THE EFFECTS OF TEMPERATURE ON THE ETHIOPIAN BUSH-CROW AND THE WHITE-TAILED SWALLOW

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DECLARATION

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University of similar institution except as declared in the Preface and specified in the text

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SUMMARY

Understanding the factors which determine the distributions of species is challenging. In response to recent anthropogenic climate change species' ranges are already changing, adding to the complexity of describing their ecological boundaries. The threat posed to species by climate change cannot be understated, and our ability to understand the drivers and mechanisms which underlie species' responses is critical to our strategies to conserve them.

The Ethiopian Bush-crow's *Zavattariornis stresemanni* distribution was recently described by an envelope of cooler, drier climate than the surrounding area. This finding raised an intriguing possibility; could this abundant, generalist and charismatic species be limited to a tiny corner of the world by its response to climatic variables alone? That the White-tailed Swallow *Hirundo megaensis* occurs in a near identical area only adds to this curiosity; how can two unrelated species be globally restricted to the same small area?

I address the following questions. What are the effects of temperature on the distribution and local density of the Ethiopian Bush-crow and White-tailed Swallow? How is Bush-crow behaviour affected by temperature? What are the effects of temperature on the breeding success of the White-tailed Swallow? What are the consequences of climatic range-restriction for the conservation of the two species?

I found that both species' ranges are neatly described by distribution models, in which the most important variable was maximum temperature of the warmest month. Bush-crow local density declines as temperatures rise, and their foraging behaviour is negatively impacted by high temperatures, compared to two sympatric starling species. The White-tailed Swallow shows similar negative trends in abundance, and displays a reduction in breeding success as ambient temperatures increase during its breeding season. In both cases, wider-ranging sympatric species do not show the same negative responses to temperature. Both the Ethiopian Bush-crow and White-tailed Swallow are projected to lose a significant proportion of their range over the coming century, raising the level of conservation concern for the species.

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CONTENTS

LIST OF ABBREVIATIONS AND ACRONYMS

AIC: Akaike’s Information Criterion

AIC_c: Corrected Akaike’s Information Criterion

ANN: Artificial Neural Networks

ANOVA: Analysis of Variance

AUC: Area Under (the Receiver-Operator) Curve

BMR: Basal Metabolic Rate

BRT: Boosted Regression Trees

CTA: Classification Tree Analysis

DT: Decision Tree Analysis

EAS: Effective Area Surveyed

EVI: Enhanced Vegetation Index

EWL: Evaporative Water Loss

FDA: Flexible Discriminant Analysis

FDR: False Discovery Rate

FNR: False Non-Discovery Rate

GAM: Generalised Additive Model

GBM: Generalised Boosting Model

GCM: Global Circulation Model

GLM: Generalised Linear Model

GPS: Global Positioning System

HESW: Half Effective Strip Width

ISRIC: International Soil Reference and Information Centre

LST: Land Surface Temperature

MARS: Multiple Adaptive Regression Splines

MaxEnt: Maximum Entropy

ML: Maximum Likelihood

MODIS: Moderate Resolution Imaging Spectroradiometer

NASA: North American Space Agency

NDVI: Normalised Difference Vegetation Index

OLS: Ordinary Least Squares

PCA: Principal Components Analysis

pFDR: positive False Discovery Rate

RCP: Representative Concentration Pathway

REML: Restricted Maximum Likelihood

RF: Random Forests

ROC: Receiver-Operator Characteristic

RSPB: Royal Society for the Protection of Birds

RSS: Residual Sum of Squares

RTA: Regression Tree Analysis

SD: Standard Deviation

SDM: Species Distribution Model

SRE: Surface Range Envelope

TEWL: Total Evaporative Water Loss

TNZ: Thermoneutral Zone

WLS: Weighted Least Squares

VCF: Vegetation Continuous Fields

1 THE EFFECTS OF TEMPERATURE IN LIMITING THE GEOGRAPHICAL RANGES OF BIRDS

"In Bale mountains National Park, ambasha is recommended."

1.1 Introduction

Understanding the reasons why the boundaries of species' geographical ranges are located where they are is difficult, because there are often many variables acting directly and indirectly in different ways in different parts of the species' distribution (Pearson and Dawson, 2003; Warren et al., 2001). In addition, the response of a species will often depend on the interaction of multiple factors even at a single range boundary (Araújo and Luoto, 2007; Hersteinsson and MacDonald, 1992; Mason et al., 2014b). For some species, limited dispersal ability can be an important factor limiting occupancy of suitable patches of habitat isolated from the core range (Bibby and Tubbs, 1975; Komdeur, 1994). For more mobile species, physical or ecological barriers may still prevent suitable habitat patches from being occupied, as demonstrated by the invasion of non-native species when introduced to new continental land masses (Gammon and Maurer, 2002; Veech et al., 2011).

Birds are highly mobile endotherms which have colonised every continent and large island. They are able to withstand temperature extremes and habitat variation, and most can move readily from one location to another. Despite this, some species breed over remarkably restricted areas. This range restriction is caused by ecological conditions, including anthropogenic factors (Newton, 2003; Orme et al., 2006).

Brommer and Møller (2010) suggested that birds' high latitude range margins are more likely to be determined by abiotic factors, including temperature, whilst their low latitude margins are more likely to be driven by biotic interactions. This assumes that low, rather than high, temperatures are more likely to limit bird distributions. However many studies have found a range of effects of high temperature on birds, from physiological limitations to impacts on breeding success, phenology and behaviour (Salaberria et al., 2014). Ultimately, any of these effects can be responsible for determining a species' distribution.

A number of studies have found indirect effects of temperature on birds, predominantly because temperature affects prey abundance or habitat suitability (Bolger et al., 2004; Forcada et al., 2006; Jones et al., 2003; Mantyka-Pringle et al., 2012; Ward et al., 2005). Here, I will review the physiological, behavioural and demographic mechanisms by which high temperatures limit birds' ranges. A better understanding of these mechanisms is required if the effects of global climate warming on the distribution of species is to be assessed.

1.2 Effects of high temperature on avian physiology

As endotherms, birds are able to regulate their body temperatures independently from the environment. However, there is significant variation between species in their ability to cope with high air or body temperatures (Boyles et al., 2011). Birds typically maintain a higher body temperature than mammals, both when resting and when active (Prinzinger et al., 1991). The thermoneutral zone (TNZ) of an animal defines the range of ambient temperatures within which its Basal Metabolic Rate (BMR) is low and constant, and expenditure of energy on thermoregulation is not required (Tieleman and Williams, 1999). Below the lower bound of the TNZ, endotherms must increase their metabolism to generate heat and maintain body temperature as air temperature falls, while above the upper bound of the TNZ the rate of heat gain increases, and they begin to suffer the effects of heat stress unless they expend energy on thermoregulation, for example by panting, gular fluttering or sweating to increase evaporative cooling (Tieleman and Williams, 1999).

Nevertheless, many birds are able to maintain a body temperature far below ambient air temperature during acute heat exposure. Three species of ploceid weaver, which naturally experience air temperatures up to 43^{o}C, can tolerate experimental exposure to air temperatures ranging from 48–54^{o}C, with evaporative heat dissipation reaching 141–222% of metabolic heat production (Whitfield et al., 2015). Evaporative heat loss between 227 and 446% of metabolic production enables arid-zone columbids (Namaqua Dove *Oena capensis*, Laughing Dove *Spilopelia senegalensis*, Cape Turtle Dove *Streptopelia capicola* and Crested Pigeon *Ocyphaps lophotes*) to maintain body temperatures below 45^{o}C when exposed to air temperatures up to 62^{o}C (McKechnie et al., 2016).

When exposed to consistently high temperatures, birds exhibit a reduction in BMR and an increase in the upper limit of the TNZ. This occurs over two scales, evolutionary adaptation and behavioural plasticity. Lark species which are found in hot, arid environments have evolutionary adaptations which allow their BMRs at high temperatures to be lower on average than those of similar species native to more mesic environments (Tieleman et al., 2002, 2003a). The Arabian Babbler *Turdoides squamiceps* has a lower rate of oxygen consumption, and higher overall thermal conductance (the rate of heat loss), than expected for a passerine of its body mass. Low oxygen consumption is indicative of a low BMR, whilst high thermal conductance enables body temperature to be kept constant at higher air temperatures, which raises the upper threshold of the TNZ (Anava et al., 2001).

Individual birds, when exposed to seasonal variations in temperature, are also able to adjust their BMR in response (Tieleman et al., 2003b). In cooler seasons, increased energy demands require higher food intake, leading to an increase in body mass. This generates a higher oxygen requirement, which necessitates an increase in BMR (Williams and Tieleman, 2000). In warmer seasons, body mass, energy expenditure and BMR are reduced (Tieleman and Williams, 2000). A lower BMR means that the bird produces less heat itself, which when air temperatures are high means that it has less heat to try to dissipate. However, low BMR does not necessarily confer greater tolerance to high air temperatures (Hayworth and Weathers, 1984).

Birds are also able to maintain a higher-than-normal body temperature for short periods in warmer environments, allowing them to function normally, at least for a period. As air temperature rises towards body temperature, birds raise their body temperature by 2–4°C above normal, thus maintaining a small gradient between body temperature and the surrounding air temperature for longer, which facilitates greater dry heat transfer and reduces the requirement for evaporative water loss (Tieleman and Williams, 1999).

Birds living in deserts may be better able to employ this strategy than conspecifics in semi-desert sites. White-browed Sparrow Weavers *Plocepasser mahali* living in desert environments exhibit higher body temperatures than conspecifics from cooler semi-desert environments during the warmest part of the day. This enables the desert birds to continue foraging at higher temperatures than the semi-desert birds (Smit et al., 2013). Despite this, a cross-species review found no difference in the degree of hyperthermia exhibited by desert and non-desert species when exposed to air temperatures of 45°C (Tieleman and Williams, 1999).

Over short timescales, birds also respond to high temperatures by changing their behaviour (Section 1.3). When the upper limit of the TNZ is exceeded, panting or gular fluttering are often used as a mechanism to increase evaporative cooling, but the muscular effort requires energy expenditure and an increase in metabolic rate, and affects the birds' water balance (Tieleman and Williams, 1999). Air temperature thresholds at which behaviours that increase evaporative water loss are triggered range from 31.3–37.5°C in ten passerines endemic to, or resident in, the Fynbos in South Africa. Above their respective thresholds, all ten species show panting behaviour (Milne et al., 2015). In species that experience water shortage, the water loss required to regulate body temperature may exceed water intake rates on hot days, which may force birds to face a trade-off between thermoregulation, hydration and activity (Smit and McKechnie, 2015). If temperature regulation and hydration are prioritised, and activity levels are forced to decrease, then regular temperature exceedance of the TNZ's upper bound may limit the ability of a species to survive in hotter areas because it cannot commit enough time to foraging or breeding behaviour.

Flight is particularly expensive in terms of heat production. When flying at a constant altitude at 33°C air temperature, White-necked Ravens *Corvus cryptoleucus* are close to the limit of their ability to dissipate endogenous heat. The need to stabilise body temperatures may force them either to fly higher, where the air is cooler, or to engage in shorter flights during hot periods (Hudson and Bernstein, 1981).

The existence of a TNZ, above the upper bound of which animals either suffer the effects of heat stress or have to expend energy and water on cooling, suggests that physiological responses to temperature are non-linear, and this has led authors to suggest that species-specific threshold temperatures (T_{Thres}) exist, above which organisms incur fitness costs (Cunningham et al., 2013a, 2013b; du Plessis et al., 2012). Regular exceedance of such thresholds would cause fitness costs to accumulate, and eventually restrict the ability of a species to survive in a climate which is more extreme than its preferred range. California Spotted Owls *Strix occidentalis occidentalis* show a faster rise in BMR above 35.2^{o}C (the upper limit of their TNZ) than is predicted from their body size, and inhabit old-growth forests where more favourable microclimates are found (Weathers et al., 2001). The owls exhibit behavioural responses to heat-stress at relatively modest temperatures (30–34^{o}C), and physiological thresholds are most often detected by observing species’ behavioural responses to temperature.

1.3 Effects of high temperature on behaviour

The physiological impacts of temperature lead animals to change their behaviour to reduce exposure to temperature extremes and allow for physiological recovery (Kelly et al., 2004). These behavioural changes involve fitness trade-offs because behaviours adopted to achieve thermoregulation require time and effort that could otherwise be spent on other behaviour such as foraging or territory defence (Oswald et al., 2008).

Behaviours such as panting and wing fanning are used to increase heat dissipation, but can lower the time committed to, or efficiency of, foraging. When daily maximum air temperatures exceed 35.5^{o}C in the Kalahari desert, increasing behavioural thermoregulation by Southern Pied Babblers *Turdoides bicolor* reduces foraging efficiency to such an extent that they are unable to gain sufficient weight to replace typical overnight weight loss (du Plessis et al., 2012). In the Arctic, Great Skuas *Catharacta skua* spend more time bathing in freshwater on hot days, meaning they are absent from their territories for longer, which leaves their nests at greater risk of predation (Oswald et al., 2008).

