± 7.542	0.3				
Rwenzori Turaco	Black-billed Turaco	0.276 ± 0.207	0.202	10.166 ± 4.164*	**0.027**	-12.512 ± 4.079	**0.01**	-1.357 ± 4.678	0.775	-10.496 ± 4.685	**0.04**

4.5 Discussion

My results show that abundance of competitor species had little effect on that of endemic and threatened species in the Albertine Rift, being significant for just one endemic species (blue-headed sunbird (*Cyanomitra alinae*) (endemic species) with purple-breasted sunbird (*Nectarinia purpureiventris*) (competitor species)), and this relationship was positive. There was more evidence for habitat as a driver of population densities for the endemic and threatened species, being significant for at least one habitat in five species pairs (out of the 15 pairs observed in more than one habitat). Observation of the graphs in Figure 4.1 also suggests that habitat is a much more important driver. In eight species pairs, abundances of the endemic and threatened species were higher when occurring with the competitor species than when occurring in isolation, and in habitats in which both species of a pair occurred, abundances increased together in every case, rather than an increase in one species resulting in a decrease in another. This could be attributable to a range of factors, such as better habitat quality benefitting both species, leading to higher abundances of both, and suggests that an increase in commoner generalist species may not be detrimental to the abundances of threatened and endemic species of the Albertine Rift.

Previous studies into the effects of competition and habitat on species distributions have shown mixed conclusions. There is widespread evidence of competition playing a major role in determining species ranges (Terborgh and Weske, 1975; Jankowski *et al*., 2010; Laube *et al*., 2013). However, recent work in the Himalayas found little evidence for this or for congeneric competitors limiting species' elevational ranges, with model results suggesting that displaced habitat and differing temperature profiles were better predictors of any observed elevational shifts (Elsen *et al*., 2017). Whilst with purely congeneric competitors, resource partitioning to avoid competition is likely to allow sympatry (MacArthur, 1958; Price, 1991), it was assumed that calculating a species' nearest competitor using measurements of bill and body mass would be more likely to result in species that compete more for resources, particularly when foraging, so the limited evidence for competitor abundance driving endemic/threatened species abundance suggests competition does not play a large role in driving abundances of these endemic and threatened species in the Albertine Rift. The proportion of species pairs in which habitat was a significant factor in endemic and threatened species density was much higher, with a third of species showing significant relationships with at least one habitat type. The often local and specialist nature of endemic and threatened species means they are likely to be tied to particular habitats. A species' requirements for reproduction or foraging reduce the range of resources it can use, and therefore impose range limits (Terborgh, 1985; Price, 1991). Previous work suggests that spatial exclusion is common in tropical ecosystems, whereas in temperate ecosystems habitat may be more important, with separate habitat selection among congeners resulting from competitive interactions (Robinson and Terborgh, 1995; Patterson *et al.*, 1998; Elsen *et al.*, 2017).

The data used for this study were the result of 16 years of consistent monitoring across the Albertine Rift. Although densities could not be estimated for many species as they received insufficient observations, these species are less likely to be limiting a species that is more abundant, for which a density could be estimated. Therefore, although it is plausible that a species for which a density could not be calculated may have been a closer competitor than those which I was able to select from, it remains unlikely that these species would exert significant pressure on endemic and threatened species. More observation data would have helped the inclusion of more endemic and threatened species in the analysis, as only 17 could be included here. However, the local and rare nature of several of the endemic and threatened species makes this difficult. Densities used in this analysis were calculated for species receiving at least 30 observations. This threshold falls below the minimum of 40 suggested by Buckland *et al.* (2001), and well below their preferred requirement of 60-80 observations (Buckland *et al.*, 2001), but was used due to the rarity and subsequent low recording rates of several of the species in the dataset. Whilst this study considers the effects of habitat and competitor abundance, it is widely acknowledged that abiotic factors play a significant role in driving species distribution and range patterns (Root, 1988b; Rubidge *et al.*, 2011; Alofs and Jackson, 2015). Future study that included the effects of these would give a clearer picture of the drivers of populations for endemic and threatened species in the Albertine Rift. There is also the question of the accuracy of the density estimates calculated in Chapter *3*. When future studies are carried out, recording of distances as exact measurements is preferable. In this case, distances were placed into bins. This increases the uncertainty around the resulting density estimates and makes it harder to fit models.

Despite the importance of determining the relative importance of specific abiotic and biotic factors on species, work to achieve this is complicated due to the difficulty associated with performing controlled experiments (Terborgh, 1971). However, work that investigates the drivers of population densities for endemic and threatened species has significant implications. Endemic and threatened species are often at higher risk of extinction (Bibby *et al.*, 1992b); threatened species have low, commonly decreasing populations, and endemic species tend to have limited ranges. In the Albertine Rift, many of these species are found in montane tropical forest and alpine habitats, areas of habitat which are often separated from similar areas by large regions of unsuitable habitat. This means the probability of successful dispersal to new suitable areas is low, so endemic and threatened species in montane regions such as this are of high conservation concern. The results here imply it is habitat quality that is more important than lower abundance of competitors. This could be used when looking at prioritisation of sites for conservation, particularly in an area such as the Albertine Rift, where resources for conservation are limited and the human population is rising rapidly, leading to increasing habitat destruction. There are also implications for the translocation of species to aid species persistence under the threat of climate change. I find that the occurrence of potential competitor species has little impact on endemic and threatened species abundance, suggesting that translocation between different peaks of the Albertine Rift should have few detrimental effects on potential competitor species present at recipient sites.

5

General Discussion

5.1 Synthesis

In this thesis, I compared bird density estimates obtained from line transects and point counts, using data from almost simultaneous studies using the two methods in the same area of arid-zone Australia (Chapter 2). Then, using a large standardised dataset of bird point counts carried out over 16 years across six key core conservation areas of central Africa's Albertine Rift, I estimated populations for this region (Chapter 3), and investigated the effects of biotic factors on abundances of the endemic and threatened bird species found here (Chapter 4).

5.2 Summary of findings

In Chapter 2 of this thesis, I used distance sampling to compare the merits of line transects and point counts when surveying Australian arid-zone birds. Relatively little work has been carried out into the efficacy of these two survey methods, despite their widespread use in obtaining baseline data which are, in turn, of critical importance in ecological studies, particularly those with conservation applications. Studies using line transects and point counts have wide-ranging applications, helping to determine the best way to target and allocate the limited funds and resources available to conservation (IUCN, 2004). Such applications include designating species as being of conservation concern (IUCN, 2004) and prioritising locations and habitat types for conservation (Gregory and Baillie, 1998**;** Pérez-Arteaga *et al*., 2005). Previous work comparing methodologies has not managed to produce a general consensus, with studies showing preference for point counts (e.g. Verner and Ritter, 1985; Yinting *et al*., 2010), others for line transects (e.g. Wilson *et al*., 2000), and others no significant difference between them (e.g. Dobkin and Rich, 1998). My results illustrated that density estimates derived from point counts were significantly greater than those from line transects for birds in the Australian Outback. Foraging strategy (arboreal or ground-based) had a significant effect, suggesting that, typically, arboreal foragers are better detected by point counts, and ground foragers by line transects. Consequently, ground foragers had higher density estimates when estimated by line transects, and arboreal foragers had higher estimates from point counts, presumably due to the differing methodologies of the two methods lending themselves to better detecting certain species.

In Chapter 3, I used distance sampling on a large dataset of point count observations for birds in central Africa's Albertine Rift to calculate population densities and, from these, abundances. Despite its extremely high biodiversity levels (the region harbours the highest levels of vertebrate species endemism and richness in Africa), as well as the significant pressures from threats such as climate change and a growing human population, the region has received relatively little study. The results provide important baseline data for the region, and have wide-ranging applications, particularly relating to future conservation work to aid species persistence in this region. I found non-uniform patterns of species richness across the six surveyed core conservation areas of the Albertine Rift used in this analysis, with greatest richness of species in the Murchison-Semliki and Greater Virunga areas, and the greatest richness of endemic and threatened species in the Greater Virunga and Maiko-Itombwe regions. Average species density in the same habitat also varied significantly across regions, and in some cases was as much as 25 times higher in one region than another (as was the case for shrubland in the Maiko-Itombwe region and Murchison-Semliki region). The habitats with greatest species richness were woodland-grassland (535), shrubland (392) and tropical forest (366 and 307 in forest above and up to 1400m, respectively), although looking at richness of species that received at least 30 observations reduces the importance of shrubland. Richness of endemic and threatened species was highest in woodland-grassland, montane tropical forest and shrubland, although many of these species were observed extremely infrequently. When just considering richness of endemic and threatened species that received at least 30 observations, montane tropical forest was the highest, with 15 species (out of 18 for which densities could be produced). Of the species for which densities could be produced, several existed in both montane and lower elevation tropical forest, although this applied to just one endemic/threatened species. For these species, densities tended to be higher in lower elevation forest. Average densities also different by feeding guild, with nectarivores highest by some margin (average density = 169 individuals km^{-2}), and birds of prey, unsurprisingly, lowers (1.72 individuals km^{-2}).

In Chapter 4, I focused on the effects of biotic factors on abundances of endemic and threatened bird species of the Albertine Rift. There is widespread evidence of the role biotic factors play in determining species range boundaries and distributions (e.g. Terborgh, 1985; Terborgh and Weske, 1975; Pearson and Dawson, 2003; Bascompte, 2009; Jankowski *et al.*, 2010 Wiens, 2011; Wisz *et al.*, 2013; Godsoe *et al.*, 2015). Using beak trait and body mass data, I determined a nearest likely competitor species for each endemic and threatened species for which I was able to calculate a density in Chapter 3. Although previous work has often used congeneric competitor species (e.g. Terborgh and Weske, 1975; Jankowski *et al.*, 2010; Cahill *et al.*, 2014) due to ecological similarity, resource partitioning to avoid competition is highly likely (MacArthur, 1958; Price, 1991). Therefore, as an alternative approach, I performed principal component analysis using the beak trait and body mass data to determine a likely nearest competitor in the same feeding guild and primary habitat. Using the resulting species pairs, I then compared the corresponding density estimates in different habitats to investigate whether competitor abundance or habitat type have a significant effect on the abundance of endemic and threatened species in the Albertine Rift. Contrary to previous studies demonstrating the role of competition in determining species distributions and range boundaries, competitor abundance was a significant factor in just 6% of cases (and this was a positive interaction), and habitat in 33%. This suggests competitor abundance plays little role in driving abundance of endemic and threatened species in the Albertine Rift, and, unsurprisingly, habitat is a significant factor.

5.3 Implications and future directions

5.3.1 Survey choice

The findings from Chapter 2 highlight the importance of survey choice when calculating bird abundances. The influence that survey choice has, and the wide-ranging applications of baseline data such as population abundances that these survey methods are used for, means careful consideration should be taken of which method to use, so sampling design should be considered on a case-by-case basis, factoring in both species and habitat of the study. Different behavioural traits of target species may lead to one or other method being preferred; my results suggested that arboreal foragers may be better detected by point counts and ground foragers by line transects. When considering which method to use, efficiency must be considered, as time will likely be limited; line transects can survey a larger area, but often take longer (Raman, 2003). All these factors need to be taken into account to pick the most suitable survey method in the scenario. There are still relatively few studies that investigate the relative efficacy of point counts and line transects via surveys carried out in the same location, as close together in time as possible. More work using data collected in a similar manner to the long-term study design carried out to collect data used in this analysis would provide further insights for more habitats and help contribute to a greater picture of when one method may be preferred over another.

5.3.2 Bird populations in the Albertine Rift

The populations calculated in Chapter 3 provide important baseline data for bird abundances in the Albertine Rift, and illustrate the relative importance of various regions of the Albertine Rift in terms of species richness. These results could be used in prioritisation of sites for conservation, particularly given that large areas of the Albertine Rift remain unprotected, and are therefore at significant risk from an expanding human population. The abundances provide many opportunities for future study, particularly with regard to the impacts of climate change, which will likely result in upslope movement of ecosystems as they attempt to keep up with the climate envelope shifting to greater elevations (Shoo *et al*., 2005). Some possibilities include determining abundance peaks to investigate possible future effects of climate change, and forecasting what percentage of current habitat areas will be lost in future and the effects this may have on species in the Albertine Rift. Although the data used were the result of 16 years of consistent monitoring across the Albertine Rift, densities could not be calculated for many species, particularly some of the endemic and threatened species, as they are often scarce and local, and so did not meet the required number of observations. Of the 694 species observed during surveying, densities could only be calculated for 239. Of greater concern was that, of the 57 endemic and threatened species observed, I was able to produce density estimates for just 18. This is despite many years of detailed surveying in species-rich tropical habitats. It is vital to have baseline data such as population densities and sizes on species for efficient conservation, but it is also clear that obtaining sufficient observations of cryptic, rare or local species is extremely difficult, particularly in habitats with poor visibility. Continuation of the bird surveys in the Albertine Rift would mean this analysis could be applied to a greater proportion of the endemic and threatened species in the region.

5.3.3 Competitors

The results from Chapter 4 show that competitor abundance has little effect on abundance of endemic and threatened species in the Albertine Rift, but the effect of habitat was more pronounced. Endemic and threatened species are of greater conservation concern, as they are generally more vulnerable to extinction (Bibby *et al*., 1992b). Ecotourism can provide valuable and substantial income (e.g. Xie, 2012 – unpublished; Balmford *et al*., 2015), and endemic and threatened can be a more attractive draw for ecotourists (Meuser *et al*., 2009; Biggs *et al*., 2011; Booth *et al*., 2011). Many of these endemic and threatened species in the Albertine Rift are found in montane habitats on mountain peaks often separated from other areas of similar conditions by large lowland expanses, comprising either unsuitable natural ecosystems, or habitat that has been converted to agriculture or settlement (Seimon *et al*., 2011; Seimon and Plumptre, 2012; Ayebare *et al*., 2013). This means the likelihood that many species will be able to successfully disperse unaided to new areas of suitable conditions is low. Therefore, the fact that competitor abundance has little effect means translocation of endemic and threatened species to new areas of suitable conditions to aid persistence under the threat of future climate change should have few negative effects on potential competitor species already present at the recipient sites. Future work that investigates the importance of abiotic factors in driving species distributions and abundances is also important, as abiotic factors are well-known to be significant determinants (Root, 1988b; Rubidge *et al*., 2011; Alofs and Jackson, 2015). Taking account of these factors as well as biotic factors would give greater insight into drivers of populations for endemic and threatened bird species in the Albertine Rift.