When ambient temperatures rise to a point where behaviours to increase heat dissipation cannot regulate body temperature, animals are forced to take refuge in cooler microhabitats or reduce activity levels (Ricklefs and Hainsworth, 1968). In environments where temperatures regularly exceed the upper bound of an organism's TNZ, the presence of cooler thermal refugia is a prerequisite for survival (Cunningham et al., 2015). Magpies *Pica pica* actively select their thermal environment when temperatures rise above 31^{o}C, spending more time perched in the shade and less time foraging (Kelly et al., 2004), and similar responses have been recorded in desert birds (Austin and Miller, 1982). Cactus Wrens *Campylorhynchus brunneicapillus* select cooler microhabitats when temperature in the sun rises above 35^{o}C, and when the minimum available temperature reaches 35^{o}C they decrease their activity (Ricklefs and Hainsworth, 1968). Bobwhites *Colinus virginia* avoid habitat patches at times when they exceed 39^{o}C. This equates to not using about 50% of available habitat across all seasons, and up to 74% of potential habitat in the hot season (July-Sept). This preference, driven by thermoregulation, therefore has a serious impact on both the species' abundance within its range, and its range extent (Forrester et al., 1998).

For some birds, particularly in sparsely-vegetated deserts, shade can be hard to find, and other methods of behavioural cooling need to be employed. Black-crowned Sparrow-Larks *Eremopterix nigriceps* in Kuwait create small hollows in damp ground near to pools, and sit there, exposed to the sun, during the hottest part of the day. Similarly, Temminck's *Eremophila bilopha* and Bar-tailed *Ammomanes cinctura* Larks seek out mats of low-growing, heavily transpiring gourds. In dry summers, when the gourd mats did not develop, the birds were not seen in the study area. Both appear to be behavioural strategies to encourage heat loss (Brown, 2009).

Populations of the same species which inhabit different thermal environments also differ in their choice of habitat. Phainopeplas *Phainopepla nitens* inhabiting warm interior woodlands use sites exposed to direct sunlight 56% less than birds from cooler coastal locations. This reduces the time during which they experience temperatures above their upper critical temperature threshold of 43^{o}C (Walsberg, 1993).

Shifting between different environments in response to temperature changes can incur other costs for a bird. Southern Fiscals *Lanius collaris* prefer to hunt from sunny perches, but when air temperatures exceed 35^{o}C they switch to shaded perches, which are always cooler. However, foraging success rates are 50% lower when using shaded perches (Cunningham et al., 2015). Hoopoe larks *Alaemon alaudipes* prefer to nest in open areas, as this reduces the risk of predation whilst incubating. However as the breeding season progresses they shift their nest locations to the shade of bushes, which reduces the thermoregulatory costs of incubation, but increases the rate of nest predation (Tieleman et al., 2008). The frequency or duration of hotter periods, when birds are forced to incur other behavioural costs of keeping cool, may then determine where a species can and cannot survive (Cunningham et al., 2013a).

Species vary in their behavioural responses to temperature. This variation may reflect differences in their physiological ability to tolerate higher temperatures without expending energy and water on evaporative cooling. When air temperatures exceed 35^{o}C, two ground-foraging species (Scaly-feathered Finch *Sporopipes squamifrons* and Kalahari Scrub-Robin *Erythropygia paeana*) in South Africa show an increased preference for trees (*Boscia albitrunca*) that provide the most shade. However, while the Scrub-Robin only changes its preference during the mid-afternoon, when temperatures are highest, the Scaly-feathered Finch changes in the late morning, suggesting that it has a lower physiological tolerance of temperature (Martin et al., 2015).

Within a species, there is seasonal variation in behavioural responses to temperature. In cool conditions in winter, Chukars *Alectoris chukar* spend most of the day foraging on low-energy food in shaded environments. In the summer, however, they switch to feeding on high-energy food in exposed areas, but restrict the foraging time to the morning and evening, when temperatures are lowest, and spend the rest of the day resting in the shade. This seasonal change facilitates their persistence in areas which are warmer than would otherwise be habitable (Carmi-Winkler et al., 1987).

1.4 Effects of high temperature on demographic rates

The physiological and behavioural impacts of temperature on birds affect their reproductive success and survival.

Parent birds must regulate nest temperatures because developing embryos and newly hatched chicks are not able to thermoregulate. In general, hyperthermia is more dangerous to embryos and young birds than hypothermia (Bennett and Dawson, 1979; Webb, 1987). Parent bird must therefore select nest sites which are not likely to be exposed to lethal temperatures, or shade their offspring during the hottest parts of the day (Bennett and Dawson, 1979; Tieleman et al., 2008). As chicks develop, their thermoregulatory capacity increases. This occurs through the development of panting behaviour, to dissipate heat, and the growth of feathers and deposition of fat reserves, which offer insulation (O'Connor, 1975a; Thomas et al., 1993). Additionally, nestlings exhibit a rise in body temperature during development, as they transition from embryonic to mature tissue (O'Connor, 1975b).

Once nestling thermoregulatory capacity has developed, warmer nest environments tend to be beneficial to chick growth and survival (Pérez et al., 2008; Reid et al., 2000). However, negative effects of high temperature also occur. In Spotless Starlings *Sturnus unicolor* high ambient temperatures during the nestling period negatively affect mass and wing length in second broods, and nestling dehydration increases at high temperatures (Salaberria et al., 2014). The frequency with which daily maximum air temperatures exceed 33^{o}C, 37^{o}C and 35^{o}C (respectively), reduces body mass and tarsus length at fledging and delays fledging in Common Fiscals *Lanius collaris* (Cunningham et al., 2013b).

High temperatures can also affect the behaviour of adult birds tending nests. When maximum daytime temperature exceed 30^{o}C, Rufous Treecreepers *Climacteris rufa* decrease their provisioning rates to nests, which may impact chick survival (Luck, 2001). At a population scale, these effects are likely to have an impact on the suitability of areas for breeding, and therefore limit the potential range of the species.

Effects of temperature on demographic rates can cause geographical variation in the rate of population growth. Bird populations in areas which are amongst the warmest that their species inhabits tend to have less positive growth rates at a given population density, below carrying capacity, than populations living in the coolest parts of the species' range, with a graded linear response through the centre of the range between these extremes (Jiguet et al., 2010). This reflects an effect of temperature on demographic rates. Moreover, species that have only a small range in temperature between the warmest and coolest parts of their range tend to show the sharpest declines in population when exposed to heat wave events (Jiguet et al., 2006).

In general, the effects of temperature on population parameters across taxa, including birds, tend to be more positive at higher latitudes than at lower latitudes, whilst precipitation tends to have a more positive effect at low latitudes than at high latitudes

(Pearce-Higgins et al., 2015). This is suggestive of negative effects of rising temperatures at lower latitudes, which could be mediated via direct thermal intolerance (Section 1.2), or via an indirect interaction effect with limited water availability for evaporative thermoregulation (Smit and McKechnie, 2015).

High temperatures can indirectly affect bird demographic rates, such as the effect of temperature on prey, predators or diseases. Such effects require careful study and ecological knowledge to detect because the ecology of the focal species needs to be well known. In addition, such effects may involve time lags. An example is provided by the Eurasian Golden Plover *Pluvialis apricaria* in the UK. Tipulid flies with soil-dwelling larvae are an important food resource for breeding adults and their precocial chicks. Tipulid abundance and plover breeding success were found to be negatively affected by high temperatures in the late summer (August) in the year preceding a plover breeding season (Pearce-Higgins et al., 2010). This was probably because high temperatures affected the soil moisture and thermal conditions during and soon after egg deposition in the soil by the adult flies and therefore reduced larval survival. Lagged effects like these would not be detected, or would be dismissed as spurious correlations, without detailed ecological knowledge.

1.5 Effects of high temperature on distribution

Despite the clear existence of physiological limits to birds’ tolerance of high temperatures, and of behavioural mechanisms to avoid daily or seasonal periods of unfavourably high temperature, evidence for direct climatic limitation of species’ ranges by high temperature is rare (Thomas, 2010). This is due to the fact that, even if temperature defines a potentially suitable area for a species, other factors, such as habitat availability, ecological competition, or dispersal ability, often influence the realised range of the species, and high temperature may influence distribution indirectly through the effects on prey, predators or diseases (Milne et al., 2015; Newton, 2003; Pearce-Higgins and Green, 2014). Nonetheless, combining observed physiological or behavioural thresholds with range limits does provide some evidence for species’ distributions being directly limited by climatic factors.

Catharacta skuas in both northern and southern hemispheres are confined to breeding at high latitudes where summer temperatures are below ~13^{o}C, despite the presence of abundant prey and suitable breeding habitat at lower latitudes (Furness, 1988).

Behavioural observations show a marked increase in the frequency of bathing, a strategy for keeping cool, on days on which temperatures exceed 14°C, which suggests that a physiological intolerance of high temperatures may determine the distribution of these skuas (Oswald et al., 2008).

Black-billed Magpies *Pica pica* appear to be physiologically restricted to their Cold Type Steppe Dry Climate habitat. Experimental exposure of captive birds to ambient temperatures of 40°C led to the death of three out of nine birds, whilst all 12 congeneric Yellow-billed Magpies *P. nuttalli*, whose range covers lower latitudes, survived. However both species are less tolerant of high temperatures than most other passerines, having very low upper critical temperatures (32.5°C and 33.5°C respectively) and limited capabilities for evaporative cooling at high temperatures (Hayworth and Weathers, 1984). Similarly, the Palila *Psittirostra bailleui* is less heat tolerant than other passerines, and is probably physiologically restricted to cool mountain forests (Weathers and van Riper, 1982).

Chukars, whose upper critical threshold lies at 38.5°C, died when exposed to experimental temperatures of 43°C, while Sand Partridges *Ammoperdix heyi*, which inhabit hotter environments, showed no increase in BMR up to 51°C (Frumkin et al., 1986). Together with the Chukars' seasonal behavioural response (Section 1.3), this suggests that the species' range is determined by the time it can remain active and meet energy requirements without compromising heat balance (Carmi-Winkler et al., 1987).

Recent changes in species' distributions are also suggestive of strong limitations of geographical range by high temperatures. Pied Crows *Corvus albus* have shifted their range south-westwards across South Africa over the last 25 years, with the highest abundances tracking a mean annual temperature of 19°C, and a sharp decline in population density in areas warmer than this. This response suggests that the Pied Crow's temperature preference reflects a fundamental aspect of its physiology (Cunningham et al., 2016).

However, caution must be taken not to ascribe a direct causal effect of high temperatures to correlations between changes in distribution or abundance and changes in mean or maximum temperature. Endemic Fynbos species initially occupying the coolest regions have experienced the greatest reductions in range and population size since the late 1980s. Those species with the largest increases in air temperature in their range have suffered the greatest declines. But only one species, the Cape Rockjumper, exhibited signs of a low physiological thermal threshold. It had the lowest air temperature threshold at which evaporative water loss (EWL) started to increase (31.3^{o}C), and showed the greatest increase in EWL between 30^{o}C and 38^{o}C. For the other 11 species studied, evidence of physiological intolerance of high temperatures was equivocal, suggesting it was not the direct cause of declining population trends (Milne et al., 2015).

1.6 The consequences of temperature limitation

If temperature directly limits species' distributions, then it is to be expected that warming as a result of anthropogenic climate change will directly impact species' populations, and might cause extinctions. However, reviews of the subject suggested that no climate-driven extinctions to date have been caused directly; that is, by straightforward limited tolerances to high temperature (Cahill et al., 2012), and that most population-level impacts occurred via indirect, biotic mechanisms (Ockendon et al., 2014).

As anthropogenic climate change increases, it becomes increasingly likely that physiological intolerances will become a more prevalent cause of extinction (Cahill et al., 2012). The impacts of higher temperatures on species, and their ranges, will therefore become an ever more important concern for conservation. Moreover, the choice of index used to measure warming trends, and their impact on a species, is important when looking to detect biologically meaningful effects. Cunningham *et al.* (2013) found that in South Africa, while all heat wave indices increased, the most rapid increases were in the annual number of hot days (days exceeding a critical threshold) and in the maximum intensity of the heat waves (Cunningham et al., 2013a), and these are the same variables which impact bird species there (Cunningham et al., 2013b; du Plessis et al., 2012). Warming trends were not uniform across their study area, meaning that both high risk areas and refugia could be identified.

The ability of species to tolerate climatic changes will be determined by their ability to either 1) withstand climatic changes due to a pre-existing, already evolved tolerance of higher temperatures than they currently experience, 2) evolve new physiological or behavioural adaptations which allow them increase their tolerance of higher temperatures (Visser, 2008), or 3) move to areas where cooler climate remains without any change in tolerance (Devictor et al., 2008). The last of these depends on both the availability of such refugia and the species' ability to move to them (Jiguet et al., 2007). In addition to large-scale refugia which may shelter a population, small-scale refugia (Kelly et al., 2004; Ricklefs and Hainsworth, 1968) available to individuals for the warmest periods of a day or in the hottest season may allow persistence in areas which have otherwise become more climatically unsuitable (Carmi-Winkler et al., 1987; Cunningham et al., 2015; Hindle et al., 2015).

1.7 Conclusions

The physiological and behavioural impacts of high temperature operate at a range of scales from individual animals to populations. They can determine where a species does, and does not, occur. Effects can be driven by physiological limitations or can occur indirectly because of the effects of temperature on other ecological factors (Milne et al., 2015). Some authors suggest that birds, being highly mobile, may be better able to escape physiological impacts, and that their distributions are driven more by the ecological consequences of climate (Weathers and van Riper, 1982). However, thermoregulatory differences between similar species inhabiting different environments (Frumkin et al., 1986; Hayworth and Weathers, 1984; Weathers and van Riper, 1982), and the climatically adaptive BMR and heat loss strategies of many species (Anava et al., 2001; McKechnie et al., 2016; Smit et al., 2013; Tieleman et al., 2003a; Weathers, 1979; Whitfield et al., 2015), suggest that physiological constraints can be important in determining bird species distributions.

2 INTRODUCTION TO THE STUDY SPECIES

Babaro, qaaqaa fi raarree! Akam?

The two species studied in this thesis, the Ethiopian Bush-crow *Zavattariornis stresemanni* and the White-tailed Swallow *Hirundo megaensis*, are both severely under-studied, and there is scant previously published research. This chapter, therefore, combines a literature review of the available published information on each species with both my own field notes and a summary of further observations and findings which have arisen from work over the last decade, and have been collated as part of this PhD. Both parts have been published (Bladon et al., 2016, 2015), and reformatted for inclusion in this thesis.

2.1 The Ethiopian Bush-crow

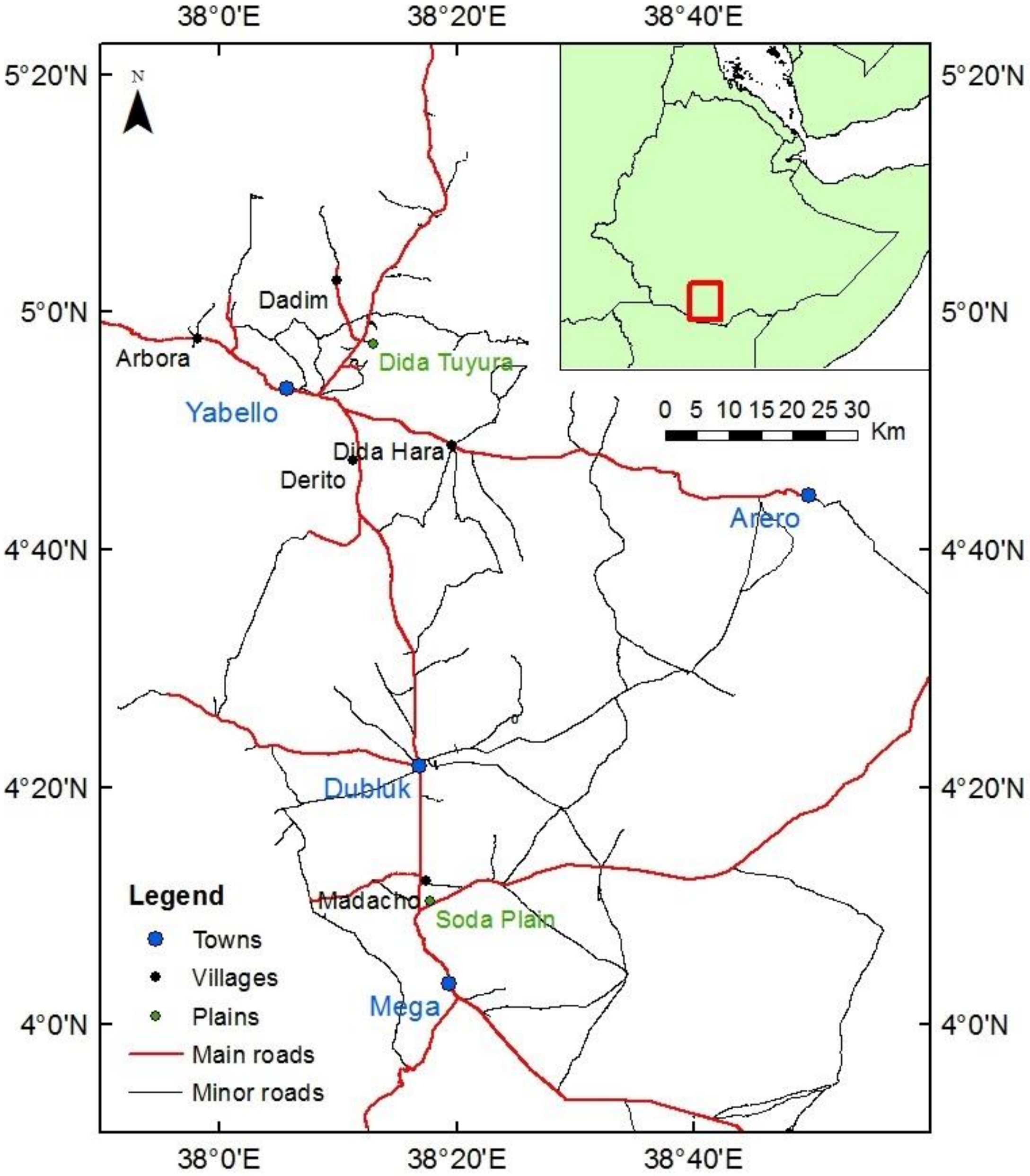
The Ethiopian Bush-crow *Zavattariornis stresemanni* is an enigmatic species of corvid, apparently most closely related to Asian ground-jays *Podoces* (Ericson et al., 2005), and is confined to an area of open thornbush, short-grass savanna and pastures in southern Ethiopia. Ten years ago a reported decline in numbers (Borghesio and Giannetti, 2005) led to its upgrading to the IUCN Red List category Endangered, and this treatment has been maintained until the present (BirdLife International, 2016a). This triggered new initiatives to assess its ecological requirements more precisely (Donald et al., 2012; Mellanby et al., 2008). The Bush-crow is a co-operative breeder (Benson, 1942; Fry et al., 2002) that lives in small groups, occasionally congregating in flocks of up to 30 birds, and exhibits a number of interesting social behaviours, e.g. allofeeding, allopreening and the use of bare skin around the eye in signalling (Gedeon, 2006). Its range is confined to a pocket of cooler, drier and more seasonal climate than is found elsewhere in southern Ethiopia and northern Kenya, which is thought to limit this otherwise common and seemingly generalist species to a global distribution of <6,000 km^2 (Donald et al., 2012). Here I assemble observations collected during research between 2008 and 2014 by myself and others (acronyms given in Table A1), to supplement the natural history notes already provided by Dellelegn (1993), Gedeon (2006) and Ross et al. (2009). The locations of sites mentioned in the text are shown in Figure 2.1.

2.1.1 Breeding season

The Bush-crow was initially reported to breed in February–March, in response to the primary wet season in the region (Benson, 1942). However, breeding has since been more commonly observed in May–June, prompting the suggestion that birds ‘may be double-brooded or have an extended breeding season’ (Collar and Stuart, 1985). There is still no solid evidence for double-brooding, but observations support the existence of a variable or extended breeding season. Breeding activity is influenced by annual variations in the timing and intensity of rains, as is true of the sympatric White-tailed Swallow *Hirundo megaensis* (Bladon et al., 2015) and many other African arid-zone birds (Craig, 2012; Immelmann, 1973).

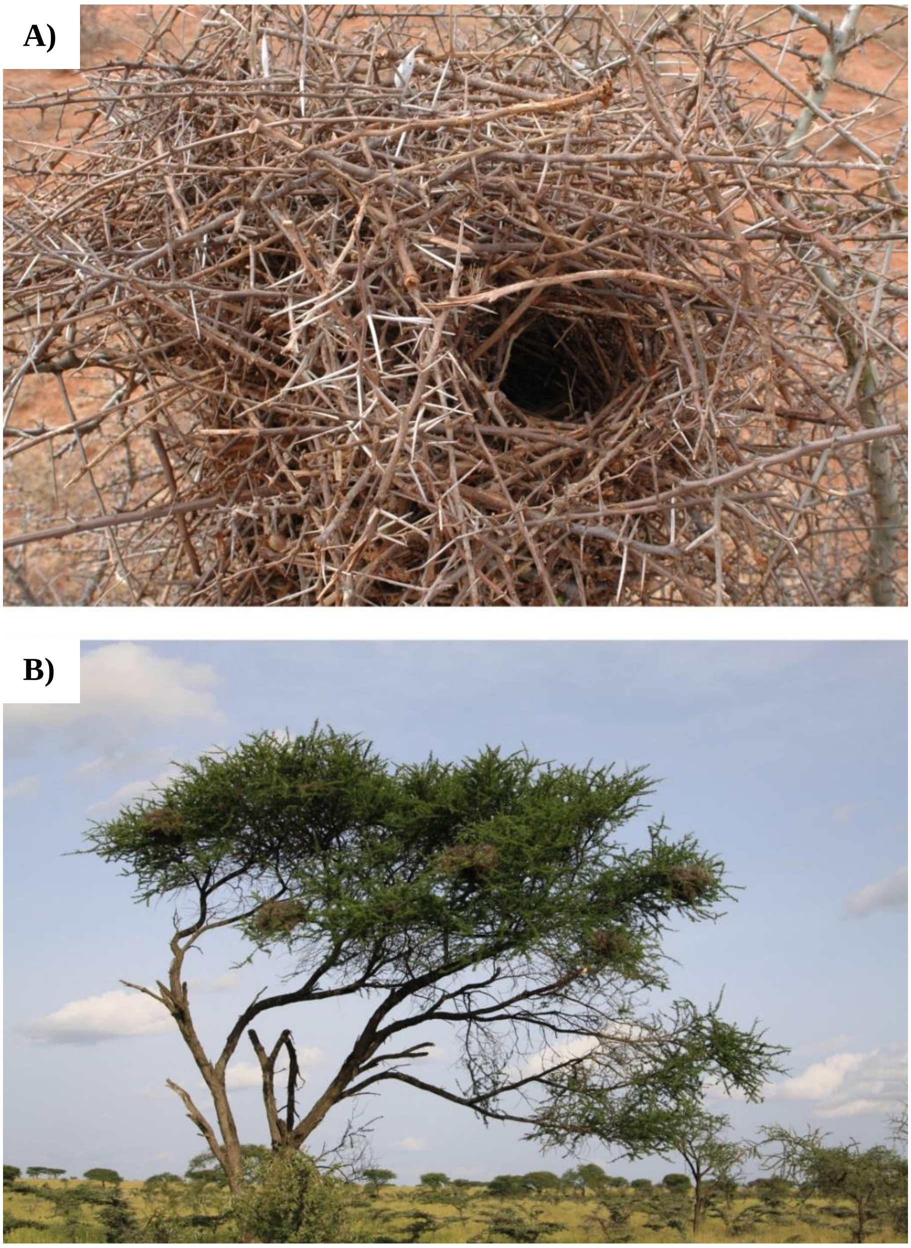
Gedeon (2006) reported that the first rains in 2005 fell on 27th February, stimulating much Bush-crow nest-building activity, none of which had been completed by 6th March. Between 20th and 31st May 2011, KG found a family at Dida Hara with at least one fledged but dependent juvenile, whereas most other groups were still tending nests. In 2013, I recorded the onset of rain at the end of March, saw birds visiting two nests on 27th March, and heard young begging in nests on 29th March and 6th April. The first fledgling was observed on 9th May, but another pair was observed building a new nest as late as 11th May, and some were still tending young in the nest at the end of the month; possibly these were inexperienced birds or individuals that had ceased helping other groups partway through the season (Section 2.1.6). In 2014 the rains started in mid-March (JD), and I observed nest-building and tending regularly throughout April, and saw the first juvenile on 17th May. However, a nest with chicks heard begging was found a month later on 15th June. Clearly, Bush-crows breed in response to the onset of rain, but if conditions are favourable the breeding season can be prolonged. Given the continual and protracted care that groups show for juveniles, it seems probable that Bush-crows produce only a single brood per season and that late nests represent either re-nesting attempts or inexperienced birds trying to breed.

Figure 2.1: Map of the study region, showing the locations of sites referred to in the text. Inset: the location of the study region within Ethiopia.



A second, less intense rainy season between September and November (EWNHS, 2001) also stimulates some breeding activity. On 17th November 2012, I made two observations of nesting: the first 4km east of Yabello, where a group of Bush-crows was tending a nest, and the second on Soda Plain where a group was observed building a nest (it is, however, unclear whether or not Bush-crows maintain nests year-round, and this observation may not represent evidence of breeding). On 19th and 20th November, a further three nests were being visited by Bush-crows, two east of Dida Hara and one on Soda Plain. On 28th October 2013, also on Soda Plain, a fledged juvenile was observed repeatedly being fed by 1–2 adults (NJC). We have also recorded courtship behaviour at this time of year (Section 2.1.3). Two individuals captured in May 2013 (Section 2.1.7) appeared to be immatures, which were probably raised in the second wet season of the previous year (Section 2.1.4).