5.3.4 The importance of large datasets

The work carried out in this thesis was only possible due to large datasets resulting from many years of consistent monitoring. The establishment of baseline data such as population abundances is crucial to conservation, with wide-ranging applications such as prioritising locations and habitats for conservation (Gregory and Beillie, 1998; Pérez-Arteaga *et al*., 2005), assessing a species' conservation status (IUCN, 2004) and examining drivers of species abundances. Using abundance data also provides greater insight than presence absence metrics, as it is population size and trends that are used for examining a species' conservation status (IUCN, 2001; Mace *et al*., 2008). However, calculation of population densities by distance sampling is only possible with numerous observations of a species. The minimum number of observations to accurately calculate a density using distance sampling is 40 (Buckland *et al*., 2001), with a preferred threshold of 60-80 (Buckland *et al*., 2001) which, for species that are local, scarce or cryptic, can be extremely hard to reach. In this thesis I have used data from two long-term studies in Outback Australia and central Africa's Albertine Rift, lasting six years and sixteen years, respectively. Despite this, a significant proportion of species still fell below the minimum observation threshold, set by me as 40 for the Australian data and 30 for the Albertine Rift (a lower threshold was used for the Albertine Rift data due to the scarce nature of many of the species; goodness of fit tests were still carried out to ensure the models fitted appropriately). However, projecting the number of species that would receive 40 observations in the Outback Australia study if surveying was continued showed that even if its duration were to be extended from 6 to 30 years, a large proportion of species would still remain under the minimum threshold (see Chapter 2, Figure 2.4). Another issue to consider is the difficulty of estimating accurate abundances for endemic and threatened species. These are often scarce and/or local, which can make it difficult to obtain sufficient observations to calculate abundances accurately. Out of 57 endemic and threatened species found in the Albertine Rift, I was only able to calculate a density for 18. These species can be desirable to conservationists, as often they are at greater risk of extinction; the nature of threatened species means they tend to be suffering population declines, or have extremely small populations, and the often-local nature of endemics means they are more vulnerable to extinction (Bibby *et al*., 1992b). Therefore, during surveying of a large area such as occurred in the Albertine Rift, particular effort should be made to ensure that sufficient observations of endemic and threatened species are made to allow accurate calculation of abundances, which have crucial applications to their conservation.

5.4 Summary

In this thesis, I have demonstrated that density estimates tend to be greater when arising from point counts compared to line transects. However, species traits may mean that one survey method is preferable to another. Future analyses into the efficacy of these two methods of data collection will help clarify when one method may be preferred over the other. When determining which method to use, careful consideration of a range of factors should be taken, such as landscape, topography, vegetation and target species, in order to achieve the most accurate results. I have also provided population sizes for 239 bird species across six core conservation areas of central Africa's Albertine Rift. Baseline data such as these are vital in conservation work, and have a wide range of opportunities for future work, particularly relating to potential impacts of climate change on birds in this region. Finally, I have shown that competitor species abundance has little effect on the abundances of endemic and threatened bird species of central Africa's Albertine Rift. This has implications for conservation of these species, and suggests that translocation to alternative areas of suitable montane habitat will have few detrimental effects on species already present in the recipient areas. This thesis has demonstrated the importance of appropriate survey method choice, and provided baseline data for one of the world's biodiversity hotspots that is facing severe threats. These results should help to conserve biodiversity, through an increased understanding into the relative methods of two widely-used methods of data collection and calculation of important baseline data which will provide useful in future work to aid conservation in the Albertine Rift.

References

Able, K. and Noon, B. (1976). Avian community structure along elevational gradients in the northeastern United States. *Oecologia*, 26(3), pp.275-294.

Achard, F. (2002). Determination of Deforestation Rates of the World's Humid Tropical Forests. *Science*, 297(5583), pp.999-1002.

Achard, F., Eva, H., Mayaux, P., Stibig, H. and Belward, A. (2004). Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. *Global Biogeochemical Cycles*, 18(2).

Acharya, B. J., Sanders, N. J., Vijayan, L. and Chettri, B. (2011). Elevational Gradients in Bird Diversity in the Eastern Himalaya: An Evaluation of Distribution Patterns and Their Underlying Mechanisms. *PLoS ONE*, 6(12), e29097.

African Studies Center (2010). East Africa living Encyclopedia. University of Pennsylvania (2010) http://www.africa.upenn.edu/NEH/kenergy.htm, Accessed 04/10/2017

Akinyemi, F. (2013). *Socio-economic development in the Albertine Rift and its impact on the environment*. S. Kanyamibwa (Ed.), Albertine rift conservation status report, ARCOS, Series No 1. Uganda and UK, pp.69-74.

Alofs, K. and Jackson, D. (2015). The abiotic and biotic factors limiting establishment of predatory fishes at their expanding northern range boundaries in Ontario, Canada. *Global Change Biology*, 21(6), pp.2227-2237.

Anderson, D., Burnham, K. and Thompson, W. (2000). Null Hypothesis Testing: Problems, Prevalence, and an Alternative. *The Journal of Wildlife Management*, 64(4), p.912.

Araújo, M. and Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16(6), pp.743-753.

Asner, G., Rudel, T., Aide, T., Defries, R. and Emerson, R. (2009). A Contemporary Assessment of Change in Humid Tropical Forests. *Conservation Biology*, 23(6), pp.1386-1395.

Ayebare, S., Ponce-Reyes, R., Segan, D., Watson, J., Possingham, H., Seimon, A. and Plumptre, A. (2013). Identifying climate resilient corridors for conservation in the Albertine Rift. *Unpublished report to the Wildlife Conservation Society to MacArthur Foundation*.

Baker, T., Phillips O., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T., Laurance, S., Laurance, W., Lewis, S., Monteagudo, A. Neil, D., Vargas, P., Pitman, N., Silva, J. and Martínez, R. (2004). Increasing biomass in Amazonian forest plots. *Philos Trans R Soc Lond B Biol Sci.* 359(1443), pp. 353-365

Balmford, A., Green, J., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. and Manica, A. (2015). Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. *PLOS Biology*, 13(2), p.e1002074.

Barlow, J., Mestre, L., Gardner, T. and Peres, C. (2007). The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation*, 136(2), pp.212-231.

Barlow, J. and Peres, C. (2004). Ecological responses to El Nino-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.367-380.

Barlow, J. and Peres, C. (2008). Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1498), pp.1787-1794.

Barnosky, A., Matzke, N., Tomiya, S., Wogan, G., Swartz, B., Quental, T., Marshall, C., McGuire, J., Lindsey, E., Maguire, K., Mersey, B. and Ferrer, E. (2011). Has the earth's sixth mass extinction already arrived?. *Nature*, 471, pp.51-57.

Barraclough, R. K. (2000). Distance sampling: a discussion document produced for the Department of Conservation. Wellington, New Zealand Department of Conservation.

Bascompte, J. (2009). Mutualistic networks. *Frontiers in Ecology and the Environment*, 7(8), pp.429-436.

Beaugrand, G., Reid, P., Ibañez, F., Lindley, J. and Edwards, M. (2002). Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science*, 296(5573), pp.1692-1694.

Beier, P. and Noss, R. (1998). Do Habitat Corridors Provide Connectivity? *Conservation Biology*, 12(6), pp.1241-1252.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), pp.365-377.

Bibby, C., Burgess, N. and Hill, D. (1992a). *Bird census techniques*. London: Academic Press.

Bibby, C., Collar, N., Crosby, M., Heath, M., Imboden, C., Johnson, T., Long, A., Stattersfield, A. and Thirgood, S. (1992b). *Putting biodiversity on the map: priority areas for global conservation*. Cambridge: International Council for Bird Preservation.

Biggs, D., Turpie, J., Fabricius, J. C. and Spenceley, A. (2011). The value of avitourism for conservation and job creation – An analysis from South Africa. *Conservation and Society*, 9(1), pp.80-90.

Bober, S. O., Herremans, M., Louette, M., Kerbis Peterhans, J.C. and Bates, J.M. (2001). Geographical and altitudinal distribution of birds endemic to the Albertine Rift. Proceedings 10th Pan African Ornithological Congress, Kampala, Uganda. *Ostrich Supplement* 15, pp.189-196.

Booth, J. E., Gaston, K. J., Evans, K. L. and Armsworth, P. R. (2011). The value of species rarity in biodiversity recreation: A birdwatching example. *Biological Conservation*, 144(11), pp.2728-2732.

Boren, J., Engle, D., Palmer, M., Masters, R. and Criner, T. (1999). Land Use Change Effects on Breeding Bird Community Composition. *Journal of Range Management*, 52(5), p.420.

Both, C. and Visser, M. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411, pp.296-298.

Both, C., van Asch, M., Bijlsma, R., van den Burg, A. and Visser, M. (2009). Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, 78(1), pp.73-83.

Boucher-Lalonde, V., Kerr, J. and Currie, D. (2014). Does climate limit species richness by limiting individual species' ranges? *Proceedings of the Royal Society B: Biological Sciences*, 281(1776), pp.20132695-20132695.

Bradshaw, C., Sodhi, N. and Brook, B. (2009). Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7(2), pp.79-87.

Brashares, J., Arcese, P. and Sam, M. (2001). Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society B: Biological Sciences*, 268(1484), pp.2473-2478.

Bregman, T. P., Lees, A.C., MacGregor, H.E.A, Darski, B., de Moura, N.G., Aleixo, A., Barlow, J. and Tobias, J.A. (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, 283(1844), 20161289.

Bridgman, H. and Oliver, J. (2006). *The Global Climate System: Patterns, Processes, and Teleconnections*. Cambridge University Press.

Brook, B., Bradshaw, C., Koh, L. and Sodhi, N. (2006). Momentum Drives the Crash: Mass Extinction in the Tropics1. *Biotropica*, 38(3), pp.302-305.

Brook, B., Sodhi, N. and Bradshaw, C. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, 23(8), pp.453-460.

Brook, B., Sodhi, N. and Ng, P. (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature*, 424(6947), pp.420-426.

Brooks, T., Balmford, A., Burgess, N., Fjeldså, J., Hansen, L., Moore, J., Rahbek, C. and Williams, P. (2001). Toward a Blueprint for Conservation in Africa. *BioScience*, 51(8), p.613.

Brooks, T.M., Hoffmann, M., Burgess, N., Plumptre, A., Williams, S., Gereau, R. E., Mittermeier, R. A., Stuart, S. (2004). Eastern Afromontane. In: Mittermeier, R. A., Robles-Gil, P., Hoffmann, M., Pilgrim, J. D., Brooks, T. M., Mittermeier, C. G., Lamoreux, J. L., Fonseca, G. (Eds.), *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*, second en., Cemex, Mexico, pp. 241-242

Brown, J., Valone, T. and Curtin, C. (1997). Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences*, 94(18), pp.9729-9733.

Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. (1993). Distance Sampling: Estimating Abundance of Biological Populations. London: Chapman and Hall.

Buckland, S., Anderson, D., Burnham, K., Laake, J. and Borchers, D. (2001). *Introduction to Distance Sampling: Estimating Abundance of Biological Population*. New York: Oxford University Press.

Bull, J. W., Gordon, A., Law, E. A., Suttle, K. B. and Milner-Gulland, E. J. (2014). Importance of Baseline Specification in Evaluating Conservation Intentions and Achieving No Net Loss of Biodiversity. *Conservation Biology*, 28(3), pp.799-809.

Burgess, N., D'Amico Hales, J., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. and Newman, K. (2004). *Terrestrial Ecoregions of Africa and Madagascar: A Continental Assessment*. 1st ed. Washington DC: Island Press, p.550.

Burrows, M., Schoeman, D., Richardson, A., Molinos, J., Hoffmann, A., Buckley, L., Moore, P., Brown, C., Bruno, J., Duarte, C., Halpern, B., Hoegh-Guldberg, O., Kappel, C., Kiessling, W., O'Connor, M., Pandolfi, J., Parmesan, C., Sydeman, W., Ferrier, S., Williams, K. and Poloczanska, E. (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, 507(7493), pp.492-495.

Bush, G. K., Nampindo, S., Aguti, C. and Plumptre, A. J. (2004). Valuing Uganda's Forests: A Livelihood and Ecosystems Approach. Unpublished report to National Forest Authority, Uganda. www.albertinerift.org

Butchart, S., Walpole, M., Collen, B., van Strien, A., Scharlemann, J., Almond, R., Baillie, J., Bomhard, B., Brown, C., Bruno, J., Carpenter, K., Carr, G., Chanson, J., Chenery, A., Csirke, J., Davidson, N., Dentener, F., Foster, M., Galli, A., Galloway, J., Genovesi, P., Gregory, R., Hockings, M., Kapos, V., Lamarque, J., Leverington, F., Loh, J., McGeoch, M., McRae, L., Minasyan, A., Hernández Morcillo, M., Oldfield, T., Pauly, D., Quader, S., Revenga, C., Sauer, J., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S., Symes, A., Tierney, M., Tyrrell, T., Vié, J. and Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, 328, pp.1164–1168.

Cabeza, M. and Moilanen, A. (2001). Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution*, 16(5), pp.242-248.

Cahill, A., Aiello-Lammens, M., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C., Ryu, H., Sbeglia, G., Spagnolo, F., Waldron, J. and Wiens, J. (2014). Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, 41(3), pp.429-442.

Cahill, A., Aiello-Lammens, M., Fisher-Reid, M., Hua, X., Karanewsky, C., Yeong Ryu, H., Sbeglia, G., Spagnolo, F., Waldron, J., Warsi, O. and Wiens, J. (2012). How does climate change cause extinction?. *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), pp.20121890-20121890.

Cardinale, B., Duffy, J., Gonzalez, A., Hooper, D., Perrings, C., Venail, P., Narwani, A., Mace, G., Tilman, D., Wardle, D., Kinzig, A., Daily, G., Loreau, M., Grace, J., Larigauderie, A., Srivastava, D. and Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, pp.59-67.

Catchpole, E., Morgan, B., Coulson, T., Freeman, S. and Albon, S. (2000). Factors influencing Soay sheep survival. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 49, pp.453-472.

Central Intelligence Agency (2015). Uganda. In: The World Factbook. Retrieved from https://www.cia.gov/library/publications/the-world-factbook/geos/ug.html

Chambers, J. and Silver, W. (2004). Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.463-476.

Chapin III, F., Zavaleta, E., Eviner, V., Naylor, R., Vitousek, P., Reynolds, H., Hooper, D., Lavorel, S., Sala, O., Hobbie, S., Mack, M. and Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405, pp.234-242.

Chen, I., Hill, J., Ohlemuller, R., Roy, D. and Thomas, C. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, 333(6045), pp.1024-1026.

Christie, M. and Knowles, L. (2015). Habitat corridors facilitate genetic resilience irrespective of species dispersal abilities or population sizes. *Evolutionary Applications*, 8(5), pp.454-463.

Clark, D. (2004). Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.477-491.

Conservation Ecology Group, Durham University: https://www.conservationecology.org

Coomes, D. and Grubb, P. (2000). Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. *Ecological Monographs*, 70(2), p.171.