Figure 2.2: Structure and location of Ethiopian Bush-crow nests. *A*) The entrance to a nest found low in a tree (Claire Spottiswoode). *B*) A large *Acacia* containing seven nests (Paul Donald).

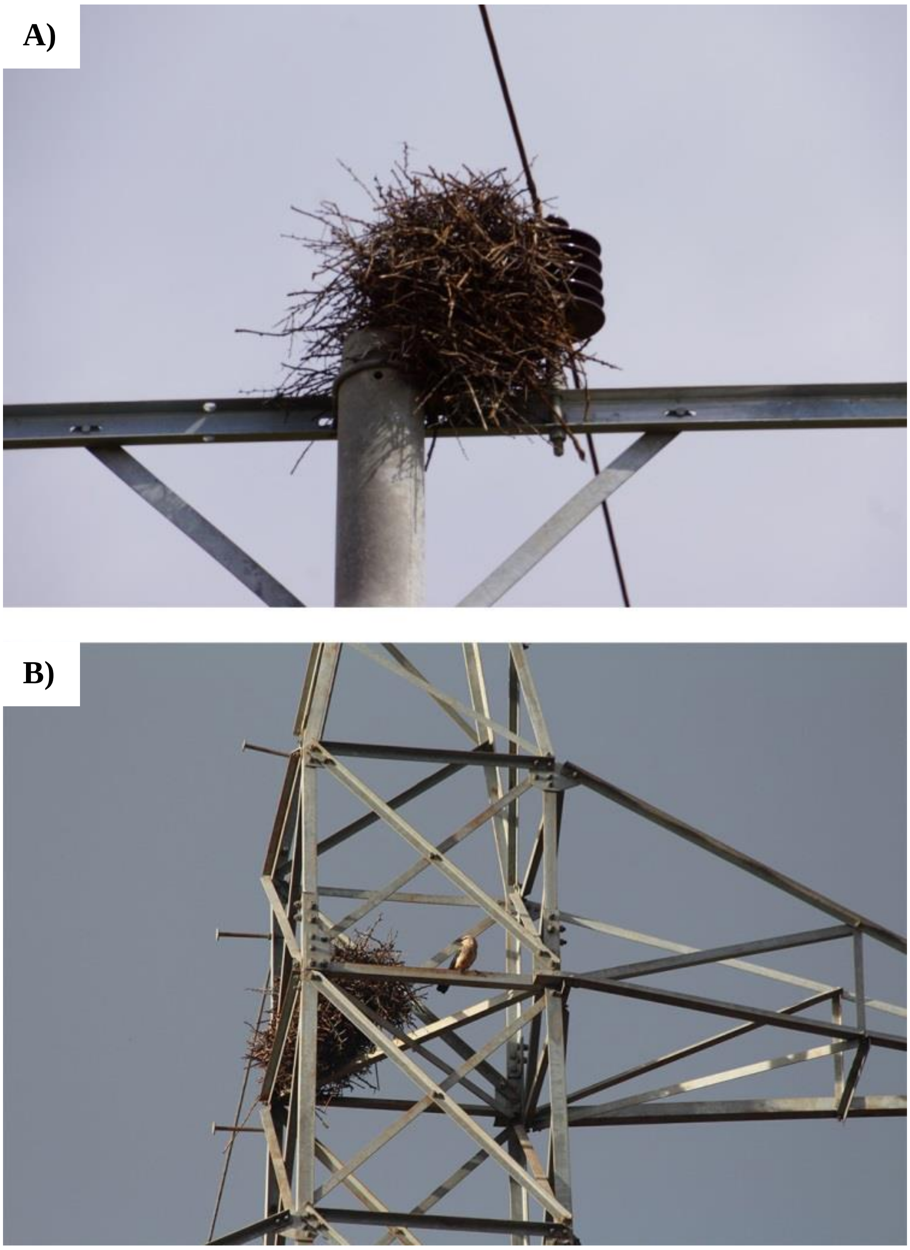


2.1.2 Nest sites

Bush-crows construct large, crudely spherical or semi-cylindrical nests of thick thorny twigs, surrounding a dung- and mud-lined inner chamber reached by a tunnel with an entrance in the upper part of the structure (Figure 2.2, top). These are placed in the crowns of trees, the upper half sometimes sitting proud of the canopy (Benson, 1942; Dellelegn, 1993; Töpfer and Gedeon, 2012). Nests are usually built in *Acacia* spp., *Balanites aegyptiaca* or *Commiphora africana*, mostly between 3.0 and 6.5m above ground (mean = 4.88m: Töpfer and Gedeon, 2012) and are normally solitary (Fry et al., 2002). However, we have several observations of two, one of four and one of seven nests in a single tree (Figure 2.2, bottom), but we lack evidence of whether more than one nest was in use simultaneously. Nest height is necessarily limited by the height of the trees used; the highest of 210 nests around Dida Hara was 14m above ground (Töpfer and Gedeon, 2012). During transects across the range in 2013 and 2014 (Chapter 3), I found only 17 of 243 nests to be higher than 15m above ground, with a mean height of 8.9m, in trees with a mean height of 9.6m. This compares to a mean tree height of 7.1m across transects, suggesting that Bush-crows preferentially select taller trees to nest in, presumably to allow them to gain extra height for the nest.

The use of man-made structures had not previously been reported, but two instances have recently been observed. On 26th October 2013, near Madacho, NJC found a nest on a power distribution pole c.7m above ground: it was balanced on the metal cross-arm and apparently wedged between the top of the central pole and both the central cable and insulator (Figure 2.3, top). None of the twigs appeared to be intertwined with any part of the powerline to hold the nest in place, and its vulnerability was evident from the substantial remains of an earlier nest (in two halves; or possibly two nests) below the same pole. The line ran through scattered trees of similar height and structure to others often used for nesting, and past some village huts; the nest itself was judged to be roughly as high as or possibly a little higher than the upper canopies of the adjacent trees. On 10th May 2014, west of the main road 29km north-east of Yabello and only 6.5km from the edge of the Bush-crow’s range, I found a nest on an electricity pylon. The nest was c.90% up the main tower, at a height of at least 25m, making it by far the highest nest reported. It was supported by, but seemingly not secured to, the framework of the pylon. Two birds were seen visiting the nest (Figure 2.3, bottom). The immediate vicinity again contained trees similar in height to those in which nests are frequently found, but these contained no nests.

Figure 2.3: The first reports of Ethiopian Bush-crows nesting on man-made structures. *A*) A nest on a power distribution pole found in October 2013 (Nigel Collar). *B*) An active nest on an electricity pylon found in May 2014, high above the surrounding trees (Andrew Bladon).



The energetic costs of visiting the high pylon nest must be greater than for lower nests in trees (Zach, 1979), and nesting on pylons may increase the risk to Bush-crows from aerial predator attack. However, it is perhaps the case that the extra height better cools the nest, reducing heat-stress and perhaps increasing breeding success given the species' apparent temperature sensitivity (Donald et al., 2012; Töpfer and Gedeon, 2014, 2012). This might explain the difference in mean height of 4.88m found by Töpfer & Gedeon

(2012) and 8.9m presented here, as the 2012 figure comes from Dida Hara, near the centre of the range, which is perhaps cooler on average than sites across the range, which produced the new, higher mean (Donald et al., 2012). Cooling might also explain why many nests in trees sit proud of the canopy.

Figure 2.4: Ethiopian Bush-crow displaying to another; stretching its head up and forwards, fanning its tail and exaggerating its steps (Paul Donald).

2.1.3 Display

Gedeon (2006) described some display behaviours related to allofeeding, nest building and courtship. On 26th October 2013, just north of Soda Plain, NJC and PFD encountered two Bush-crows that were remarkably confiding in their behaviour, first in a low tree and then on the ground, permitting the observers to approach within a few metres. On the ground one bird walked a few yards behind the other, with the observers quietly following them. After a minute or so the bird following adopted a posture recalling a displaying male dove, in which it stretched its neck up and forward at c.45°, raising the crown feathers so that its head appeared larger (with seemingly an inflated bulge on the neck-sides), tilting the head forward so the bill pointed 30° downwards, exaggerating its steps so that they appeared slightly higher and slower, and fanning its tail to twice its usual width and tilting it downwards so that its tip dragged along the ground (Figure 2.4). During this display, the fleshy patch behind the blue eye-ring was prominently displayed, and the eye appeared to be bulging and half-closed. This appeared to be a courtship display by a male to a female, but it might conceivably have been a mate-guarding display if the bird in question was somehow registering the human observers as threats to its mate or status. Gedeon (2006) recorded a similar display, except that the performer led rather than followed the second bird; he judged it to be a courtship display by a nest-building pair.

Figure 2.5: Colour-marked Ethiopian Bush-crow and its partner reciprocally allopreening (Andrew Bladon).

Gedeon (2006) noted that ‘allofeeding and allopreening remained, as far as could be observed, unreciprocated’. However, on 24th May 2014, I observed two birds reciprocally allopreening (Figure 2.5). These birds appeared to be a pair, perched in a separate tree and paid little attention to the rest of their group, so it may be that, although allopreening is widespread, reciprocation is limited to breeding pairs. Allopreening of juveniles by their attendant adults is also common.

2.1.4 Nestlings and juveniles

Benson (1942) described the eggs of the Bush-crow when he collected two clutches (one of four eggs and one of six). On 14th June 2008, a few kilometres north of Dubluk, an occupied nest was found in a tree so low that the nest chamber could be accessed by hand from the roof of a vehicle, by PD. It contained two naked and blind nestlings probably less than one week old, apparently the first time young in the nest have been photographed (Figure 2.6). This nest was attended by at least five adults; four were seen to fly out of it in succession as it was approached, one of them carrying a faecal sac, which it smeared on the first branch of a nearby tree on landing.

Figure 2.6: Ethiopian Bush-crow nestlings taken from a nest in June 2008, showing large, pale gape flanges typical of chicks raised in dark nests (Claire Spottiswoode).

Dellelegn (1993) and Fry et al. (2002) briefly described the differences between adult and juvenile plumage; the most obvious of which are the grey-white tint to the juvenile head and neck feathers (which in adults are often brown-white, due to staining from the local soil; Figure 2.7), and the dark skin around the eye (cobalt-blue in adults). Feathering covering the nares is duskier in young, creating (in conjunction with the dark ocular/loral skin) a dark ‘saddle’ over the bill (Figure 2.8). Juveniles also display a distinctive pale pink bill base, and the gape is bright pink-red (Figure 2.7). In late June 2014, juveniles a few weeks post-fledging were still readily distinguishable from adults.

Figure 2.7: Ethiopian Bush-crow family in an *Acacia*, permitting comparison of the differences in plumage between adults (right) and juveniles (Paul F. Donald).

Two birds captured on 6th May 2013 near Madacho displayed characteristics of juveniles from a previous breeding season. Both had noticeably darker blue facial skin with the residual pink bill base (Figure 2.9; compare top, a presumed subadult, with bottom, an adult). Notably, these birds were not recently fledged (judged by wear to the remiges and rectrices). These characteristics were observed on no other individual captured (*n* = 55) nor observed in the field.

Figure 2.8: Juvenile Ethiopian Bush-crows lack the cobalt-blue eye-ring of adults, instead possessing a black mask, darker feathering over the nares and a distinctive pale pink bill base; *cf*. Figure 2.9 *B* (Sam Jones).

Two calls were documented from juveniles, adding to the vocal repertoire of the species previously described by Dellelegn (1993) and Gedeon (2006). Young in the nest emit a constant soft and squeaky *kew*, recordings of which have been archived online (www.xeno-canto.org/131679, 131678). During the post-fledging period, young emit a series of loud and insistent *kah* and *kew* notes, which are distinctly muffled during feeds, resembling the allofeeding *kaw kaw kaw* described by Gedeon (2006) (Figure 2.10). These begging calls are similar to the juvenile contact call described by Dellelegn (1993), but the tone is sharper and the usage clearly for begging rather than contact. The calls are distinctive and almost constant during active periods, making location of post-fledging groups particularly easy. They have been documented and archived online (www.xeno-canto.org/140133, 140131).

Figure 2.9: Comparison of the facial features of Ethiopian Bush-crows in *A*) a presumed subadult and *B*) an adult bird (Sam Jones).

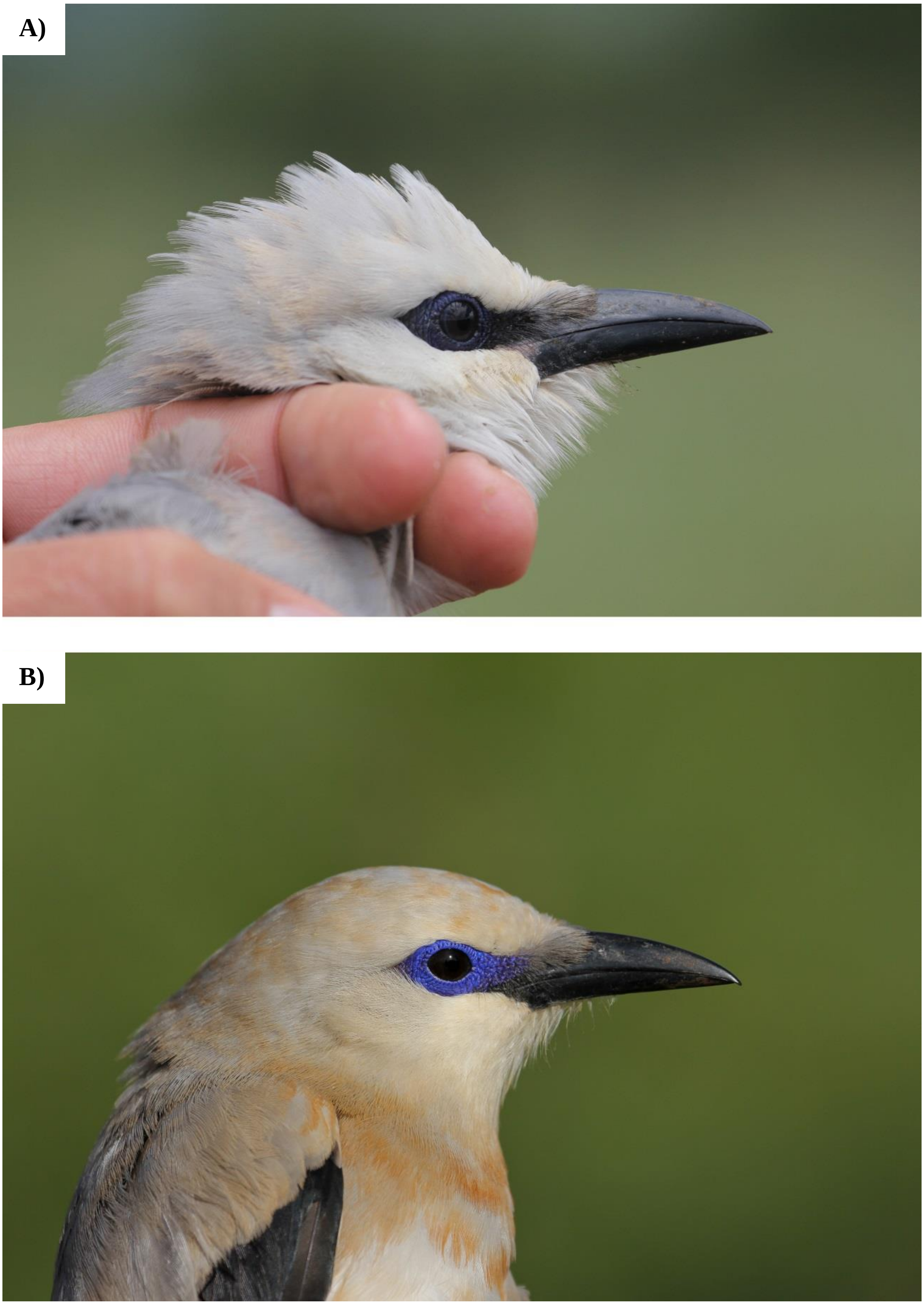


Figure 2.10: Adult Ethiopian Bush-crow feeding a juvenile; the attendance of juveniles by the adults demonstrates the high levels of post-natal care (Andrew Bladon).

Figure 2.11: Young Ethiopian Bush-crow fanning its wings; the reason for this behaviour is not apparent (Paul Donald).

On a number of occasions, juveniles have been observed fanning their open wings, both while perched and on the ground (Figure 2.11). This behaviour does not seem to be related to begging, and its function is unclear, but it is notable that we have observed it only in juveniles.

2.1.5 Morphology and moult

Biometrics

Biometric data have not previously been collated for the species, with quoted figures (e.g. mass of c.130g) in Madge (2009) probably speculation. Table 2.1 presents biometrics of 57 live individuals trapped in the field in May 2013, and 14 specimens at the Natural History Museum, Tring, UK. Biometrics were examined for bimodality, but there was little evidence to suggest these are useful for sexing individuals. We also found a range of biometric values in individuals with well-developed brood patches. If these are presumed to be females, then the lack of biometric bimodality is supported, but it is possible that males assist with incubation, and develop brood patches too, although this is rare in corvids (Goodwin, 1986). Biometric bimodality is recorded in other corvids, but with a sufficient degree of overlap between the distributions to present uncertainty if used alone for sexing individual birds (Fletcher and Foster, 2010; Giammarino et al., 2012).

Table 2.1: Biometric summary of 57 Ethiopian Bush-crows trapped for colour-marking in 2013 and, except for last two variables, 14 specimens at the British Natural History Museum, Tring, UK.

	Birds caught in 2013 *n* = 57		**NHMUK, Tring, specimens *n* = 14**	
Value	**Mean ± 1 SD**	**Range**	**Mean ± 1 SD**	**Range**
Flattened wing chord (mm)	141.8 ± 3.7	135–149	141.4 ± 3.5	137–148
Tail (mm)	125.2 ± 5.6	108–135	125.0 ± 3.8	121–135
Culmen–skull (mm)	35.5 ± 2.0	31.1–41.1	34.2 ± 2.2	30.3–37.7
Head and bill (mm)	63.1 ± 1.9	59.5–67.5	65.6 ± 4.0	55.8–71.7
Maximum tarsus (mm)	45.2 ± 1.5	41.1–48.6	-	-
Mass (g)	109 ± 6.1	97–124	-	-

Feather and plumage morphology

Simple morphology was examined on trapped birds. Bush-crows have ten primaries, six secondaries and three tertials. The outer primaries, 10–5, are emarginated. As in many corvids, the first tertial (outermost from the body) is longer than the sixth secondary. There are 12 rectrices. Feathers were noticeably lightweight and low-density, particularly on the belly, breast, axillaries and crural areas (Figure 2.12), which is interesting when considering the species' apparent climatically driven range-restriction (Donald et al., 2012). Perhaps light, low-density feathers serve to allow better heat dissipation for effective thermoregulation, in addition to the use of the exposable flange on the side of the head (Töpfer and Gedeon, 2014).

Plumage aberrations have not been reported in the species previously, but SEIJ observed a bird with a single leucistic primary (Figure 2.13).

Figure 2.12: Typical light feathering observed on the belly, breast, axillaries and crural areas of Ethiopian Bush-crows (Sam Jones).

Figure 2.13: Ethiopian Bush-crow showing a single leucistic fourth primary; note the 'fork-tailed' appearance caused by rectrix moult, with the central pair dropped (*cf*. Figure 2.14) (Sam Jones).

Moult

A high proportion of trapped birds (80%, *n* = 57) were synchronously moulting and tending nests. Many of these were in an advanced stage of wing moult, indicating they had started their moult early in the breeding cycle. Moulting and breeding simultaneously is uncommon in birds, but has been reported in similar arid-zone species such as the Pale-winged Starling *Onychognathus nabouroup* (Craig, 2012) and the Southern Pied Babbler *Turdoides bicolor* (A. Ridley *pers. comm.*), of which the latter also breeds cooperatively. Such synchrony may be driven by physiological stressors, such as high temperatures, which, if greater during the non-breeding season, necessitate moulting during the breeding season.

Remex moult patterns are centrifugal as in most passerines, beginning with the greater coverts and moving from the first primary outwards, with secondary moult probably starting simultaneously with primaries 4–6. A lack of apparent pattern, however, was observed in rectrix moult in a large proportion of trapped birds, where in some circumstances up to three generations of feathers were present (Figure 2.14). The explanation is unclear, but is the likely cause of regular observations of Bush-crows displaying a fork-tailed appearance in flight (Figure 2.13). Rectrix moult was observed to be more uniform in some birds, however, commencing with the central pair.

Figure 2.14: Peculiar rectrix moult present in many Ethiopian Bush-crows captured in 2013, showing heavy wear and three separate generations of rectrices (Sam Jones).

The extent of post-juvenile moult is unknown, although both trapped individuals thought to be young from the previous season showed no moult limits or feather attributes normally associated with young birds (e.g. pointed tips to primary-coverts or rectrices). Considering the controlled and protected nest environment of the Bush-crow (Benson, 1942; Töpfer and Gedeon, 2012), juveniles may be able to take more time to grow better-quality feathers than other passerines, which they then retain for a protracted period before moulting into subsequent plumage. While uncommon in a passerine, this strategy would offer more effective thermoregulatory ability under high temperatures that appear to restrict their behaviour (Chapter 5), and would reduce metabolic stress in already physiologically challenging conditions.

2.1.6 Group dynamics

Breeding groups

Bush-crows breed co-operatively and several helpers tend active nests, although their specific roles and fidelity to nests are unknown. Benson (1942) noted that it was usual for three birds to tend a nest, but that there was no evidence for more than one female laying. Donald et al. (2012) observed three nest helpers (additional to the breeding pair) at each of four nests, while observations by Gedeon (2006) suggest that helpers may tend several nests simultaneously. However, PFD has observed a group where helpers visited several crudely constructed nests in between visiting one that was clearly active, so an alternative explanation is that helpers build ‘practice’ nests while tending ‘real’ ones. The same apparent ‘nest infidelity’ was observed on a couple of occasions by AJB & SEIJ in 2013 while observing colour-marked birds.

While undertaking behavioural observations on post-fledging groups (frequently containing colour-marked birds) in 2013 and 2014 (Section 2.1.7; Chapter 5), SEIJ and AJB observed at least 24 groups across eight sites for protracted periods. Modal group size was 9–10 birds, comprising 2–6 adults (all appearing to possess some role in post-natal care) and 1–5 juveniles. The ratio of adults to juveniles in each group varied from 6:1 to 3:4, although roughly equal proportions were most common. The high adult to juvenile ratio highlights the attentive post-natal care given to young birds by the group. The two smallest groups contained two adults and one juvenile. However, at least one of these groups was almost certainly not the product of bi-parental care as one of the adults had been caught and colour-marked attending a nest amongst a larger group. It is therefore possible that these observations pertain to birds defecting, or being expelled, from their original social group.

As noted by Gedeon (2006), these groups occasionally form larger flocks, or separate into sub-units while foraging, but the number of parent and tending birds appears stable within a group across multiple visits. While observing a nest in Dida Hara, KG observed a parent pair and two stable helpers, who were occasionally joined by a third individual. However, the latter was not well received by the parents, who even tried to prevent it from approaching the nest, perhaps indicating that genetic or social bonds may play a role in acceptance of helpers. Bush-crows are often observed playing with sticks, and the arrival of a bird at a nest with a stick is greeted by a cacophony of calling (Gedeon 2006; pers. obs.), suggesting that nest construction may be important in affirming group structure.

Non-breeding groups

During behavioural observations, SEIJ and AJB noted several small parties of up to eight adults (mode = 4–5) without chicks, with two observations of a lone adult. In 2013, many such groups included colour-marked individuals that had been trapped while attending nests, indicating that some helper birds may leave the group after the young fledge.

2.1.7 Post-breeding ranging behaviour

In 2013, 57 birds were trapped, measured and individually colour-marked. Active nests were identified by observing the birds’ regular flight paths and nest visits, and these were used to target breeding birds. Data on individual groups’ ranges were subsequently collected by SEIJ, broadly following a methodology outlined by Bowden et al. (2008): a set aspect (south) and distance (25m) to a focal bird was adopted and the group followed on foot by ‘shadowing’ the bird’s movements while the observer tracked the path using the ‘track’ function on a Garmin GPSMAP 62s unit. Coordinates were then adjusted by 25m north to assess ‘true’ movements.

The dispersal area from the nest for up to five weeks after fledging was measured for four colour-marked groups, followed on at least three separate days over at least a two-week period (Table 2.2).

These preliminary results indicate that at least some groups possess a high fidelity to the natal area. However, many groups with ringed birds were not relocated, particularly at the edge of the range near Dadim, where 18 birds were ringed but only two seen again during five days of searching. This is in keeping with reports given to KG, AJB & SEIJ by local people, in particular at the edges of the species' range, that birds are present in some seasons and absent in others, suggesting a degree of seasonal movement, as previously mentioned by other authors (Collar and Stuart, 1985; Dellelegn, 1993; Redman et al., 2009).

Table 2.2: Summary of group sizes, observation coverage and dispersal area for four post-fledging Bush-crow groups followed in 2013 by SEIJ.