Corlett, R. (1992). The Ecological Transformation of Singapore, 1819-1990. *Journal of Biogeography*, 19(4), p.411.

Corlett, R. (2007). The Impact of Hunting on the Mammalian Fauna of Tropical Asian Forests. *Biotropica*, 39(3), pp.292-303.

Crick, H., Dudley, C., Glue, D. and Thomson, D. (1997). UK birds are laying eggs earlier. *Nature*, 388(6642), pp.526-526.

Davey, C., Chamberlain, D., Newson, S., Noble, D. and Johnston, A. (2012). Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, 21(5), pp.568-578.

DeFries, R., Rudel, T., Uriarte, M. and Hansen, M. (2010). Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, 3(3), pp.178-181.

Devictor, V., Julliard, R., Couvet, D. and Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, 275(1652), pp.2743-2748.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. and Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, 2(2), pp.121-124.

Diamond J. (1989) Overview of recent extinctions. In: *Conservation for the Twenty-First Century* (eds Western, D. and Pearl, M.C.), pp. 37–41. Oxford University Press, New York.

Dirnboeck, T., Essl, F. and Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17, pp.990-996.

Dirzo, R. and Raven, P. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, 28, pp.137-167.

Dobkin, D. and Rich, A. (1998). Comparison of line-transect spot-map, and point-count surveys for birds in Riparian habitats of the Great Basin. *Journal of Field Ornithology*, 69(3), pp.430-443.

Dobson, A.P., Ralls, K., Foster, M., Soule, M.E., Simberloff, D., Doak, D., Estes, J.A., Mills, L.S., Mattson, D., Dirzo, R., Arita, H., Ryan, S., Norse, E.A., Noss, R.F. and Johns, D. (1999). Corridors: reconnecting fragmented landscapes. In: Soule, M.E., Terborgh, J. (Eds), Continental conservation: Scientific foundations of regional reserve networks, Island Press, Washington DC, pp. 129-170.

Dobson, A., Rodriguez, J., Roberts, W. and Wilcove, D. (1997). Geographic Distribution of Endangered Species in the United States. *Science*, 275(5299), pp.550-553.

Elsen, P., Tingley, M., Kalyanaraman, R., Ramesh, K. and Wilcove, D. (2017). The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. *Ecology*, 98(2), pp.337-348.

FAO (2001). *Forest Resources Assessment 2000,* FAO Forestry Papers 140, Rome.

Fearnside, P. (2000). Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climate Change*, 46, pp.115-158.

Fisher, B. and Christopher, T. (2007). Poverty and biodiversity: Measuring the overlap of human poverty and the biodiversity hotspots. *Ecological Economics*, 62(1), pp.93-101.

Fitter, A. and Fitter, R. (2002). Rapid Changes in Flowering Time in British Plants. *Science*, 296(5573), pp.1689-1691.

Fletcher, R. (2007). Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology*, 76(3), pp.598-606.

Fuller Lab, University of Queensland: https://www.fullerlab.org

Gardner, T., Barlow, J., Parry, L. and Peres, C. (2007). Predicting the Uncertain Future of Tropical Forest Species in a Data Vacuum. *Biotropica*, 39(1), pp.25-30.

Gardner, T., Barlow, J., Sodhi, N. and Peres, C. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation*, 143(10), pp.2293-2300.

Gibson, L., Lee, T., Koh, L., Brook, B., Gardner, T., Barlow, J., Peres, C., Bradshaw, C., Laurance, W., Lovejoy, T. and Sodhi, N. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 505(7485), pp.710-710.

Gibson, M. R. (2018). Movement ecology of Australian arid-zone birds. Doctoral thesis, Durham University.

Gilbert-Norton, L., Wilson, R., Stevens, J. and Beard, K. (2010). A Meta-Analytic Review of Corridor Effectiveness. *Conservation Biology*, 24(3), pp.660-668.

Gilman, S., Urban, M., Tewksbury, J., Gilchrist, G. and Holt, R. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, 25(6), pp.325-331.

Godsoe, W., Murray, R. and Plank, M. (2015). The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, 38(11), pp.1071-1079.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. and Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), pp.111-115.

Grace, J., Malhi, Y., Lloyd, J., McIntyre, J., Miranda, A., Meir, P. and Miranda, H. (1996). The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology*, 2(3), pp.209-217.

Grant, P.R. (1968). Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Systematic Zoology*, 17, pp.319-333.

Gregory, R. and Baillie, S. (1998). Large-scale habitat use of some declining British birds. *Journal of Applied Ecology*, 35(5), pp.785-799.

Gregory, R.D., Gibbons, D.W. and Donald, P.F. (2004). Bird census and survey techniques. In: Sutherland, W.J., Newton, I. and Green, R. (Eds.), Bird Ecology and Conservation: A Handbook of Techniques, Oxford Scholarship, pp. 17-56.

Groombridge, B. and Jenkins, M. (2002). *World atlas of biodiversity*. Berkeley, Calif.: University of California Press.

Hambler, C. and Canney, S. (2013). *Conservation*. Cambridge: Cambridge University Press.

Hamel, P. B., Smith, W. P., Twedt, D. J., Woehr, J. R., Morris, E., Hamilton, R. B. and Cooper, R. J. (1996). A Land Manager's Guide to Point Counts of Birds in the Southeast. Gen. Tech. Rep. SO-120. New Orleans, LA: U.S. Dept of Agriculture, Forest Service, Southern Forest Experiment Station. 39 p.

Handbook of the Birds of the World Alive. Accessed at https://www.hbw.com

Hanski, I. (2005). Landscape fragmentation, biodiversity loss and the societal response. *EMBO reports*, 6(5), pp.388-392.

Hantson, S., Pueyo, S. and Chuvieco, E. (2015). Global fire size distribution is driven by human impact and climate. *Global Ecology and Biogeography*, 24(1), pp.77-86.

Hartter, J. and Southworth, J. (2009). Dwindling resources and fragmentation of landscapes around parks: wetlands and forest patches around Kibale National Park, Uganda. *Landscape Ecology*, 24(5), pp.643-656.

Hartter, J., Ryan, S., Southworth, J. and Chapman, C. (2011). Landscapes as continuous entities: forest disturbance and recovery in the Albertine Rift landscape. *Landscape Ecology*, 26(6), pp.877-890.

Harvell, C., Mitchell, C., Ward, J., Altizer, S., Dobson, A., Ostfeld, R. and Samuel, M. (2002). Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science*, 296(5576), pp.2158-2162.

Hawkins, B., Field, R., Cornell, H., Currie, D., Guégan, J., Kaufman, D., Kerr, J., Mittelbach, G., Oberdorff, T., O'Brien, E., Porter, E. and Porter, J. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, pp.3105–3117.

Heikkinen, R., Luoto, M., Virkkala, R., Pearson, R. and Körber, J. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, 16(6), pp.754-763.

Herremans, M., Louette, M. and Meirte, D. (2002). The importance of historical collections for in-situ conservation in Africa. *Abstracts 23° International Ornithological Congress, Beijing*

Hill, J., Thomas, C., Fox, R., Telfer, M., Willis, S., Asher, J. and Huntley, B. (2002). Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society B: Biological Sciences*, 269(1505), pp.2163-2171.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, 50(8), p.839.

Hughes, A., Byrnes, J., Kimbro, D. and Stachowicz, J. (2007). Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters*, 10(9), pp.849-864.

Huntley, B., Collingham, Y., Green, R., Hilton, G., Rahbek, C. and Willis, S. (2006). Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, 148, pp.8-28.

Huntley, B., Collingham, Y., Willis, S. and Green, R. (2008). Potential Impacts of Climatic Change on European Breeding Birds. *PLoS ONE*, 3(1), p.e1439.

Hurtt, G., Chini, L., Frolking, S., Betts, R., Feddema, J., Fischer, G., Fisk, J., Hibbard, K., Houghton, R., Janetos, A., Jones, C., Kindermann, G., Kinoshita, T., Klein Goldewijk, K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., van Vuuren, D. and Wang, Y. (2011). Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic Change*, 109(1-2), pp.117-161.

IPCC (2007). Climate Change 2007: Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland

IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (ed. R.K.P.a.L.A.M. Core Writing Team). IPCC, Geneva, Switzerland.

IUCN (2001). IUCN Red List categories and criteria. Version 3.1. IUCN Species Survival Commission. Cambridge.

IUCN (2004). Guidelines for Using the IUCN Red List Categories and Criteria. IUCN, Gland, Switzerland, and Cambridge, UK. (Available at http://www.redlist.org)

Jankowski, J., Merkord, C., Rios, W., Cabrera, K., Revilla, N. and Silman, M. (2013). The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, 40(5), pp.950-962.

Jankowski, J., Robinson, S. and Levey, D. (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, 91(7), pp.1877-1884.

Jenni, L. and Kery, M. (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, 270(1523), pp.1467-1471.

Kanowski, J. (2001). Effects of elevated CO2 on the foliar chemistry of seedlings of two rainforest trees from north-east Australia: Implications for folivorous marsupials. *Austral Ecology*, 26(2), pp.165-172.

Khaliq, I., Hof, C., Prinzinger, R., Bohning-Gaese, K. and Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B*, 281: 20141097

Koon, L.C. & Earl of Cranbrook (2002). *Swiftlets of Borneo — Builders of Edible Nests*. Natural History Publication (Borneo) SDN., B.H.D. Sabah , Malaysia.

Korner, C. (2004). Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.493-498.

Körner, C. (2002). Mountain biodiversity, its causes and functions: an overview. In: Körner, C. and Spehn, E.M. (Eds.), Mountain biodiversity: a global assessment. Parthenon Publishing, London, pp. 3-20.

Laube, I., Graham, C. and Böhning-Gaese, K. (2013). Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. *Global Ecology and Biogeography*, 22(2), pp.223-232.

Laurance, W. (1999). Reflections on the tropical deforestation crisis. *Biological Conservation*, 91(2-3), pp.109-117.

Laurance, W. (2007). Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution*, 22(2), pp.65-70.

Laurance, W., Oliveira, A., Laurance, S., Condit, R., Nascimento, H., Sanchez-Thorin, A., Lovejoy, T., Andrade, A., D'Angelo, S., Ribeiro, J. and Dick, C. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428(6979), pp. 171-175.

Laurance, W. and Peres, C. (2006). *Emerging threats to tropical forests*. Chicago: University of Chicago Press.

Lawler, I., Foley, W., Woodrow, I. and Cork, S. (1997). The effects of elevated CO 2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia*, 109(1), pp.59-68.

Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J., Reif, J., Van Turnhout, C. and Devictor, V. (2012). More and more generalists: two decades of changes in the European avifauna. *Biology Letters*, 8(5), pp.780-782.

Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarres, J.F., Proenca, V., Scharlemann, J.P.W., Walpole, M.J., (2010). Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services.
In: *Secretariat of the Convention on Biological Diversity* (ed. Diversity SotCoB).

Published by the Secretariat of the Convention on Biological Diversity, Montreal, p. 1–132. Technical Series no. 50.

Leakey, R. and Lewin, R. (1996). *The sixth extinction: patterns of life and the future of humankind*. New York: Doubleday.

Lemoine, N., Bauer, H., Peintinger, M. and Böhning-Gaese, K. (2007). Effects of Climate and Land-Use Change on Species Abundance in a Central European Bird Community. *Conservation Biology*, 21(2), pp.495-503.

Lewis, S. (2006). Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1465), pp.195-210.

Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T. A. and Laurance, W. F. (2009). Changing Ecology of Tropical Forests: Evidence and Drivers. *Annual Review of Ecology, Evolution and Systematics*, 40(1), pp.529-549.

Lewis, S., Malhi, Y. and Phillips, O. (2004b). Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.437-462.

Lewis, S., Phillips, O., Baker, T., Lloyd, J., Malhi, Y., Almeida, S., Hihuchi, N., Laurance, W., Neil, D., Silva, J., Terborgh, J., Torres Lezama, A., Vásquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P. and Vinceti, B. (2004a). Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philisophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp.421-436.

Li, R., Xu, M., Wong, M. H. G., Qiu, S., Sheng, Q., Li, X. and Song., Z. (2015). Climate change-induced decline in bamboo habitats and species diversity: implications for giant panda conservation. *Diversity and Distributions*, 21, pp.379-391.

Lindström, Å., Green, M., Paulson, G., Smith, H. and Devictor, V. (2012). Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography*, 36(3), pp.313-322.

Loarie, S., Duffy, P., Hamilton, H., Asner, G., Field, C. and Ackerly, D. (2009). The velocity of climate change. *Nature*, 462, pp.1052-1057.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., Huston, M., Raffaelli, D., Schmid, B., Tilman, D. and Wardle, D. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, pp.804–808.

MacArthur, R. (1958). Population Ecology of Some Warblers of Northeastern Coniferous Forests. *Ecology*, 39(4), pp.599-619.

MacArthur, R. H. and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton (NJ): Princeton University Press.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., AkÇakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J. and Stuart, S. N. (2008). Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species.

MacKinnon, S. and Phillipps, K. (1993). *A Field Guide to the Birds of Borneo, Sumatra, Java and Bali*, Oxford University Press, Oxford.

MacLean, I., Tinch, R., Hassall, M. and Boar, R. (2003). *Social and economic use of wetland resources: a case study from Lake Bunyonyi, Uganda*. Centre for Social and Economic Research on the Global Environment, Norwich.

Malcolm, J., Liu, C., Neilson, R., Hansen, L. and Hannah, L. (2006). Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots. *Conservation Biology*, 20(2), pp.538-548.

Malhi, Y., Aragao, L., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C. and Meir, P. (2009). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences*, 106(49), pp.20610-20615.

Martin, P. and Martin, T. (2001). Behavioral Interactions between Coexisting Species: Song Playback Experiments with Wood Warblers. *Ecology*, 82(1), p.207.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecol. Biogeogr.*, 18, pp.346-360.

McCain, C. M. and Colwell, R. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, 14(12), pp.1236-1245.

McEntee, J.P., Tobias, J.A., Sheard, C.S. and Burleigh, G. (2018). Tempo and timing of ecological trait divergence in bird speciation. *Nature Ecology and Evolution*, 2, pp.1120-1127.

McMahon, T., Murphy, R., Peel, M., Costelloe, J. and Chiew, F. (2008). Understanding the surface hydrology of the Lake Eyre Basin: Part 1—Rainfall. *Journal of Arid Environments*, 72(10), pp.1853-1868.

Menéndez, R., Megias, A., Hill, J., Braschler, B., Willis, S., Collingham, Y., Fox, R., Roy, D. and Thomas, C. (2006). Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences*, 273(1593), pp.1465-1470.

Menzel, A., Sparks, T., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A., Wielgolaski, F., Zach, S. and Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), pp.1969-1976.