Site	Group size (adult : juvenile)	Observation coverage	Total ranging area
Dida Hara	9 (4:5)	16 hours 29 minutes 5 days over 3 weeks	41.0 ha
Dida Tuyura	10 (5:5)	12 hours 33 minutes 4 days over 2 weeks	37.3 ha
Soda Plain	7 (4:3)	8 hours 40 minutes 3 days over 2 weeks	107.4 ha
Soda Plain	8 (4:4)	5 hours 43 minutes 3 days over 2 weeks	60.8 ha

Visits to the region since the 2013 ringing season have provided further evidence for site fidelity. In April–May 2013 57 birds were ringed at four sites: Dida Hara (*n* = 17), Dida Tuyura (*n* = 6), between Soda Plain and Madacho (*n* = 16), and Dadim (*n* = 18). In October 2013 PFD, NJC & MW resighted nine ringed birds at Dida Hara and six on Soda Plain: of the latter, three could be individually identified, and all were within 1.5km of where they had been caught. In April–June 2014, I observed nine ringed birds; at Dadim (*n* = 1), Dida Hara (*n* = 2), Dida Tuyura (*n* = 3) and Soda Plain (*n* = 3), all of which were within 2km of where they were ringed in 2013. These observations were made during opportunistic rather than systematic searching, and overall more time was spent in areas where birds had been caught, meaning that any dispersers would be less likely to be detected. Nonetheless, the sightings provide evidence that some birds are strongly site faithful.

A single observation suggests that Bush-crows may, occasionally, move around with other species. On 26th October 2013, PFD observed a single bird associating closely with a flock of Red-billed Buffalo Weavers *Bubalornis niger* (Figure 2.15). When the flock was disturbed (presumably by an unseen raptor) and flew off far and high, the Bush-crow accompanied them, despite the presence of a Bush-crow group foraging nearby.

Figure 2.15: Solitary Ethiopian Bush-crow taking flight with a group of Red-billed Buffalo Weavers (Paul Donald).

2.1.8 Interspecific interactions and behaviours

Predation

Gedeon (2006) reported observations of interspecific relations with potential predators, but, to date, known predators are few, although reports exist of a Tawny Eagle *Aquila rapax* opening the top of a nest (Collar and Stuart, 1985) and an Eastern (Pale) Chanting Goshawk *Melierax poliopterus* successfully plundering a nest (Töpfer and Gedeon, 2012). SEIJ observed a pair of Abyssinian Ground Hornbills *Bucorvus abyssinicus* apparently attempting to raid a Bush-crow nest in May 2013, although this was some time after the young had fledged.

Predation of a Bush-crow was observed for the first time by SEIJ on 3rd June 2013. Widespread alarm behaviour by a post-fledging Bush-crow group was elicited on detection of an Eastern (Pale) Chanting Goshawk, but the raptor managed to take a juvenile. On capture, the juvenile uttered a repeated distress call, attracting mass mobbing of the goshawk by other group members. This distress call was previously unknown, but first heard (and recorded) during the handling of birds in mist-nets (www.xeno-canto.org/140117).

Birds trapped in nets exhibited intriguing responses. Most initially gave the distress call described above, although some varied in their alarms, while a few remained relatively quiet. The distress call served quickly to attract other members of the group, many of which were also caught in the nets. After a short time, however, the remaining birds appeared to assess the situation and would skillfully fly around or over the net, sometimes perching on it, and occasionally mobbing SEIJ and AJB as they extracted caught birds (Figure 2.16). The distress calls acted as a stimulus to other species, commonly resulting in multiple-species captures, as was also the case from distress calls of other taxa.

Gedeon (2006) noted the confiding nature of Bush-crows, which do not scare easily at the sight of people. However, SEIJ and AJB found that, while some groups are easy to approach to within 5m, and will confidently forage around the feet of an observer, others are very wary, making approach closer than c.30–40m difficult, with one or more birds alarming and causing the group to fly off. Both response extremes were exhibited by colour-marked birds, so this does not seem to be an artefact of handling; nor did the presence of juveniles in groups appear related to degree of wariness. Possibly it simply reflects individual ‘personalities’, with wary birds producing wary behaviour in their groups, but our overall impression was that groups that nest close to villages were much more habituated to people.

Antagonistic behaviour

Bush-crows have been observed readily joining other species (most frequently Superb Starlings *Lamprotornis superbus*, White-crowned Starlings *Lamprotornis albicapillus* and Red-billed Buffalo Weavers) in mobbing snakes, including Puff Adders *Bitis arietans* on multiple occasions and a single cobra *Naja* sp. In 2013 SEIJ observed a Bush-crow group harrying a domestic dog, and we have watched groups initiate the mobbing of Grey Kestrels *Falco ardosiaceus*, Gabar Goshawks *Micronisus gabar*, Tawny Eagles and Pearl-spotted Owlets *Glaucidium perlatum* (SEIJ), and a perched

Verreaux's Eagle Owl *Bubo lacteus* (AJB); on the last occasion they were joined by single White-crowned and Superb Starlings. Despite this, Bush-crows did not respond to artificial snakes or owls, which we attempted to use as lures to nets.

Bush-crows have also been observed to respond to benign species. In 2013 SEIJ observed groups mobbing innocuous targets such as a Cape Hare *Lepus capensis*, while KG has observed Bush-crows taking an interest in large tortoises, hopping around them and even perching on their carapaces.

Figure 2.16: An Ethiopian Bush-crow, perched on the mist-net shelf, investigates how to free its companion from the net (Sam Jones).

Nest proximity to other species

Bush-crows occasionally nest close to other species. Of 250 nests, four were found in the same tree as a White-crowned Starling nest, two were among Red-billed Buffalo Weaver colonies, and once a single Bush-crow nest was in the same tree as a Black-capped Social Weaver *Pseudonigrita cabanisi* colony. This would seem beneficial if the birds utilise one another's alarm calls for protection.

Other species sometimes use Bush-crow nests. On 22 April 2013 SEIJ observed a pair of Shelley's Rufous Sparrows *Passer shelleyi* apparently tending an active nest in the base of an active Bush-crow nest. On separate occasions in 2013, I witnessed a Superb Starling and a White-crowned Starling perched at the entrances of old Bush-crow nests, and KG has observed both these species feeding their young inside old Bush-crow nests.

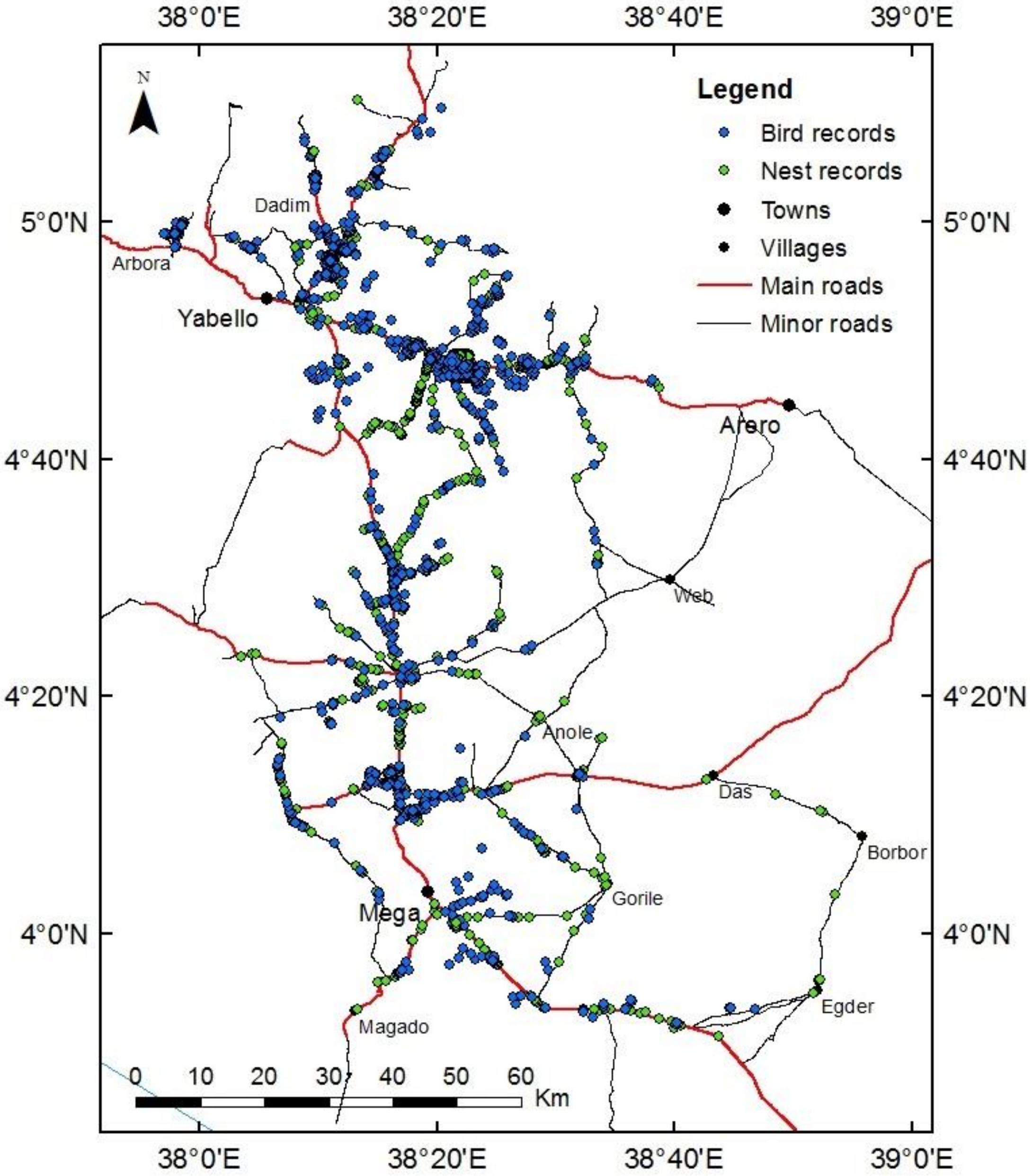
Kleptoparasite avoidance

Gedeon (2006) briefly reported a Bush-crow's avoidance of kleptoparasitism by a Northern Red-billed Hornbill *Tockus erythrorhynchus*. The Bush-crow was digging at the ground with its bill to extract food. The hornbill approached and waited next to the Bush-crow, seemingly ready to steal the prey. The Bush-crow ceased digging and flew a few metres away where it 'pretended' to forage. When the hornbill followed, the Bush-crow quickly flew back to the first point, took the prey from the exact spot where it had previously dug, and flew away, apparently having deceived the hornbill.

2.1.9 Range boundary changes

The global range of the Ethiopian Bush-crow is relatively easily defined (Figure 2.17), owing to the abundance and conspicuous nature of nests in the tops of trees (Donald et al., 2012). A range of hills with unsuitable habitat was believed to define the limit of the species west of Yabello, despite a stretch of seemingly suitable habitat along the Yabello–Consu road immediately west of the hills and a single record from the area in 1983 (Collar and Stuart, 1985). Benson (1946) reported that Bush-crows were absent west of Yabello, and this road has been regularly driven since 2005 without the species or its nests being encountered. However, on 11th April 2014, I was taken along this road to an area of woodland north of the village of Arbora, 16km north-west of Yabello. Here Abduba Huka, a local scout, had discovered Bush-crows three weeks earlier.

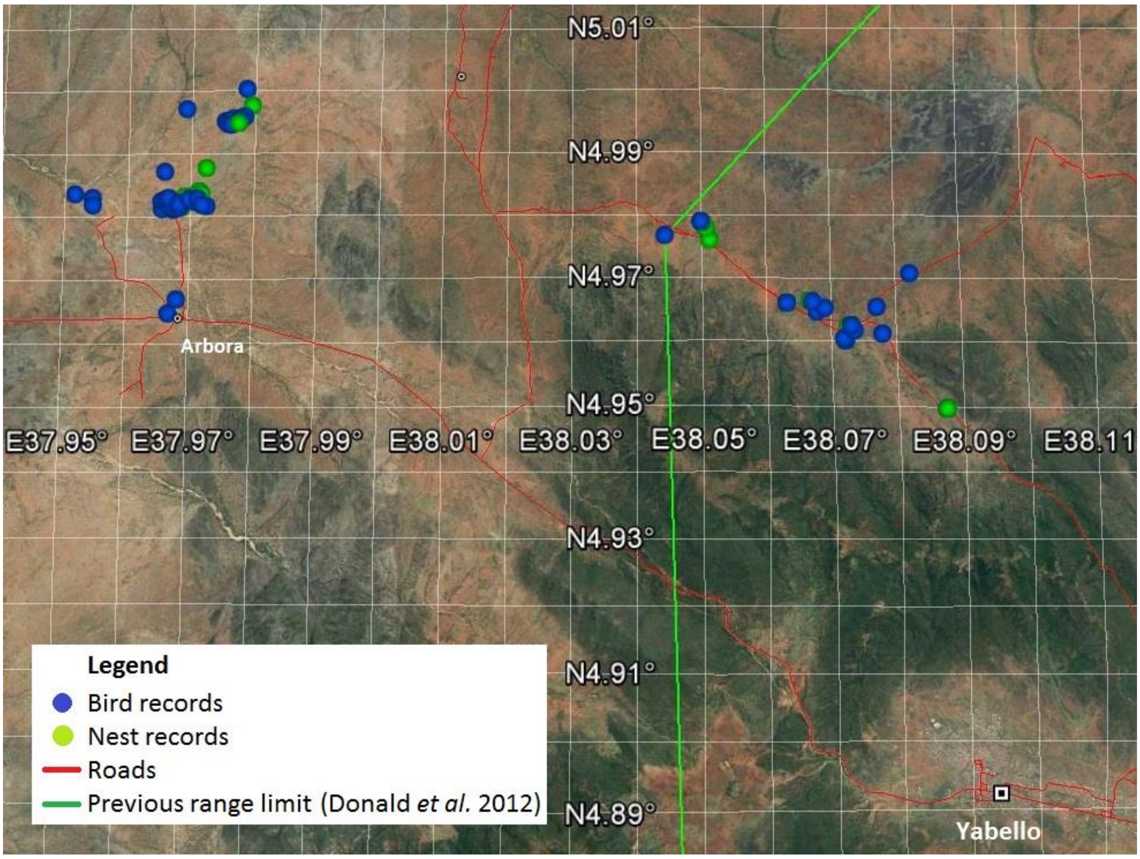
Figure 2.17: All Ethiopian Bush-crow records from 2005 to 2014, showing areas on the edge of the range where nests have been found, but birds have never been recorded. The extent of these records represents the species' apparent global range.