Meuser, E., Harshaw, H. W. and Mooers, A. Ø. (2009). Public preference for endemism over other conservation-related species attributes. *Conservation Biology*, 23(4), pp.1041-1046.

Miles, D.B. and Ricklefs, R.E. (1984). The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, 65, pp.1629-1640.

Miller, D.L. (2016). Distance: Distance Sampling Detection Function and Abundance Estimate. R package version 0.9.6 https://CRAN.R-project.org/package=Distance

Møller, A. and Szép, T. (2005). Rapid evolutionary change in a secondary sexual character linked to climatic change. *Journal of Evolutionary Biology*, 18(2), pp.481-495.

Morton, S., Stafford Smith, D., Dickman, C., Dunkerley, D., Friedel, M., McAllister, R., Reid, J., Roshier, D., Smith, M., Walsh, F., Wardle, G., Watson, I. and Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, 75(4), pp.313-329.

Munroe, D., Southworth, J. and Tucker, C. (2004). Modeling spatially and temporally complex land-cover change: the case of Western Honduras. *The Professional Geographer*, 56, pp.544-559.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G. and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(333), pp.853-858.

Nagendra, H. (2008). Do Parks Work? Impact of Protected Areas on Land Cover Clearing. *AMBIO: A Journal of the Human Environment*, 37(5), pp.330-337.

Nagendra, H., Pareeth, S., Sharma, B., Schweik, C. and Adhikari, K. (2008). Forest fragmentation and regrowth in an institutional mosaic of community, government and private ownership in Nepal. *Landscape Ecology*, 23(1), pp.41-54.

National Vegetation Information System (NVIS) – Major Vegetation Groups version 4.2; Table S2.

Newbold, T., Hudson, L., Hill, S., Contu, S., Lysenko, I., Senior, R., Börger, L., Bennett, D., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M., Feldman, A., Garon, M., Harrison, M., Alhusseini, T., Ingram, D., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D., Martin, C., Meiri, S., Novosolov, M., Pan, Y., Phillips, H., Purves, D., Robinson, A., Simpson, J., Tuck, S., Weiher, E., White, H., Ewers, R., Mace, G., Scharlemann, J. and Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, pp.45-50.

Newson, S., Evans, K., Noble, D., Greenwood, J. and Gaston, K. (2008). Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*, 45(5), pp.1330-1338.

Nix, H. and Switzer, M. (1991). *Rainforest animals: atlas of vertebrates endemic to the wet tropics*. Canberra: Australian National Parks and Wildlife Service.

O'Grady, J., Reed, D., Brook, B. and Frankham, R. (2004). What are the best correlates of predicted extinction risk? *Biological Conservation*, 118(4), pp.513-520.

Olson, D. and Dinerstein, E. (1998). The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology*, 12(3), pp.502-515.

Olupot, W., Barigyira, R. and Chapman, C. (2009). The status of anthropogenic threat at the people-park interface of Bwindi Impenetrable National Park, Uganda. *Environmental Conservation*, 36(01), p.41.

Owiunji, I. and Plumptre, A. J., 2011. The importance of cloud forest sites in the conservation of endemic and threatened species of the Albertine Rift. In: Hamilton, L. S., Bruijnzeel, L. A. and Scatena, F. N. (Eds), Tropical Montane Cloud Forests: Science for Conservation and Management, first ed., Cambridge University Press, Cambridge, pp. 164-171.

Parmesan, C. (1996). Climate change and species' ranges. *Nature*, 382, pp.765-766.

Parmesan, C., Burrows, M., Duarte, C., Poloczanska, E., Richardson, A., Schoeman, D. and Singer, M. (2013). Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, 16, pp.58-71.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J., Thomas, C., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W., Thomas, J. and Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, pp.579-583.

Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), pp.37-42.

Patterson, B., Stotz, D., Solari, S., Fitzpatrick, J. and Pacheco, V. (1998). Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, 25(3), pp.593-607.

Paudel, P. K. and Sipoš, J. (2014). Conservation status affects elevational gradient in bird diversity in the Himalaya: A new perspective. *Global Ecology and Conservation*, 2, pp.338-348.

Pearce-Higgins, J. and Green, R. (2014). *Birds and Climate Change: Impacts and Conservation Responses*. Cambridge University Press.

Pearson, R. and Dawson, T. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12(5), pp.361-371.

Pérez-Arteaga, A., Jackson, S., Carrera, E. and Gaston, K. (2005). Priority sites for wildfowl conservation in Mexico. *Animal Conservation*, 8(1), pp.41-50.

Peterson, A., Martínez-Meyer, E., Soberón, J., Araújo, M., Nakamura, M., Pearson, R. and Anderson, R. (2011). *Ecological niches and geographic distributions. No. 49 in Monographs in Population Biology*. Princeton University Press.

Peterson, A., Ortega-Huerta, M., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R. and Stockwell, D. (2002). Future projections for Mexican faunas under global climate change scenarios. *Nature*, 416(6881), pp.626-629.

Peterson, G., Allen, C. and Holling, C. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, 1, pp.6-18.

Pettingill, O. (1970). *Ornithology in laborotary and field*. 1st ed. Minneapolis: Burgess Publishing Company.

Phillips, O., Arago, L., Lewis, S., Fisher, J., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A., Cardozo, N., Czimczik, C., Feldpausch, T., Freitas, M., Gloor, E., Higuchi, N., Jimènez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D., Nepstad, D., Patiño, S., Peñuela, M., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A., ter Steege, H., Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E., Andelman, S., Andrade, A., Chao, K., Erwin, T., Di Fiore, A., Honorio C., E., Keeling, H., Killeen, T., Laurance, W., Cruz, A., Pitman, N., Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J.

and Torres-Lezama, A. (2009). Drought sensitivity of the amazon rainforest. *Science*, 323(5919), pp.1344–1347.

Phillips, O. and Gentry, A. (1994). Increasing Turnover Through Time in Tropical Forests. *Science*, 263(5149), pp.954-958.

Phillips, O., Vásquez Martínez, R., Arroyo, L., Baker, T., Killeen, T., Lewis, S., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez Vargas, P., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. and Vinceti, B. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature*, 418(6899), pp.770-774.

Pigot, A.L., Trisos, C.H. and Tobias, J.A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 283(1822), 26740616.

Pigot, A.L. and Tobias, J.A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, 16(3), pp.330-338.

Pimm, S. and Raven, P. (2000). Extinction by numbers. *Nature*, 403, pp.843-845.

Plumptre, A. J., Ayebare, S., Segan, D., Watson, J. and Kujirakwinja, D. (2016). Conservation Action Plan for the Albertine Rift. Unpublished Report for the Wildlife Conservation Society and its Partners.

Plumptre, A., Behangana, M., Davenport, T., Kahindo, C., Kityo, R., Ndomba, E., Nkuutu, D., Owiunji, I., Ssegawa, P. and Eilu, G. (2003). The Biodiversity of the Albertine Rift. Albertine Rift Technical Reports Series Number 3. Wildlife Conservation Society.

Plumptre, A., Davenport, T., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J., Pilgrim, J., Wilson, M., Languy, M. and Moyer, D. (2007). The biodiversity of the Albertine Rift. *Biological Conservation*, 134(2), pp.178-194.

Plumptre, A., Kayitare, A., Rainer, H., Gray, M., Munanura, I., Barakabuye, N., Asuma, S., Sivha, M. and Namara, A. (2004). *The Socio-economic Status of People Living Near Protected Areas in the Central Albertine Rift*. Albertine Rift Technical Reports Series Number 4. Wildlife Conservation Society.

Poloczanska, E., Brown, C., Sydeman, W., Kiessling, W., Schoeman, D., Moore, P., Brander, K., Bruno, J., Buckley, L., Burrows, M., Duarte, C., Halpern, B., Holding, J., Kappel, C., O'Connor, M., Pandolfi, J., Parmesan, C., Schwing, F., Thompson, S. and Richardson, A. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), pp.919-925.

Polovina, J. (1996). Decadal variation in the trans-Pacific migration of northern bluefin tuna (*Thunnus thynnus*) coherent with climate-induced change in prey abundance. *Fisheries Oceanography*, 5(2), pp.114-119.

Ponce-Reyes, R., Reynoso-Rosales, V. H., Watson, J. E. M., VanDerWal, J., Fuller, R. A., Pressey, R. L. and Possingham, H. P. (2012). Vulnerability of cloud forest reserves in Mexico to climate change. *Nature Climate Change*, 2, pp.448-452.

Ponce-Reyes, R., Plumptre, A., Segan, D., Ayebare, S., Fuller, R., Possingham, H. and Watson, J. (2017). Forecasting ecosystem responses to climate change across Africa's Albertine Rift. *Biological Conservation*, 209, pp.464-472.

Poulsen, B. O., Krabbe, N., Frølander, A., Hinojosa, B. M. and Quiroga, O. C. (1997). A rapid assessment of Bolivian and Ecuadorian montane avifaunas using 20-species lists: efficiency, biases and data gathered. *Bird Conservation International*, 7, pp.53-67.

Pounds, J., Fogden, M. and Campbell, J. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398, pp.611-615.

Prentice, I.C., Bondeau A., Cramer W., Harrison, S.P., Hickler, T., Lucht, W., Sitch, S., Smith, B. and Skies, M.T. (2007). Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell, J.G., Pataki, D.E. and Pitelka, L.F. (Eds.), Terrestrial ecosystems in a changing world. Springer, Berlin, pp. 175–192.

Price, T. (1991). Morphology and Ecology of Breeding Warblers Along an Altitudinal Gradient in Kashmir, India. *The Journal of Animal Ecology*, 60(2), p.643.

Price, T., Mohan, D., Tietze, D., Hooper, D., Orme, C. and Rasmussen, P. (2011). Determinants of Northerly Range Limits along the Himalayan Bird Diversity Gradient. *The American Naturalist*, 178(S1), pp.S97-S108.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raman, T. (2003). Assessment of census techniques for interspecific comparisons of tropical rainforest bird densities: A field evaluation in the Western Ghats, India. *Ibis*, 145, pp.9-21.

Ramanathan, V., Crutzen, P., Kiehl, J. and Rosenfeld, D. (2001). Aerosols, Climate, and the Hydrological Cycle. *Science*, 294(5549), pp.2119-2124.

Reynolds, R., Scott, J. and Nussbaum, R. (1980). A Variable Circular-Plot Method for Estimating Bird Numbers. *The Condor*, 82(3), p.309.

Ricklefs, R. and Cox, G. (1977). Morphological Similarity and Ecological Overlap among Passerine Birds on St. Kitts, British West Indies. *Oikos*, 29(1), p.60.

Robbins, C. S. (1981). Effect of time of day on bird activity. In: Ralph, C. J. and Scott, J. M. (Eds), Estimating Numbers of Terrestrial Birds, *Studies in Avian Biology*, 6, pp.275-286.

Robinson, S. and Terborgh, J. (1995). Interspecific Aggression and Habitat Selection by Amazonian Birds. *The Journal of Animal Ecology*, 64(1), p.1.

Rödenbeck, C., Houweling, S., Gloor, M. and Heimann, M. (2003). CO_2 flux history 1982–2001 inferred from atmospheric data using a global inversion of atmospheric transport. *Atmospheric Chemisty and Physics*, 3, pp.1919-1964.

Roland Berger (2011). Trend Compendium 2030: Demographic Dynamics, Roland Berger Strategy Consultants.

Root, T. (1988a). Environmental factors associated with avian distributional boundaries. *Journal of Biogeography*, 15, pp. 489-505.

Root, T. (1988b). Energy Constraints on Avian Distributions and Abundances. *Ecology*, 69(2), pp.330-339.

Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C. and Pounds, J. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421(6918), pp.57-60.

Rosenstock, S., Anderson, D., Giesen, K. and Carter, M. (2002). Landbird Counting Techniques: Current Practices and an Alternative. *The Auk*, 119(1), pp.46-53.

Rubidge, E., Monahan, W., Parra, J., Cameron, S. and Brashares, J. (2011). The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. *Global Change Biology*, 17(2), pp.696-708.

Rudnick, D., Beier, P., Cushman, S., Dieffenbach, F., Epps, C.W., Gerber, L., Hartter, J., Jenness, J., Kintsch, J., Merenlender, A.M., Perkle, R.M., Preziosi, D.V., Ryan, S.J., and S. C. Trombulak (2012). Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. Issues in Ecology. Report No. 16. Ecological Society of America. Washington, DC.

Ryan, S., Palace, M., Hartter, J., Diem, J., Chapman, C. and Southworth, J. (2017). Population pressure and global markets drive a decade of forest cover change in Africa's Albertine Rift. *Applied Geography*, 81, pp.52-59.

Ryan, S., Southworth, J., Hartter, J., Dowhaniuk, N., Fuda, R. and Diem, J. (2015). Household level influences on fragmentation in an African park landscape. *Applied Geography*, 58, pp.18-31.

Sagarin, R., Barry, J., Gilman, S. and Baxter, C. (1999). Climate-Related Change in an Intertidal Community over Short and Long Time Scales. *Ecological Monographs*, 69(4), p.465.

Schoener, T. (1965). The Evolution of Bill Size Differences Among Sympatric Congeneric Species of Birds. *Evolution*, 19(2), p.189.

Schonewald-Cox, C. and Bayless, J. (1986). The boundary model: A geographical analysis of design and conservation of nature reserves. *Biological Conservation*, 38(4), pp.305-322.

Seimon, A., Picton-Phillipps, G. and Plumptre, A. J. (2011). A climatological assessment for the Albertine Rift. In: Plumptre, A. J. (Ed), The Ecological Impact of Long-term Changes in Africa's Rift Valley, Nova Science Publishers, New York.

Seimon, A. and Plumptre, A. J., (2012). Africa's Albertine Rift: planning for predicted climate change in a global biodiversity hotspot. In: Chester, C. C., Hilty, J. A. and Cross, M. S. (Eds.), Climate and Conservation: Landscape and Seascape Science, Planning and Action, Island Press, pp. 33-44

Shmida, A. and Wilson, M. (1985). Biological Determinants of Species Diversity. *Journal of Biogeography*, 12(1), p.1.

Shoo, L., Williams, S. and Hero, J. (2005). Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, 125(3), pp.335-343.

Smith, F., Browning, H. and Shepherd, U. (1998). The influence of climate change on the body mass of woodrats Neotoma in an arid region of New Mexico, USA. *Ecography*, 21(2), pp.140-148.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), pp.1115-1123.

Southworth, J., Nagendra, H. and Cassidy, L. (2012). Forest transition pathways in Asia–studies from Nepal, India, Thailand, and Cambodia. *Journal of Land Use Science*, 7(1), pp.51-65.

State of the Tropics leadership group et al. (2014). *State of the Tropics*. James Cook University.

Stattersfield, A., Crosby, M., Long, A. and Wege, D. (1998). *Endemic bird areas of the world: priorities for biodiversity conservation*. 1st ed. Cambridge: BirdLife International.