Thirty minutes of searching yielded three nests and at least two groups of birds. I returned to the area on four more occasions until the end of June, finding further nests and groups. Curiously the central area, which contained most of the nests, held birds on the earlier visits but not on later ones, when searching further afield led to the discovery of groups elsewhere, including right next to the main road at Arbora itself (Figure 2.18).

Birds have remained in the area since then (last seen on 13th April 2015; SB) and on 18th July 2014 a group was seen 5km south of Arbora (JD) but Abduba, who has worked at Arbora for four years, had never seen Bush-crows there before.

Figure 2.18: Locations of Ethiopian Bush-crows (blue dots) and their nests (green dots) found near Arbora in 2014 (western cluster), overlaid on GoogleEarth imagery. The eastern cluster contains records from 2014 and previous years, and the green line represents the previous range limit (Donald *et al.*, 2012). Red lines represent roads. Displayed units are decimal degrees. Source: GoogleEarth 4.942512° N and 38.028320° E. © 2015 Cnes/Spot Image. Image © 2015 DigitalGlobe. Imagery date: 02/02/15. Image accessed: 21/09/15.



There are other areas at the edge of the range where Bush-crow nests have been seen but birds have never been recorded (Figure 2.17, e.g. the Das–Egder road in the south-east). This suggests that there may be some fluctuation at the edges of the range, which is of particular interest given the species' close-fitting climate envelope (Donald et al., 2012). If the birds are indeed limited by some temperature-driven stressor, range expansions perhaps occur in cooler years when the birds are able to survive further from their core range, and this is when nests are built in places such as Arbora and Borbor. In hotter years the birds retreat from these areas, leaving their robust nests, which evidently survive a number of years, as indications of their former presence. Observations of the disappearance of large numbers of Bush-crows post-breeding from the edge of the range offer further anecdotal support for this hypothesis.

2.2 The White-tailed Swallow

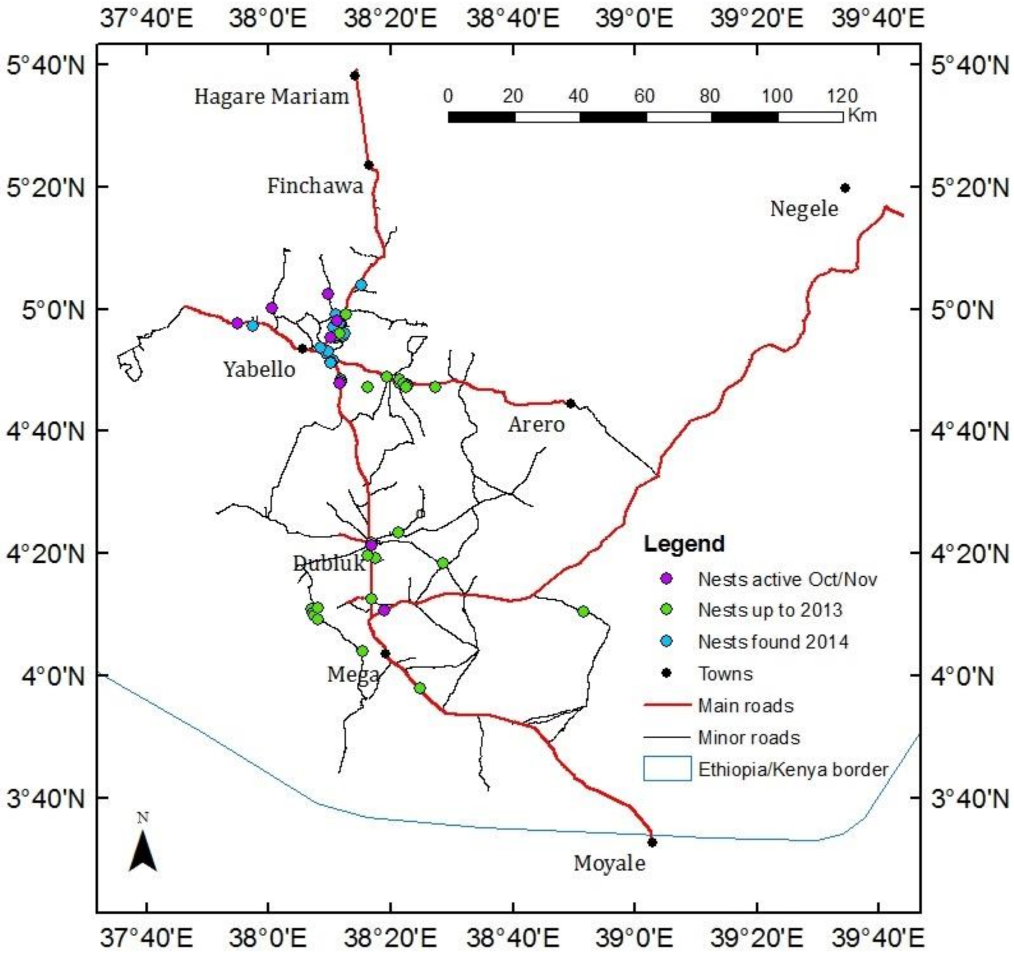
The White-tailed Swallow *Hirundo megaensis* is a globally threatened (Vulnerable) species restricted to c.5,500km^2 of *Acacia–Commiphora* savanna woodland around the towns of Yabello and Mega in southern Ethiopia (Benson, 1942; BirdLife International, 2016b; Collar and Stuart, 1985), with a few recent sightings from other places, notably the Liben Plain 120km to the east (Gabremichael et al., 2009). This tiny range largely overlaps with that of the Ethiopian Bush-crow (Endangered), which appears to be limited primarily by climate (BirdLife International, 2016a; Donald et al., 2012). The White-tailed Swallow is extremely closely related to the Pearl-breasted Swallow *H. dimidiata* of southern Africa, differing in mtDNA by only 0.7%, less than the genetic distance between many of the subspecies of Barn Swallow *H. rustica* (Dor et al., 2010).

The White-tailed Swallow was first described to science as recently as 1942, and it was not until 1996 that its nest was documented (Holtam, 1998). Despite, or perhaps because of, its highly restricted distribution, the White-tailed Swallow has remained understudied, with scant information on its abundance, behaviour and habitat preferences (Ash and Gullick, 1989; Mellanby et al., 2008; Syvertsen and Dellelegn, 1991). Over the past ten years numerous visits to the Yabello–Mega region by a number of people (Table A1) have been made to develop work on the Ethiopian Bush-crow, and between 2010 and 2014 a total of 67 White-tailed Swallow nests (2 in 2010, 11 in 2011, 9 in 2012, 11 in 2013 and 34 in 2014: Figure 2.19) have been found. Additionally, nine study skins kept at the Natural History Museum, Tring, UK (NHMUK) and one at the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK) were examined (TT). Here I document these findings.

2.2.1 Nest locations

Given that the Pearl-breasted Swallow breeds in mud huts, wells, animal burrows, buildings, bridges and rock faces (Harrison et al., 1997; Maclean, 1993), it might have been expected that White-tailed Swallows would utilise a similar breadth of locations. Benson (1946) suspected breeding took place in termite mounds, but Holtam (1998) found two nests with chicks in village huts in May, and a third in a deep well in September. In October 2000 a further four nests were reported in culverts under the main (Addis Ababa–Nairobi) road that bisects the species' range, and in October 2001 two pairs were seen frequenting a termite mound, one bird carrying food (Ash and Atkins, 2009). However, the observer has clarified that the birds seen at the culvert may not have been the builders of the nests seen, and that the birds seen at the termite mound may simply have been feeding there (N. Borrow *in litt.* 2008).

Figure 2.19: Study region, showing all White-tailed Swallow nest records to date. Nests found prior to 2014, those active in April and May 2014, and in October and November of any year, are highlighted.



Village huts

Traditional huts probably provide the most important nesting sites for the White-tailed Swallow. All but two of the 67 recent nests were built in Borana tribal domestic huts or their associated store huts, with one nest in 2010 found in a termite mound converted into a bread oven (see below) and one in 2013 against wooden beams in an isolated concrete building next to a water storage tank (Figure 2.20).

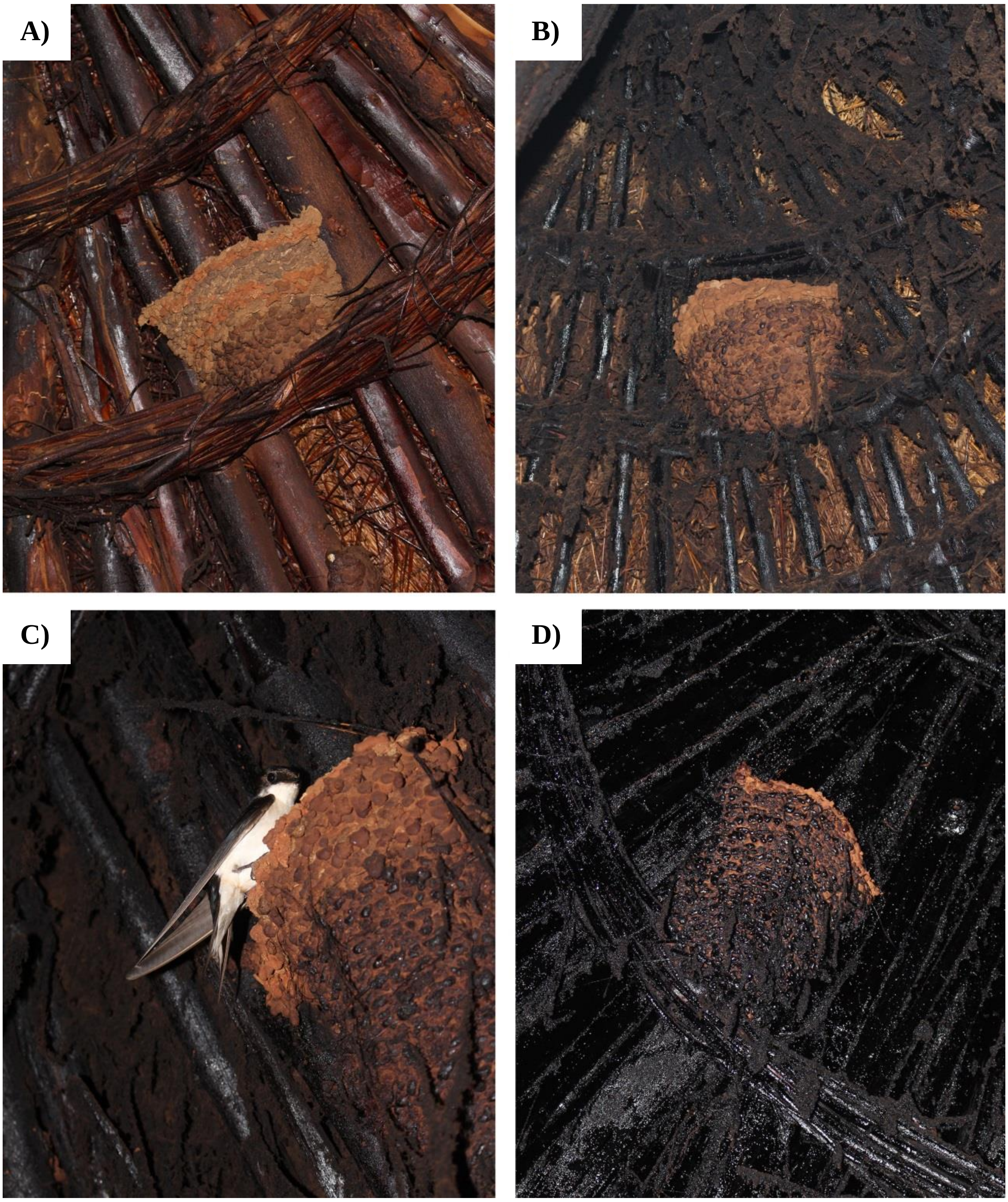
Figure 2.20: White-tailed Swallow nest found in April 2013 in a concrete building. This is the only nest record from a non-traditional human building, and it is noticeable that the nest is attached to the wooden beams (perhaps more akin to the sides of a termite mound or the thatching of a traditional hut) rather than to the horizontal corrugated iron roof (Andrew Bladon).