Stephens, P., Mason, L., Green, R., Gregory, R., Sauer, J., Alison, J., Aunins, A., Brotons, L., Butchart, S., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D., Paquet, J., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A., van Turnhout, C., Vorisek, P. and Willis, S. (2016). Consistent response of bird populations to climate change on two continents. *Science*, 352(6281), pp.84-87.

Still, C., Foster, N. and Schneider, S. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature*, 398, pp.608-610.

Templeton, A. R. (1987). Species and speciation. *Evolution*, 41, pp.233-235.

Terborgh, J. (1971). Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, 52, pp.23-40.

Terborgh, J. (1985). The role of ecotones in the distribution of Andean birds. *Ecology*, 66, pp.1237-1246

Terborgh, J. and Weske, J. (1975). The Role of Competition in the Distribution of Andean Birds. *Ecology*, 56(3), pp.562-576.

Tewksbury, J., Huey, R. and Deutsch, C. (2008). Putting the Heat on Tropical Animals. *Science*, 320(5881), pp.1296-1297.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. and Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, pp.5-14.

Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A., Midgley, G., Miles, L., Ortega-Huerta, M., Peterson, A., Philips, O. and Williams, S. (2004). Extinction risk from climate change. *Nature*, 427, pp.145-148.

Thuiller, W., Araújo, M. and Lavorel, S. (2004). Do we need land-cover data to model species distributions in Europe?. *Journal of Biogeography*, 31(3), pp.353-361.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W., Simberloff, D. and Swackhamer, D. (2001). Forecasting Agriculturally Driven Global Environmental Change. *Science*, 292(5515), pp.281-284.

Tilman, D., Reich, P. and Knops, J. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, pp.629-632.

Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. and Seddon, N. (2014). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, 506, pp.359-363.

Trisos, C.H., Petchey, O.L. and Tobias, J.A. (2014). Unravelling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *American Naturalist*, 184(5), pp.593-608.

Turner, I., Tan, H., Wee, Y., Ibrahim, A., Chew, P. and Corlett, R. (1994). A Study of Plant Species Extinction in Singapore: Lessons for the Conservation of Tropical Biodiversity. *Conservation Biology*, 8(3), pp.705-712.

Twiss, S., Thomas, C., Poland, V., Graves, J. and Pomeroy, P. (2007). The impact of climatic variation on the opportunity for sexual selection. *Biology Letters*, 3(1), pp.12-15.

Ulrich, W., Banks-Leite, C., De Coster, G., Habel, J.C., Matheve, H., Newmark, W.D., Tobias, J.A. and Lens, L. (2017). Environmentally and behaviourally mediated co-occurrence of functional traits in bird communities of tropical forest fragments. *Oikos*, 127(2), pp.274-284.

United Nations Development Programme (2007). Rwanda: Annual report 2007.

van Dam, N. (2009). How plants cope with biotic interactions. *Plant Biology*, 11(1), pp.1-5.

Van Houtan, K., Pimm, S., Halley, J., Bierregaard, R. and Lovejoy, T. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*, 10(3), pp.219-229.

Verner, J. and Ritter, L. (1985). A Comparison of Transects and Point Counts in Oak-Pine Woodlands of California. *The Condor*, 87(1), pp.47-68.

Visser, M., Noordwijk, A., Tinbergen, J. and Lessells, C. (1998). Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society B: Biological Sciences*, 265(1408), pp.1867-1870.

Vitousek, P., Mooney, H., Lubchenco, J. and Melillo, J. (1997). Human domination of earth's ecosystems. *Science*, 277, pp.494–499.

Wade, T., Riitters, K., Wickham, J. and Jones, K. (2003). Distribution and Causes of Global Forest Fragmentation. *Conservation Ecology*, 7(2).

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O. and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, pp.389-395.

Warren, M., Hill, J., Thomas, J., Asher, J., Fox, R., Huntley, B., Roy, D., Telfer, M., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S., Greatorex-Davies, J., Moss, D. and Thomas, C. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, pp.65-69.

Weishampel, J., Godin, J. and Henebry, G. (2001). Pantropical dynamics of 'intact' rain forest canopy texture. *Global Ecology and Biogeography*, 10(4), pp.389-397.

Wiens, J. (2011). The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), pp.2336-2350.

Wildlife Conservation Society: Welcome to the Albertine Rift Program. www.albertinerift.org

Williams, S. E., Pearson, R. G. and Walsh, P. J. (1995). Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. *Pacific Conservation Biology*, 2(4), p.327.

Williams, S., Bolitho, E. and Fox, S. (2003). Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society B: Biological Sciences*, 270(1527), pp.1887-1892.

Wilson, R., Twedt, D. and Elliott, A. (2000). Comparison of line transects and point counts for monitoring spring migration in forested wetlands. *Journal of Field Ornithology*, 71(2), pp.345-355.

Wisz, M., Pottier, J., Kissling, W., Pellissier, L., Lenoir, J., Damgaard, C., Dormann, C., Forchhammer, M., Grytnes, J., Guisan, A., Heikkinen, R., Høye, T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M., Normand, S., Öckinger, E., Schmidt, N., Termansen, M., Timmermann, A., Wardle, D., Aastrup, P. and Svenning, J. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, 88(1), pp.15-30.

Worm, B., Barbier, E., Beaumont, N., Duffy, J., Folke, C., Halpern, B., Jackson, J., Lotze, H., Micheli, F., Palumbi, S., Sala, E., Selkoe, K., Stachowicz, J. and Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, pp.787-790.

Wright, S. and Muller-Landau, H. (2006). The Future of Tropical Forest Species. *Biotropica*, 38(3), pp.287-301.

Wright, S., Muller-Landau, H. and Schipper, J. (2009). The Future of Tropical Species on a Warmer Planet. *Conservation Biology*, 23(6), pp.1418-1426.

Xie, P.F. (2012) Socio-economic Impacts of Birdwatching along Lake Eerie: A Coastal Ohio Analysis.

Yang, L. and Rudolf, V. (2010). Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, 13(1), pp.1-10.

Yinting, C., Xiaojing, G. and Zhijun, M. (2010). A comparison of line transect and point count surveys:a case study of spring saltmarsh birds at Chongming Dongtan. *Biodiversity Science*, 18(1), p.44.

Yom-Tov, Y., Yom-Tov, S., Wright, J., J. R. Thorne, C. and Du Feu, R. (2006). Recent changes in body weight and wing length among some British passerine birds. *Oikos*, 112(1), pp.91-101

Zuckerberg, B., Woods, A. M. and Porter, W. F. (2009). Poleward shifts in breeding bird distributions in New York State. *Global Change Biology*, 15(8), pp.1866-1883.

Appendices

Table A1: bird densities, by habitat, across the study area. ‘*’ denotes a species for which estimates failed goodness of fit tests in some, but not all, habitats. ‘-‘ denotes that a density, and therefore population, could not be calculated due to insufficient observations, or failure of model fitting, or goodness of fit tests in all habitats.

Species	**Density (km^{-2})**						
	Woodland-Grassland	**Tropical Forest (≤ 1400m)**	**Tropical Forest (> 1400m)**	**Shrubland**	**Bamboo**	**High Elevation-Alpine**	**Miombo Woodland**
Abyssinian Ground Hornbill	0.272±0.049	0	0	-	0	0	0
Afep Pigeon*	-	0.463±0.164	0.822±0.391	0	0	0	0
African Black-headed Oriole	0.016±0.015	0	0	-	0	0	0
African Broadbill	-	-	4.025±3.298	0	0	0	-
African Emerald Cuckoo	-	8.919±1.437	2.46±0.576	-	-	0	-
African Fish Eagle	-	-	0	0.121±0.311	0	0	0
African Golden Oriole	1.168±0.797	-	0	-	0	0	-
African Green Pigeon*	-	4.07±1.552	34.014±51.63	-	-	0	-
African Harrier Hawk	0.052±0.029	-	0	0.054±0.034	0	0	0
African Hill Babbler	-	-	51.003±8.739	-	41.574±25.733	0	0
African Mourning Dove*	0.653±0.223	-	0	0.492±0.213	0	0	0
African Moustached Warbler	0.653±0.125	-	0	0.343±0.079	0	0	-
African Paradise Flycatcher	21.674±21.069	36.059±7.77	101.882±29.98	-	-	0	-
African Pygmy Kingfisher	4.313±1.847	-	0	-	0	0	0
African Shrike Flycatcher	-	15.485±3.549	7.409±2.47	-	0	0	0
African Thrush	3.913±3.142	-	-	-	-	0	-

African Wattled Lapwing Plover*	1.435±0.325	-	0	0.253±0.074	0	0	0
African White-backed Vulture	0.447±0.365	0	0	-	0	0	0
Archer's Ground Robin	-	-	29.746±3.533	-	42.843±10.215	142.289±52.807	0
Banded Prinia	-	-	35.018±4.545	-	-	-	0
Bar-tailed Trogon	0	-	2.036±0.614	0	-	0	0
Barred Long-tailed Cuckoo	-	-	2.648±0.545	-	-	0	0
Bateleur*	0.158±0.047	-	0	0.095±0.049	-	0	-
Beautiful Sunbird	0.879±0.441	0	0	41.281±157.301	0	0	0
Black and White Cuckoo	0.048±0.019	0	0	-	0	0	0
Black Cuckoo	-	0.282±0.148	0.387±0.164	-	0	0	0
Black-bellied Bustard	0.11±0.026	0	0	-	0	0	0
Black-billed Turaco*	1.195±0.921	8.508±2.821	15.277±3.251	-	2.302±1.155	-	0
Black-billed Wood Dove*	0.995±0.169	-	0	0.564±0.169	0	0	0
Black-casqued Wattled Hornbill	0	2.888±1.24	-	0	0	0	0
Black-crowned Tchagra*	1.635±0.601	-	-	1.209±0.401	-	0	14.085±4.482
Black-faced Rufous Warbler*	-	51.699±17.884	80.263±11.377	-	-	0	0
Black-headed Batis	3.79±1.144	0	0	-	-	0	0
Black-headed Heron	0.063±0.026	0	-	-	-	0	0
Black-headed or Village Weaver	15.896±6.862	-	0	2.492±1.622	0	0	0
Black-lored Babbler	4.604±1.778	-	0	-	0	0	0
Black-throated Apalis	-	4.668±0.965	21.149±2.034	0	-	0	0
Black-winged Kite*	0.205±0.031	0	-	0.144±0.046	0	0	0
Blue-breasted Kingfisher	-	22.516±3.221	4.663±3.932	-	-	0	-
Blue-headed Coucal	-	0.256±0.128	0.075±0.057	-	-	0	0

Blue-headed Sunbird	-	-	127.438±18.825	0	-	0	0
Blue-naped Mousebird*	6.084±1.171	-	0	14.319±7.674	0	0	0
Blue-spotted Wood Dove*	0.193±0.069	3.873±2.336	-	0.757±0.438	0	0	-
Blue-throated Roller	0	5.835±3.01	-	0	0	0	0
Bocage's Bush-shrike	-	-	0.59±0.19	-	0	0	0
Broad-tailed Warbler	3.283±0.759	0	-	-	0	0	-
Bronze Mannikin	26.328±12.179	-	-	-	0	0	0
Brown Illadopsis*	-	35.11±7.768	11.942±7.506	0	0	0	-
Brown Snake Eagle	0.033±0.022	-	0	0	0	0	-
Brown-chested Alethe	-	6.781±3.189	-	0	0	0	0
Brown-crowned Tchagra	1.118±1.044	-	-	-	-	0	-
Brown-throated or Common Wattle-eye*	1.658±0.869	-	0	14.391±11.385	-	0	0
Brubru*	0.96±0.166	0	0	0.369±0.094	0	0	0
Buff-bellied Warbler	1.709±1.003	0	0	-	0	0	0
Buff-spotted Woodpecker	-	3.27±1.767	-	0	0	0	0
Cardinal Woodpecker	6.873±5.196	-	-	-	-	0	-
Cattle Egret	5.163±1.619	0	0	2.597±0.582	0	0	0
Chestnut Wattle-eye*	-	44.207±7.379	12.868±7.63	-	0	0	0
Chestnut-crowned Sparrow Weaver	4.942±1.002	0	0	1.788±0.238	0	0	0
Chestnut-throated Apalis*	-	0	54.034±5.767	-	36.05±9.034	-	0
Chin-spot Batis	-	-	3.666±1.852	-	-	0	-
Chocolate-backed Kingfisher	-	5.15±1.043	-	0	0	0	0
Chubb's Cisticola	-	-	29.672±3.112	-	16.133±3.53	-	0
Cinnamon Bracken Warbler*	10.191±5.065	0	38.593±3.393	-	181.355±35.24	283.204±70.617	0

Collared Apalis	-	-	95.709±8.677	-	92.249±28.857	-	0
Collared Sunbird	11.487±5.776	64.259±35.568	47.08±16.854	-	-	0	-
Common Bulbul*	117.214±21.971	121.943±34.294	129.432±29.478	171.485±110.793	95.898±26.393	-	288.454±59.377
Common Fiscal	0.727±0.329	0	0	0	0	0	0
Common Waxbill	9.963±5.027	-	-	-	0	0	0
Copper Sunbird	22.577±18.291	-	0	-	-	0	0
Crested Francolin*	0.426±0.192	0	0	0.703±0.345	0	0	0
Croaking Cisticola*	8.417±0.587	0	0	2.794±0.448	0	0	-
Crowned Hornbill	-	4.874±1.96	-	-	-	0	-
Dark Chanting Goshawk	0.041±0.012	0	0	-	0	0	-
Dark-backed Weaver	-	29.099±13.915	51.148±24.161	0	-	0	-
Doherty's Bush Shrike	-	0	5.254±1.327	-	1.761±0.937	-	0
Double-toothed Barbet	1.39±1.072	-	0	-	0	0	0
Dusky Long-tailed Cuckoo	-	6.922±1.44	3.56±0.997	0	0	0	0
Dusky Tit	-	13.526±4.789	65.549±19.291	-	0	0	0
Eastern Grey Plantain Eater	0.112±0.086	-	0	-	0	0	0
Emerald-spotted Wood Dove	-	-	-	0	-	0	6.468±2.697
Fire-crested Alethe	0	9.301±1.956	-	0	0	0	0
Flappet Lark*	4.625±0.528	-	0	3.693±0.609	0	0	-
Fork-tailed Drongo	3.248±1.126	-	-	-	-	0	-
Foxy Cisticola	1.464±0.521	0	0	-	0	0	0
Grasshopper Buzzard	0.021±0.01	0	0	-	0	0	0
Grauer's Rush Warbler	-	0	1.299±0.337	-	-	0	0
Grauer's Warbler	0	-	3.887±1.346	0	0	0	0

Great Blue Turaco*	-	4.585±1.754	6.491±2.17	-	-	0	0
Green Crombec*	1.786±1.403	40.834±4.559	19.536±6.103	-	-	0	0
Green Hylia*	-	84.098±8.203	17.75±2.978	-	0	0	0
Green Wood Hoopoe	0.512±0.269	-	-	-	0	0	-
Grey Apalis*	-	24.46±4.744	31±4.451	0	-	0	0
Grey Kestrel	0.211±0.031	0	0	0.178±0.055	0	0	0
Grey Parrot	-	8.47±2.829	-	-	0	0	0
Grey-backed Fiscal	3.706±0.545	0	0	0.813±0.226	0	0	0
Grey-backed or Green-backed Camaroptera*	164.154±45.523	109.664±19.326	66.584±21.155	93.376±20.788	-	0	-
Grey-capped Warbler	0.908±0.294	-	-	7.174±4.411	0	0	0
Grey-chested Illadopsis	-	-	24.604±4.764	0	-	0	0
Grey-headed Kingfisher*	2.14±0.395	0	0	0.856±0.328	0	0	-
Grey-headed Negrofinch	-	12.207±3.952	4.952±1.439	-	-	0	0
Grey-headed Sunbird	-	25.395±4.239	-	0	0	0	0
Grey-throated Barbet	-	20.063±10.864	72.947±39.066	-	-	0	0
Hadada Ibis*	0.64±0.511	-	-	0.09±0.061	-	0	0
Hairy-breasted Barbet	-	1.055±0.22	0.24±0.09	-	0	0	0
Helmeted Guineafowl*	1.251±0.307	-	0	0.535±0.159	0	0	-
Heuglin's Francolin	0.1±0.024	0	0	0.063±0.037	0	0	0
Honeyguide Greenbul	-	11.001±1.762	6.193±2.006	-	0	0	0
Icterine Greenbul	0	10.652±2.28	0	0	0	0	0
Kabobo Apalis	-	0	15.297±3.342	-	-	-	0
Klaas's Cuckoo*	0.296±0.137	5.629±5.667	-	-	-	0	-
Laughing Dove*	1.777±0.74	-	0	0.472±0.211	0	0	0

Lead-coloured Flycatcher	0.806±0.457	-	-	-	0	0	-
Least Honeyguide	0	1.903±0.468	-	0	0	0	0
Lesser Striped Swallow	3.673±1.845	-	-	-	-	0	-
Little Greenbul*	30.83±20.281	274.901±24.951	106.458±20.466	188.304±352.52	-	0	-
Little Weaver	5.851±0.92	-	0	1.761±0.881	0	0	0
Lizard Buzzard	-	8.186±5.027	0	-	0	0	-
Long-crested Eagle	0.214±0.121	-	-	-	0	0	0
Luhder's Bush Shrike	-	25.036±43.818	41.899±10.151	-	0	0	-
Marabou Stork*	0.345±0.251	-	0	0.199±0.143	0	0	0
Marico Sunbird	5.275±2.001	-	0	-	0	0	0
Martial Eagle	0.057±0.053	0	0	-	-	0	0
Masked Apalis*	-	16.442±3.814	8.304±2.426	-	0	0	0
Montane Masked Apalis	-	-	133.717±10.558	-	143.372±47.596	-	0
Montane Oriole*	-	1.989±0.638	9.476±1.932	0	-	0	0
Montane Sooty Boubou	-	-	24.816±3.194	-	7.993±2.177	-	0
Mountain Buzzard	-	0	0.639±0.221	-	-	-	0
Mountain Yellow Warbler*	-	0	16.66±2.434	-	30.785±10.58	-	0
Nahan's Francolin	0	1.411±0.719	0	0	0	0	0
Narina's Trogon*	-	11.274±2.095	5.701±1.282	-	-	0	0
Northern Black Flycatcher	1.121±0.51	-	0	-	0	0	0
Northern Carmine Bee-eater	0.063±0.018	0	0	-	0	0	0
Northern Crombec	49.533±123.942	0	0	-	0	0	0
Northern Puffback	2.59±1.041	-	14.133±4.311	-	37.999±23.019	0	0
Nubian Woodpecker*	0.388±0.112	0	0	0.291±0.235	0	0	-

Olive Long-tailed Cuckoo	-	-	0.972±0.316	-	-	0	0
Olive Pigeon	-	-	23.197±11.479	-	-	-	-
Olive Sunbird	-	481.505±52.534	267.3±54.668	-	-	0	-
Olive Thrush	0	0	2.766±1.292	-	-	-	0
Olive-bellied Sunbird	41.902±44.261	31.262±17.227	47.118±40.813	-	0	0	0
Olive-breasted Mountain Greenbul	-	0	113.507±13.172	-	167.735±68.624	0	0
Olive-green Camaroptera	-	14.611±2.34	9.845±2.453	0	0	0	0
Piapiac	12.481±1.182	-	0	1.812±0.294	0	0	0
Purple-breasted Sunbird	-	-	142.789±26.906	-	-	0	0
Rattling Cisticola	22.582±2.89	0	0	12.45±1.477	0	0	0
Red-billed Quelea	45.312±18.186	0	0	-	0	0	0
Red-capped Robin Chat	-	135.284±135.355	-	0	-	0	-
Red-cheeked Cordon-bleu	89.916±49.091	0	0	18.05±2.507	0	0	0
Red-chested Cuckoo*	0.563±0.173	4.684±1.178	0.937±0.182	0.493±0.287	0.134±0.129	-	-
Red-chested Sunbird	-	-	0	3.024±2.442	0	0	0
Red-eyed Dove*	1.271±0.648	0.393±0.141	0.355±0.12	4.527±2.192	-	0	-
Red-faced Cisticola	18.635±6.642	-	-	7.063±9.236	-	0	-
Red-faced Woodland Warbler	-	-	213.959±23.919	-	227.58±59.561	-	0
Red-headed Malimbe	0	-	15.589±4.29	0	0	0	0
Red-necked Falcon	0.091±0.021	0	0	-	0	0	0
Red-necked Spurfowl	1.081±0.545	-	0	-	0	0	0
Red-shouldered Cuckoo Shrike	0.358±0.387	-	0	-	0	0	0
Red-sided Broadbill	0	5.169±1.855	0	0	0	0	0
Red-tailed Ant Thrush	0	3.454±1.387	-	0	0	0	0

Red-tailed Bristle-bill*	-	33.718±5.078	9.009±2.835	-	0	0	0
Red-tailed Greenbul*	0	64.211±10.901	21.657±12.513	-	0	0	0
Red-throated Alethe	0	11.277±3.418	31.983±9.434	-	-	0	0
Red-throated Bee-eater	1.118±0.182	-	0	-	0	0	0
Regal Sunbird	-	-	308.721±35.146	-	386.59±110.381	-	-
Ring-necked Dove*	3.305±1.782	-	0	1.262±0.451	0	0	8.113±3.51
Ruppell's Long-tailed Starling*	4.18±1.057	-	0	3.425±1.58	0	0	0
Ruppell's Vulture	0.063±0.024	0	0	-	0	0	0
Ruwenzori Double-collared Sunbird	-	0	76.002±19.542	-	-	-	0
Rwenzori Batis	-	-	33.476±5.716	-	45.484±22.259	0	0
Rwenzori Turaco*	-	-	14.378±2.922	-	9.444±4.625	-	0
Sacred Ibis	0.121±0.051	0	0	-	0	0	0
Scaly-breasted Illadopsis	-	39.842±4.835	8.561±1.598	0	0	0	0
Scarlet-chested Sunbird	4.328±2.123	-	-	-	-	0	-
Schalow's Tauraco	-	-	-	0	-	0	5.436±2.904
Senegal Plover	0.875±0.229	0	0	-	0	0	0
Sharpe's Starling	0	0	4.527±1.412	-	-	0	0
Shelley's Rufous Sparrow	5.78±0.744	0	0	1.87±0.47	0	0	0
Siffling Cisticola	3.143±0.867	-	-	-	0	0	0
Silverbird*	3.823±0.539	0	0	2.237±0.251	0	0	0
Slender-billed Greenbul	-	28.269±4.649	28.317±6.82	-	-	0	-
Sooty Chat	5.723±1.067	0	0	0.427±0.101	0	0	-
Speckle-fronted Weaver	8.83±0.91	0	0	5.12±0.946	0	0	0
Speckled Mousebird	59.159±18.16	-	-	36.151±11.317	0	0	0

Speckled Tinkerbird*	9.799±10.26	25.513±3.872	9.226±2.649	-	0	0	0
Splendid Glossy Starling*	-	53.189±31.353	15.908±7.029	-	0	0	0
Spot-flanked Barbet	7.121±3.973	-	0	1.509±0.818	0	0	0
Spotted Greenbul	-	24.783±6.692	-	-	0	0	0
Spotted Palm-Thrush	13.33±8.506	0	0	3.704±0.704	0	0	0
Strange Weaver	-	0	14.45±3.797	0	-	0	0
Stripe-breasted Tit	-	0	28.393±11.613	-	-	-	0
Striped Kingfisher*	1.621±0.525	-	-	0.244±0.107	-	0	-
Stuhlmann's Starling	-	-	31.666±13.956	-	0	0	0
Sulphur-breasted Bush Shrike	0.964±0.205	-	0	1.13±0.707	-	0	-
Swallow-tailed Bee-eater	0.665±0.271	0	0	-	0	0	0
Tambourine Dove*	0.265±0.148	10.056±1.61	5.148±1.441	1.636±1.44	2.612±1.984	0	-
Tawny Eagle	0.017±0.008	0	0	-	0	0	0
Tawny-flanked Prinia*	60.001±13.668	-	-	14.501±2.934	-	0	-
Toro Olive Greenbul	-	2.459±0.466	-	0	0	0	0
Trilling Cisticola	5.513±0.858	-	-	2.763±2.233	-	0	-
Tropical Boubou	1.689±0.943	-	-	-	-	-	13.418±4.607
Vinaceous Dove*	0.07±0.028	0	0	0.214±0.106	0	0	0
Violet-backed Starling	18.663±14.115	-	0	-	-	0	-
Wahlberg's Eagle	0.018±0.009	0	-	-	-	0	-
Waller's Chestnut-winged Starling	0	-	20.622±4.486	-	-	0	0
Western Black-headed Oriole*	1.002±0.832	13.163±2.334	3.58±0.954	-	-	0	21.418±5.271
Western Bronze-naped Pigeon*	-	0.376±0.188	0.093±0.061	0	0	0	0
Western Green Tinkerbird	-	0	6.967±2.191	-	-	-	0

Western Nicator*	4.939±5.876	71.523±12.237	14.79±4.396	-	-	0	-
Whistling Cisticola	0.396±0.123	0.149±0.092	0	-	0	0	0
White-breasted Negrofinch*	-	16.14±3.269	3.865±1.483	-	0	0	0
White-browed Coucal*	0.652±0.193	0.272±0.164	-	0.489±0.219	-	0	-
White-browed Crombec	-	-	13.632±2.973	0	-	0	0
White-browed Scrub Robin*	5.698±3.251	-	-	8.357±4.925	-	0	-
White-chinned Prinia	-	-	57.439±46.684	-	0	0	0
White-crested Turaco	0.119±0.072	-	0	-	0	0	0
White-headed Saw-wing	4.053±2.195	-	0	-	0	0	0
White-headed Vulture	0.008±0.007	0	0	-	0	0	0
White-spotted Flufftail or White-spotted Pygmy Crake	-	2.938±0.435	0.436±0.147	-	-	0	-
White-starred Forest Robin*	-	-	83.829±30.47	-	83.915±29.39	-	0
White-tailed Ant Thrush	0	16.651±12.202	-	0	-	-	0
Winding Cisticola	3.433±2.689	-	0	-	0	0	0
Yellow Longbill	-	4.331±0.546	0	0	0	0	0
Yellow White-eye	48.333±26.893	11.469±3.519	348.324±36.045	-	347.999±105.458	-	-
Yellow-backed Weaver	9.906±5.149	-	0	5.04±3.147	0	0	0
Yellow-billed Barbet*	-	4.997±1.08	2.091±0.674	-	-	0	0
Yellow-billed Oxpecker	0.757±0.101	-	0	0.608±0.138	0	0	0
Yellow-crested Woodpecker	0	7.237±2.398	-	-	0	0	0
Yellow-fronted Canary	0.306±0.175	0	0	-	-	0	0
Yellow-fronted Tinkerbird*	1.481±0.565	-	-	0.596±0.236	0	0	-
Yellow-mantled Widowbird	0.753±0.2	0	-	-	0	0	0
Yellow-rumped Tinkerbird*	4.63±2.246	49.38±7.181	82.183±7.947	53.963±30.356	18.942±4.094	-	-

Yellow-spotted Barbet*	-	5.104±1.144	7.175±2.236	-	0	0	0
Yellow-streaked Greenbul	-	-	84.027±16.672	-	-	0	0
Yellow-throated Longclaw	3.502±0.652	-	0	2.747±1.552	0	0	0
Yellow-throated Nicator	0	3.846±1.39	0	0	0	0	0
Yellow-throated Tinkerbird*	1.381±0.545	44.739±4.033	3.288±1	-	0	0	0
Yellow-whiskered Greenbul*	71.755±30.577	144.136±13.806	282.179±21.917	215.889±178.56	156.12±34.059	-	10.502±3.863
Yellowbill	-	25.207±6.397	-	-	-	0	0

Table A2: Regional populations of bird species across the study area. '*' denotes a species for which estimates failed goodness of fit tests in some, but not all, habitats. '-' denotes that a density, and therefore population, could not be calculated due to insufficient observations, or failure of model fitting, or goodness of fit tests in all habitats.

Species	**Population**						
	Congo-Nile Divide	**Greater Mahale Ecosystem**	**Greater Virunga**	**Kabobo-Marungu**	**Maiko-Itombwe**	**Murchison-Semliki**	**TOTAL**
Abyssinian Ground Hornbill	0	0	0	0	0	7,019	7,019
Afep Pigeon*	0	0	9,537	0	41,008	2,602	53,147
African Black-headed Oriole	0	0	0	0	0	409	409
African Broadbill	672	0	10,835	0	14,986	-	26,493
African Emerald Cuckoo	17	531	73,582	22,160	513,761	8,847	618,898
African Fish Eagle	0	0	618	0	0	10	628
African Golden Oriole	0	0	0	21,699	0	0	21,699
African Green Pigeon*	1,278	6,203	125,361	2,833	77,326	15,071	228,072
African Harrier Hawk	0	0	615	0	0	928	1,543
African Hill Babbler	12,841	3,992	114,115	2,943	57,288	0	191,179
African Mourning Dove*	0	0	10,253	0	0	8,943	19,196
African Moustached Warbler	0	0	6,136	0	0	12,250	18,386
African Paradise Flycatcher	4,602	71,074	375,024	47,393	1,161,907	50,753	1,710,753
African Pygmy Kingfisher	0	0	0	0	0	111,463	111,463
African Shrike Flycatcher	0	0	227,686	0	694,599	98,863	1,021,148
African Thrush	0	2,901	31,788	0	0	7,927	42,616
African Wattled Lapwing Plover*	0	0	5,097	0	0	33,161	38,258

African White-backed Vulture	0	0	9,227	0	0	3,196	12,423
Archer's Ground Robin	7,824	0	343,649	1,734	34,576	0	387,783
Banded Prinia	9,030	0	94,667	0	91,564	-	195,261
Bar-tailed Trogon	290	0	1,091	274	4,743	0	6,398
Barred Long-tailed Cuckoo	496	0	855	472	1,463	0	3,286
Bateleur*	0	0	615	0	0	3,778	4,393
Beautiful Sunbird	0	0	0	0	0	136,159	136,159
Black and White Cuckoo	0	0	0	0	0	1,233	1,233
Black Cuckoo	49	0	3,608	9	81,246	231	85,143
Black-bellied Bustard	0	0	0	0	0	2,838	2,838
Black-billed Turaco*	1,066	0	100,267	26,367	1,510,017	19,327	1,657,044
Black-billed Wood Dove*	0	0	0	0	0	27,263	27,263
Black-casqued Wattled Hornbill	0	0	20,828	4,400	603,868	0	629,096
Black-crowned Tchagra*	0	145,129	12,152	1,808	0	20,696	179,785
Black-faced Rufous Warbler*	4,546	0	1,068,826	560	9,210,704	91,667	10,376,303
Black-headed Batis	0	0	40,143	0	0	61,569	101,712
Black-headed Heron	0	0	0	0	0	1,635	1,635
Black-headed or Village Weaver	0	0	411,293	0	0	46,366	457,659
Black-lored Babbler	0	0	128,018	0	0	3,003	131,021
Black-throated Apalis	6,324	0	81,875	308	589,431	28,983	706,921
Black-winged Kite*	0	0	0	0	0	5,691	5,691
Blue-breasted Kingfisher	0	3,068	286,795	0	3,154,043	49,007	3,492,913
Blue-headed Coucal	15	0	8,144	0	0	0	8,159
Blue-headed Sunbird	19,669	0	135,599	10,249	427,818	0	593,335

Blue-naped Mousebird*	0	0	199,136	0	0	37,905	237,041
Blue-spotted Wood Dove*	0	0	26,045	13,595	0	7,286	46,926
Blue-throated Roller	0	0	92,977	0	0	34,131	127,108
Bocage's Bush-shrike	0	0	3,427	21	0	-	3,448
Broad-tailed Warbler	0	0	82,446	3,787	0	4,873	91,106
Bronze Mannikin	0	0	632,684	0	0	107,181	739,865
Brown Illadopsis*	0	12,037	196,981	45,625	825,197	114,021	1,193,861
Brown Snake Eagle	0	0	615	0	0	294	909
Brown-chested Alethe	0	0	20,583	19,568	238,703	18,504	297,358
Brown-crowned Tchagra	0	963	7,384	0	0	833	9,180
Brown-throated or Common Wattle-eye*	0	0	82,341	0	0	30,514	112,855
Brubru*	0	0	0	0	0	25,829	25,829
Buff-bellied Warbler	0	0	35,852	0	0	11,673	47,525
Buff-spotted Woodpecker	-	0	39,304	0	268,126	17,321	324,751
Cardinal Woodpecker	0	0	192,516	0	0	3,186	195,702
Cattle Egret	0	0	0	0	0	140,557	140,557
Chestnut Wattle-eye*	0	0	470,373	0	4,672,766	246,747	5,389,886
Chestnut-crowned Sparrow Weaver	0	0	0	0	0	132,636	132,636
Chestnut-throated Apalis*	13,283	0	200,114	0	204,129	0	417,526
Chin-spot Batis	956	0	8,579	0	11,373	-	20,908
Chocolate-backed Kingfisher	0	0	11,334	7,483	748,515	19,990	787,322
Chubb's Cisticola	10,531	0	152,497	0	4,517	0	167,545
Cinnamon Bracken Warbler*	17,888	0	787,191	102,732	0	0	907,811

Collared Apalis	19,341	0	335,787	9,135	217,816	0	582,079
Collared Sunbird	7,144	65,115	158,709	177,786	1,237,629	116,712	1,763,095
Common Bulbul*	18,480	3,090,034	1,423,782	825,574	828,817	341,309	6,527,996
Common Fiscal	0	0	17,131	0	0	3,255	20,386
Common Waxbill	0	0	248,204	0	0	32,600	280,804
Copper Sunbird	0	16,465	216,506	0	0	21,748	254,719
Crested Francolin*	0	0	0	0	0	12,941	12,941
Croaking Cisticola*	0	0	108,612	0	0	128,254	236,866
Crowned Hornbill	-	872	54,531	0	574,909	13,463	643,775
Dark Chanting Goshawk	0	0	0	0	0	1,048	1,048
Dark-backed Weaver	170	20,629	74,307	83,446	1,591,359	1,079	1,770,990
Doherty's Bush Shrike	3,105	0	12,768	0	0	0	15,873
Double-toothed Barbet	0	0	29,878	0	0	8,848	38,726
Dusky Long-tailed Cuckoo	0	0	118,342	0	509,750	31,277	659,369
Dusky Tit	1,769	0	611,632	1,177	49,327	64,125	728,030
Eastern Grey Plantain Eater	0	0	1,845	0	0	1,215	3,060
Emerald-spotted Wood Dove	0	66,392	0	0	0	0	66,392
Fire-crested Alethe	0	0	62,650	0	1,614,584	46,936	1,724,170
Flappet Lark*	0	0	51,378	0	0	85,785	137,163
Fork-tailed Drongo	0	0	58,365	21,446	0	1,213	81,024
Foxy Cisticola	0	0	0	0	0	37,834	37,834
Grasshopper Buzzard	0	0	0	0	0	553	553
Grauer's Rush Warbler	1,030	0	76	0	0	0	1,106
Grauer's Warbler	536	0	6,986	277	10,965	0	18,764

Great Blue Turaco*	1,807	0	70,260	801	125,466	27,010	225,344
Green Crombec*	0	0	541,165	0	7,091,403	141,677	7,774,245
Green Hylia*	0	0	733,032	52,931	6,520,725	459,491	7,766,179
Green Wood Hoopoe	0	0	12,303	0	0	2,097	14,400
Grey Apalis*	2,339	0	142,222	59,200	4,618,715	0	4,822,476
Grey Kestrel	0	0	620	0	0	5,370	5,990
Grey Parrot	-	0	200,463	0	53,077	21,601	275,141
Grey-backed Fiscal	0	0	61,415	0	0	42,853	104,268
Grey-backed or Green-backed Camaroptera*	1,748	111,444	3,149,813	233,583	1,325,996	1,526,417	6,349,001
Grey-capped Warbler	0	0	55,161	0	0	5,680	60,841
Grey-chested Illadopsis	2,309	0	24,794	3,129	61,538	0	91,770
Grey-headed Kingfisher*	0	0	9,341	0	0	49,201	58,542
Grey-headed Negrofinch	920	544	83,614	24,784	239,210	48,676	397,748
Grey-headed Sunbird	0	0	161,404	0	0	247,172	408,576
Grey-throated Barbet	1,022	4,963	410,263	12,343	4,260,943	35,196	4,724,730
Hadada Ibis*	139	0	1,845	0	0	2,652	4,636
Hairy-breasted Barbet	0	0	12,416	0	25,158	7,894	45,468
Helmeted Guineafowl*	0	0	2,042	0	0	31,954	33,996
Heuglin's Francolin	0	0	0	0	0	2,751	2,751
Honeyguide Greenbul	0	0	206,629	0	105,269	64,529	376,427
Icterine Greenbul	0	0	56,088	0	127,541	105,049	288,678
Kabobo Apalis	0	0	0	4,130	0	0	4,130
Klaas's Cuckoo*	0	2,194	24,484	2,712	1,125,306	8,326	1,163,022
Laughing Dove*	0	0	44,224	0	0	7,412	51,636

Lead-coloured Flycatcher	0	0	11,688	5,726	0	2,267	19,681
Least Honeyguide	-	0	4,894	0	189,193	16,499	210,586
Lesser Striped Swallow	0	0	95,089	0	0	8,777	103,866
Little Greenbul*	0	117,855	2,572,880	186,241	6,121,866	949,571	9,948,413
Little Weaver	0	0	0	0	0	156,049	156,049
Lizard Buzzard	0	0	2,617	0	3,743,282	1,961	3,747,860
Long-crested Eagle	0	0	4,306	904	0	371	5,581
Luhder's Bush Shrike	1,000	8,138	269,712	23,814	6,384,178	2,796	6,689,638
Marabou Stork*	0	0	7,216	0	0	3,054	10,270
Marico Sunbird	0	0	120,558	0	0	27,105	147,663
Martial Eagle	0	0	1,210	0	0	377	1,587
Masked Apalis*	0	0	551,124	0	0	1,396	552,520
Montane Masked Apalis	28,491	0	254,166	15,747	430,669	0	729,073
Montane Oriole*	3,127	0	17,534	455	919,350	266	940,732
Montane Sooty Boubou	8,127	0	71,313	1,042	30,686	0	111,168
Mountain Buzzard	237	0	1,976	0	441	0	2,654
Mountain Yellow Warbler*	5,120	0	116,798	1,013	13,845	0	136,776
Nahan's Francolin	0	0	2,824	0	0	16,219	19,043
Narina's Trogon*	1,123	691	176,604	0	1,303,635	34,235	1,516,288
Northern Black Flycatcher	0	0	25,916	0	0	5,494	31,410
Northern Carmine Bee-eater	0	0	0	0	0	1,639	1,639
Northern Crombec	0	0	703,155	0	0	642,980	1,346,135
Northern Puffback	6,774	0	130,023	0	27,890	25,065	189,752
Nubian Woodpecker*	0	0	5,272	0	0	6,429	11,701

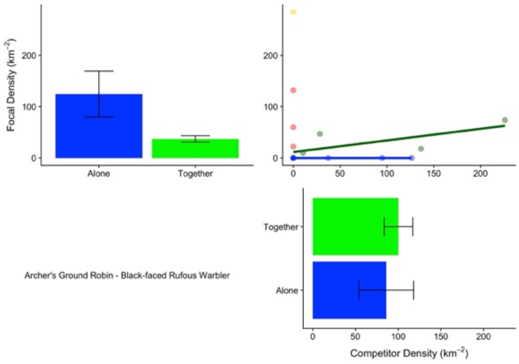
Olive Long-tailed Cuckoo	0	0	1,458	119	2,996	-	4,573
Olive Pigeon	5,535	775	76,736	378	9,499	0	92,923
Olive Sunbird	14,622	132,017	2,806,784	490,441	55,554,611	985,727	59,984,202
Olive Thrush	1,361	0	7,095	0	0	0	8,456
Olive-bellied Sunbird	0	14,951	1,464,965	5,450	85,686	198,436	1,769,488
Olive-breasted Mountain Greenbul	26,549	0	327,045	15,019	294,165	0	662,778
Olive-green Camaroptera	0	0	206,360	272	918,471	91,307	1,216,410
Piapiac	0	0	9,224	0	0	319,169	328,393
Purple-breasted Sunbird	17,509	0	217,915	11,363	443,010	-	689,797
Rattling Cisticola	0	0	0	143,173	0	418,590	561,763
Red-billed Quelea	0	0	1,169,983	0	0	110,991	1,280,974
Red-capped Robin Chat	0	142,229	269,603	0	0	20,198	432,030
Red-cheeked Cordon-bleu	0	0	1,237,382	0	0	1,253,311	2,490,693
Red-chested Cuckoo*	8	254	117,214	0	280,385	10,835	408,696
Red-chested Sunbird	0	0	8,690	0	0	3,751	12,441
Red-eyed Dove*	23	567	52,295	0	0	4,561	57,446
Red-faced Cisticola	0	0	478,877	21,216	0	49,588	549,681
Red-faced Woodland Warbler	24,226	0	592,558	31,786	564,165	0	1,212,735
Red-headed Malimbe	0	0	90,754	0	19,029	-	109,783
Red-necked Falcon	0	0	0	0	0	2,347	2,347
Red-necked Spurfowl	0	0	20,915	6,329	0	192	27,436
Red-shouldered Cuckoo Shrike	0	0	5,387	0	0	4,366	9,753
Red-sided Broadbill	0	0	22,651	0	1,313,418	20,151	1,356,220

Red-tailed Ant Thrush	0	0	26,696	0	103,200	29,000	158,896
Red-tailed Bristle-bill*	0	0	307,850	16,169	3,408,122	175,792	3,907,933
Red-tailed Greenbul*	0	0	553,188	24,009	12,070,235	231,765	12,879,197
Red-throated Alethe	6,595	0	27,090	3,636	5,375,965	0	5,413,286
Red-throated Bee-eater	0	0	0	0	0	28,886	28,886
Regal Sunbird	50,776	7,305	622,842	49,911	786,554	0	1,517,388
Ring-necked Dove*	0	84,951	47,388	0	0	10,678	143,017
Ruppell's Long-tailed Starling*	0	0	86,193	0	0	43,568	129,761
Ruppell's Vulture	0	0	0	0	0	1,624	1,624
Ruwenzori Double-collared Sunbird	19,847	0	218,227	749	150,727	0	389,550
Rwenzori Batis	6,632	0	129,908	2,941	89,151	0	228,632
Rwenzori Turaco*	3,922	0	21,821	1,466	41,101	0	68,310
Sacred Ibis	0	0	0	0	0	3,139	3,139
Scaly-breasted Illadopsis	0	0	388,314	64,214	1,197,710	153,703	1,803,941
Scarlet-chested Sunbird	0	0	80,958	0	0	38,487	119,445
Schalow's Tauraco	0	55,796	0	0	0	0	55,796
Senegal Plover	0	0	1,762	0	0	21,021	22,783
Sharpe's Starling	2,173	0	7,864	0	6,060	0	16,097
Shelley's Rufous Sparrow	0	0	0	0	0	154,519	154,519
Siffling Cisticola	0	0	38,576	31,184	0	2,886	72,646
Silverbird*	0	0	0	0	0	104,942	104,942
Slender-billed Greenbul	961	13,309	250,772	12,543	40,016	102,767	420,368
Sooty Chat	0	0	61,714	3,944	0	87,661	153,319
Speckle-fronted Weaver	0	0	0	0	0	242,263	242,263

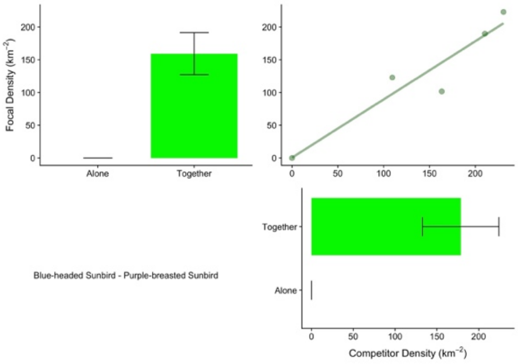
Speckled Mousebird	0	0	1,526,042	0	0	305,585	1,831,627
Speckled Tinkerbird*	0	0	290,359	37,436	2,348,615	98,162	2,774,572
Splendid Glossy Starling*	0	0	1,063,487	0	0	266,566	1,330,053
Spot-flanked Barbet	0	0	149,286	0	0	54,505	203,791
Spotted Greenbul	0	0	15,463	0	1,366,295	263,131	1,644,889
Spotted Palm-Thrush	0	0	0	0	0	354,638	354,638
Strange Weaver	2,621	0	41,259	387	34,107	0	78,374
Stripe-breasted Tit	5,826	0	36,302	3,595	22,604	0	68,327
Striped Kingfisher*	0	0	35,129	0	0	10,843	45,972
Stuhlmann's Starling	416	0	117,521	2,215	51,083	0	171,235
Sulphur-breasted Bush Shrike	0	0	26,146	0	0	6,120	32,266
Swallow-tailed Bee-eater	0	0	0	0	0	17,190	17,190
Tambourine Dove*	1,414	187	132,010	283	110,920	77,681	322,495
Tawny Eagle	0	0	0	0	0	447	447
Tawny-flanked Prinia*	0	12,509	547,889	40,291	0	770,562	1,371,251
Toro Olive Greenbul	0	0	32,274	0	0	17,180	49,454
Trilling Cisticola	0	114	91,024	41,147	0	8,246	140,531
Tropical Boubou	0	138,850	17,839	904	0	1,291	158,884
Vinaceous Dove*	0	0	0	0	0	2,392	2,392
Violet-backed Starling	0	20,066	10,994	0	0	26,846	57,906
Wahlberg's Eagle	0	0	0	0	0	460	460
Waller's Chestnut-winged Starling	7,782	0	37,051	971	16,718	0	62,522
Western Black-headed Oriole*	0	221,505	173,106	6,952	965,897	57,004	1,424,464
Western Bronze-naped Pigeon*	0	0	8,276	0	56,580	0	64,856

Western Green Tinkerbird	89	0	31,628	236	11,888	0	43,841
Western Nicator*	0	23,823	718,286	6,505	2,381,200	331,356	3,461,170
Whistling Cisticola	0	0	1,532	0	0	10,690	12,222
White-breasted Negrofinch*	0	0	302,794	0	2,619	85,627	391,040
White-browed Coucal*	0	0	18,098	2,712	0	4,363	25,173
White-browed Crombec	1,352	0	34,149	763	38,374	0	74,638
White-browed Scrub Robin*	0	3,525	42,882	0	0	48,159	94,566
White-chinned Prinia	261	13,306	90,699	695	0	-	104,961
White-crested Turaco	0	0	0	0	0	3,074	3,074
White-headed Saw-wing	0	0	0	0	0	104,745	104,745
White-headed Vulture	0	0	0	0	0	217	217
White-spotted Flufftail or White-spotted Pygmy Crake	0	0	30,083	0	169,950	20,349	220,382
White-starred Forest Robin*	8,797	5,927	137,449	8,611	263,259	0	424,043
White-tailed Ant Thrush	0	0	262,134	0	1,842,418	50,583	2,155,135
Winding Cisticola	0	0	83,972	0	0	12,652	96,624
Yellow Longbill	0	0	5,398	0	0	51,128	56,526
Yellow White-eye	42,206	6,873	920,767	429,483	4,659,450	17,517	6,076,296
Yellow-backed Weaver	0	0	259,883	0	0	38,148	298,031
Yellow-billed Barbet*	0	0	71,456	0	75,577	35,632	182,665
Yellow-billed Oxpecker	0	0	1,230	0	0	20,107	21,337
Yellow-crested Woodpecker	0	0	53,059	0	0	67,575	120,634
Yellow-fronted Canary	0	0	4,089	0	0	4,206	8,295

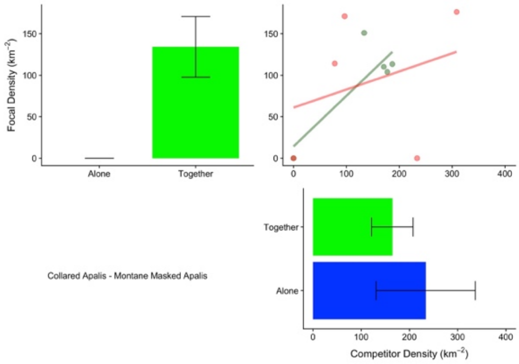
Yellow-fronted Tinkerbird*	0	0	38,147	0	0	6,048	44,195
Yellow-mantled Widowbird	0	0	0	0	0	19,471	19,471
Yellow-rumped Tinkerbird*	9,964	23,609	498,900	79,013	4,888,008	38,416	5,537,910
Yellow-spotted Barbet*	0	0	119,129	0	69,752	32,105	220,986
Yellow-streaked Greenbul	13,932	5,935	64,685	8,018	85,965	-	178,535
Yellow-throated Longclaw	0	0	85,579	0	0	25,203	110,782
Yellow-throated Nicator	0	0	116,764	0	0	0	116,764
Yellow-throated Tinkerbird*	0	0	381,666	20,691	1,846,019	359,077	2,607,453
Yellow-whiskered Greenbul*	37,232	183,029	1,175,973	192,615	20,481,691	364,238	22,434,778
Yellowbill	0	9,615	177,707	0	0	134,412	321,734



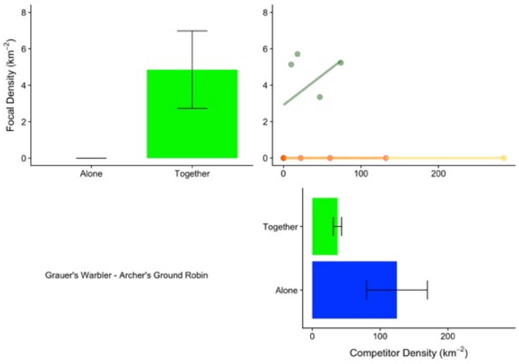
Archer's Ground Robin - Black-faced Rufous Warbler



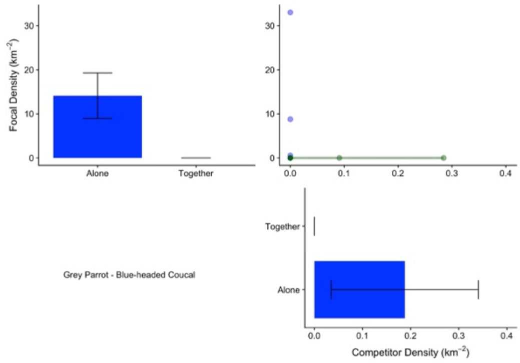
Blue-headed Sunbird - Purple-breasted Sunbird



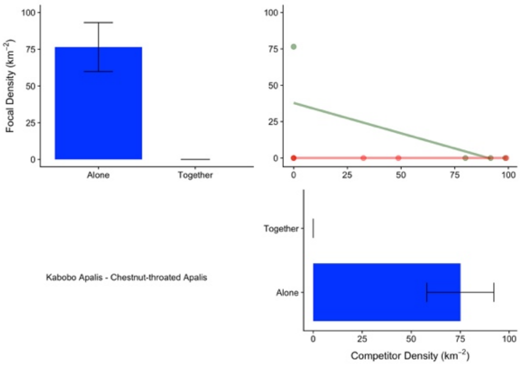
Collared Apalis - Montane Masked Apalis



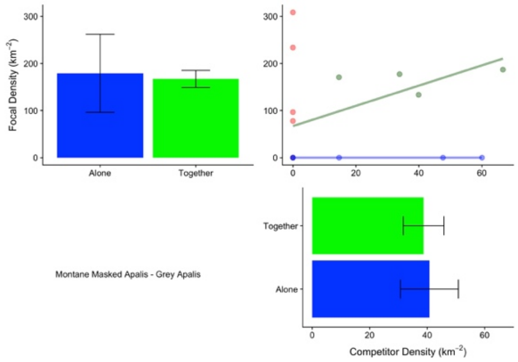
Grauer's Warbler - Archer's Ground Robin



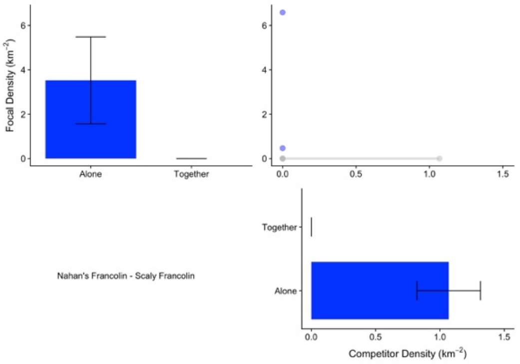
Grey Parrot - Blue-headed Coucal



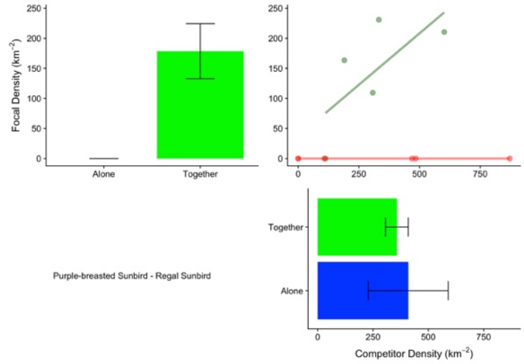
Kabobo Apalis - Chestnut-throated Apalis



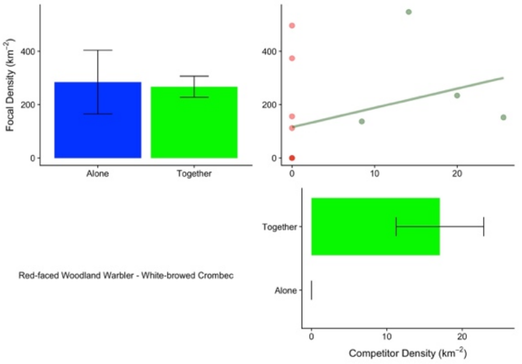
Montane Masked Apalis - Grey Apalis



Nahan's Francolin - Scaly Francolin



Purple-breasted Sunbird - Regal Sunbird



Red-faced Woodland Warbler - White-browed Crombec

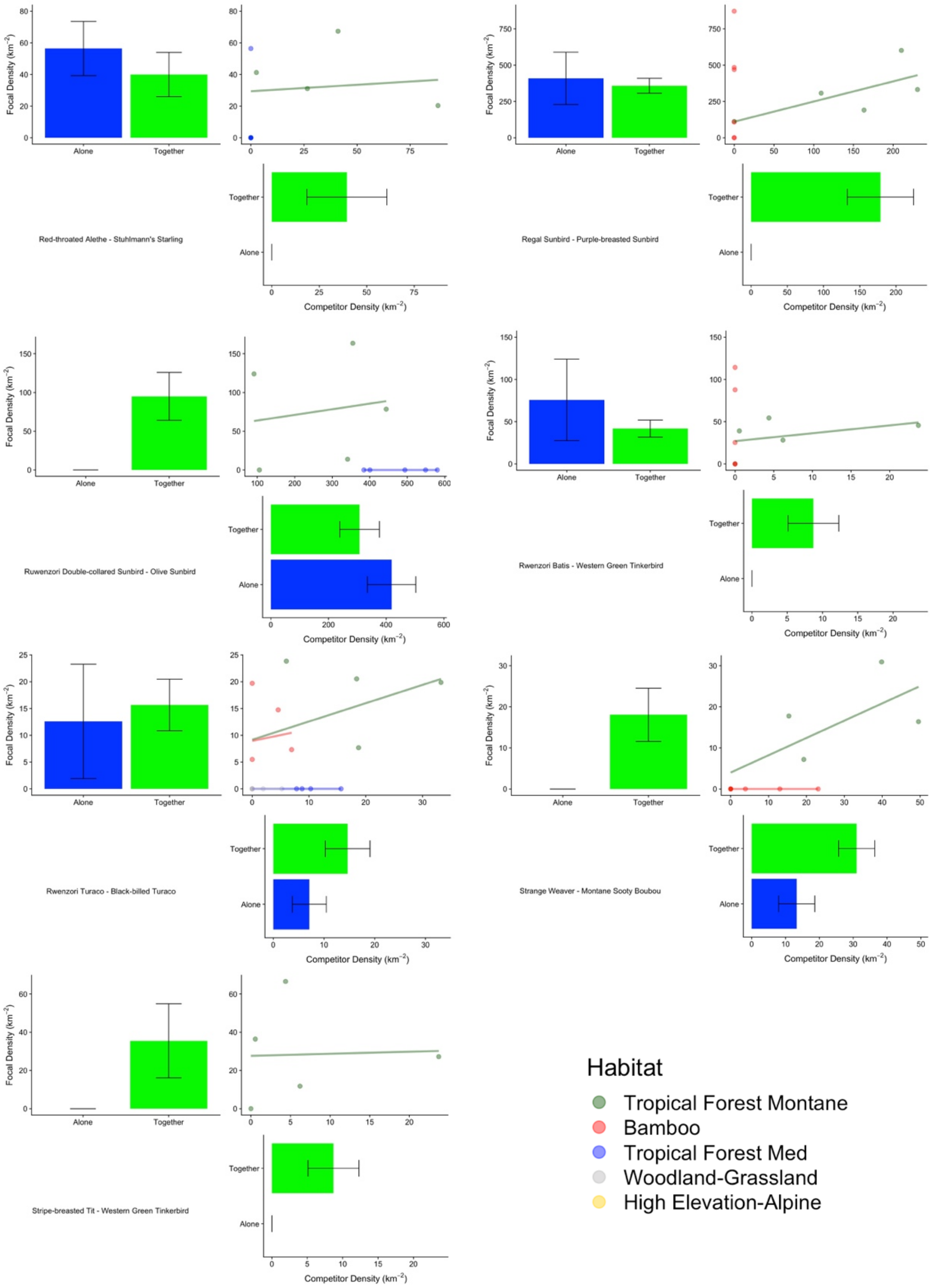


Figure A1 (clockwise for each plot): Mean focal (endemic and/or threatened species) density when alone and co-occurring with competitor species; regional densities of focal and competitor species, colour-coded by habitat (see legend at bottom of figure); mean competitor density when alone and co-occurring with focal species.