Borana huts are typically small, circular and constructed with wattle-and-daub style mud walls, a single doorway, and a low-pitched conical thatched roof supported by vertical beams and circular thatched joists (Figure 2.21). They are 2–6m in diameter, and 3–5m in height; domestic huts are generally larger than store huts. Doors (not always present) vary from a loose assembly of large sticks which roughly fill the opening to occasional solid structures with a frame. In all but the last case, access holes large enough for the adult swallows remain even when the door is closed. Occupied huts are usually solid and complete, whilst huts used for storing grain or housing animals are built to the same design but often with only partial daubing or thatching and looser doors, allowing easier access but less protection from the weather. Both constructions are numerous within villages, store huts accounting for 20–30% of the total number of buildings.

Figure 2.21: Traditional Borana huts are important nesting sites for the White-tailed Swallow. Huts number anywhere from five to a hundred per village and in the best places, such as on Dida Yabello plain, there may be one or even two White-tailed Swallow nests in each village (Andrew Bladon).

White-tailed Swallow nests are cups constructed from mud, typical of the genus *Hirundo*. The depth varies from 60 to 160mm (*n* = 28) (Figure 2.22), possibly related to the age of the nest (Section 2.2.4). Nests in huts were fixed to the circular joists of the roof construction, at heights of 2.5–4.5m (*n* = 28), normally built within a few joists of the top of the hut. It appears that White-tailed Swallows show a preference for nesting in huts occupied by people (31 nests in 2014), with only a few records from unoccupied store huts (three in 2014). In contrast, of ten Ethiopian Swallow *H. aethiopica* nests found during the same search in 2014, only two were within occupied huts and eight within store huts, a statistically significant difference ($\chi^2 = 20.8$, d.f. = 1, $P < 0.001$). This is consistent with observations of Ethiopian Swallow nests from previous years (KG, TT).

Figure 2.22: White-tailed Swallow nests of different ages. *A*) New nest in a newer hut with a clean roof. *B*) Old nest with a second layer of paler mud at the top. *C* & *D*) Older nests (here 3 and 5 years old) are deeper in construction, and the lower, older, part is blackened by carbon deposits from the hut's fire. Carbon deposits can also be seen hanging from the ceilings of these huts. This suggests the birds re-use nests from year to year, with some mud being added in later years (Andrew Bladon).



Within the core range at the right time of year (Section 2.2.3) one can walk into a village and ask for '*mana raaree*' (swallow nests) and be led straight to one, or at least directed to the next village where one can be found. On the edges of the range, however, for example the three villages where nests were found west of Yabello in 2014, people showed little awareness of the birds and frequently only the owners of the hut that actually contained the nest were conscious of the birds' presence. This is intriguing, as the Borana do not distinguish between species of swallow, '*raaree*' being their term for any hirundines or bats, but perhaps it is simply because other species nest less frequently in village huts. The same search effort in 2014 yielded only ten nests of Ethiopian Swallow, suggesting a lower density of birds, while Lesser Striped Swallows *Cecropis abyssinica*, which are common across the region, seem to nest only on concrete structures (local clinics, schools or culverts under the road) and in caves (AJB, KG, TT). Indeed, in the same region west of Yabello, I was regularly pointed towards road culverts when asking for '*raaree*', only to find *Cecropis* nests with their distinctive funnel entrance (Winkler and Sheldon, 1993).

There is much variation in local people's responses to swallow nests in their huts. Those who identify them as swallows view the nest as a sign of good luck, while those who mistake them for bats say they destroy the nests because the droppings can cause blindness. These attitudes can be split even within a village, with one lady telling me that she had kept the nest despite what her neighbours said, and was glad when the birds produced chicks.

Termite mounds

It is almost 70 years since Benson (1946) suggested that the White-tailed Swallow might nest in termite mounds, but little evidence for this ever accumulated. Birds have been seen frequenting them (Borrow, 2001; Collar and Stuart, 1985), but on only three occasions have nests been suspected or found within them. On 14th November 2007 a pair of swallows was seen entering a 40-cm-wide west-facing ground-level cavity in a 3m-tall termite mound south of Dubluk, the birds each time remaining inside for over a minute; to avoid disturbance no attempt was made to investigate further (B., W. & S. Oosterbaan *in litt.* 2010). On 20th November 2008 a nest was found stuck to the side of a large hole at the base of a broken-off termite mound on Soda Plain; it was not possible to see whether the nest was active (SR; Figure 2.23). On 3rd June 2010, in a village near to Dida Hara, an active nest was found inside an old termite mound which had previously been used as a bread oven by the villagers. The entrance to the mound was about 0.75m wide at the base, 0.9m in height, and shaped like a truncated triangle. The cavity inside was roughly 1×1×1m, with a circular base and a domed roof. The nest was fixed to the roof of the dome (Figure 2.24).

Figure 2.23: White-tailed Swallow nest inside a termite mound on Soda Plain, found by a Sunbird tour party in November 2008 (Les Colley/Sunbird).

Nesting in termite mounds, which are presumably ancestral nesting sites for the species, is thus proven, but given the relative difficulty of locating these nests (unlike nests in huts, they are not noticed by local people) it is impossible to judge whether nesting in huts or termite mounds is more frequent. However, the abundance of huts across the species' range, the lack of occupation of termite mounds searched in 2014 in areas where the birds were nesting in huts, and the apparently low frequency of suitably sized cavities within termite mounds combine to suggest that hut nesting is much commoner.

Total White-tailed Swallow nest records now number 72: 62 in village huts, five in store huts, three in termite mounds, one in a remote water storage building and one in a well. Nest records come from across the core of the bird's range (Figure 2.19), but there are still none from the Liben Plain.

Figure 2.24: An old termite mound, previously used as a bread oven by villagers, in which a White-tailed Swallow nest was found in June 2010 (Nigel Collar).

2.2.2 Observations at the nest

In 2014, I conducted a detailed study of White-tailed Swallow nesting behaviour (Chapter 7), and the observations described here relate solely to the 23 nests involved. The 11 other nests found in 2014 were either inactive (five) or inaccessible (six; too high to inspect safely or further entry to hut refused). In the case of inactive nests, the lining, presence of old eggs, and frequently the visiting or proximity of adult birds made me confident that each belonged to White-tailed Swallows. The nests were lined with grass and animal hair and the eggs were pure white, as in the Pearl-breasted (Schmidt, 1959) and Pied-winged Swallows *Hirundo leucosoma* (Fry et al., 1992). This allows easy distinction from Ethiopian Swallow nests, whose eggs are speckled chestnut (Grant and Lewis, 1984) (Figure 2.25). In only one instance were a few feathers found in a White-tailed Swallow nest, whereas they are observed occasionally in nests of Pearl-breasted Swallow (Maclean, 1993), and all ten Ethiopian Swallow nests found in 2014 were lined with feathers. Clutch size was three in nine nests and four in ten (the four others were only seen at the chick stage: two with four small chicks, one with two large chicks, and one with one large and one dead chick). The clutch size appears to be larger than in Pearl-breasted Swallow, for which two or three eggs are common but four is unusual (Fry et al., 1992; Maclean, 1993).

The incubation period was 16–17 days (*n* = 5), as in the Pearl-breasted Swallow (Schmidt, 1959). In at least five nests, which were seen within the first two days after hatching, one chick had clearly hatched a day or two after the others, while in a further nine nests (first seen slightly later) the same notably small chick remained the runt throughout development, and often fledged a day or two later, if at all. This matches the asynchrony reported in Pearl-breasted Swallows (Schmidt, 1959; Turner, 2004). In the remaining nine broods no asynchrony was evident, suggesting that either it does not always occur or some catch-up growth can redress a size difference. This asynchrony and its absence were observed in both three- and four-egg broods, suggesting that it is unconnected to clutch size.

Figure 2.25: A comparison of *A*) White-tailed Swallow and *B*) Ethiopian Swallow nests. White-tailed Swallows lay three or four pure white eggs in a simple grass- and hair-lined cup, while Ethiopian Swallows add a thick padding of feathers and lay one to four speckled eggs (mode = four) (Andrew Bladon).

2.2.3 Breeding season

The main breeding season of White-tailed Swallows is April–June (Turner, 2004), and the 23 active nests under study were found from early April through to late May 2014, following the start of the rainy season in March. When re-checked in June, none of these nests was active, suggesting that the birds do not lay a second brood. Several broods were found in early June in previous years (2010, 2011 and 2013), presumably because the rainy season started slightly later (in 2013 it began in early April). In contrast, three of the ten Ethiopian Swallow nests were active again in June 2014, all three having been among the earliest Ethiopian Swallow nests to fledge their first brood, although none earlier than the first White-tailed Swallow nest to fledge. In addition, one White-tailed Swallow nest had been lined with feathers and contained an Ethiopian Swallow brood. Intriguingly, this nest was in a hut which, although occupied, was in severe disrepair and intermediate in construction between the domestic huts favoured by White-tailed Swallows and the store huts favoured by Ethiopian Swallows.

In addition to the records from November 2007 and 2008 (Section 2.2.1), two active White-tailed Swallow nests were found on 17th November 2012 at Derito (AJB), two in October 2013 near Dida Tuyura and Dadim (PFD), and three in October 2014 at Areri, Elwayaa and Dida Yabello (JD) (Figure 2.19). The three 2014 nests were all seen with eggs or chicks. These breeding attempts are presumably a response to the smaller rainy season which occurs at this time of year (EWNHS, 2001), and their distribution across different years and much of the range suggests that there is a second breeding season, although whether individual birds breed in both seasons is unknown. However, two of the three October 2014 breeding attempts were in nests that had also been used in May 2014, and the third was in a nest found in May which was not active but did have two adult birds visiting, and which the villagers reported had been used during the previous rains. This suggests that the same pairs were using the same nests in each of the two breeding seasons.

In contrast to the White-tailed Swallow’s single brood per breeding season, the Pearl-breasted Swallow has two or even three (Schmidt, 1959). In Europe, in Great Tits *Parus major* the success of a second brood is negatively affected by the size of the first, favouring first brood reduction (Lindén, 1988). The observed larger clutches of the White-tailed compared to the Pearl-breasted Swallow (Fry et al., 1992; Maclean, 1993) might therefore be expected if the White-tailed Swallow is only able to breed once per season, compared to the Pearl-breasted Swallow’s twice (Schmidt, 1959). In House Sparrows *Passer domesticus*, clutch size also increases when the adults’ probability of survival until the next breeding attempt (which is a function of time between broods) is reduced (McGillivray, 1983). The time between the White-tailed Swallow’s April and October breeding seasons is greater than that between the Pearl-breasted Swallow’s first and second broods within a season, so again the larger clutch size in the White-tailed Swallow might be expected.

2.2.4 Nest re-use

The same nests appear to be used over several years. A number of villagers in April and May 2014 told me that the birds had nested in their huts previously. Three were reportedly new nests, two of which I saw in the process of construction, but another nest was two years old, two were three years old, and one was reported to be five years old (Figure 2.22). Additionally one nest, active in both April and October 2014, was again found active in April 2015 (SB). The re-use of old nests is known in Barn and Pearl-breasted Swallows (Møller, 1990; Turner, 2004), and evidence of this in White-tailed Swallows is further supported by the fact that active nests become blackened with carbon deposits from the hut fire, often with a noticeably lighter, and therefore presumably newer, layer or two of mud at the top of the nest (Figure 2.22). The colour variation and presence or absence of blackening at these nests suggests that nests in huts with fires visibly darken, and this should allow at least crude age estimation.

Nest re-use between seasons is perhaps a strategy to compress the breeding cycle. If the birds are limited to a shortened breeding season following each rainy season, with only time to produce one brood, then the saving of two to four weeks spent building the nest (Schmidt, 1959; Turner, 2004) might significantly increase the chances of success. Alternatively, it may allow the birds to breed even if there is a shortage of mud following a poor rainy season. The simple grass and hair lining found in White-tailed Swallow nests, and the preference for occupied huts with smoking fires, is perhaps a strategy to reduce parasite build-up between years which would otherwise hinder the re-use of old nests (Møller, 1990). The implication of this is that one or both members of the pair return to the same nest in subsequent breeding attempts, but the degree of nest-site fidelity in White-tailed Swallows is a subject for further research.

2.2.5 Behaviour around the nest

White-tailed Swallows appear to be well habituated to humans. They pay little attention to people going in and out of nest huts, and will even squeeze through a partially covered door to enter a hut full of people. Feeding rates by the pair can reach four or five times per minute, although occasionally the nest is not visited for up to half an hour (broods aged 8–14 days). When resting, the adult birds often perch on the *Acacia* fences constructed by the villagers as cattle corrals, favouring those closest to their nest hut. Juveniles also frequent them after fledging, whilst they are still being fed by their parents (Figure 2.26). Several villagers reported that the young birds continued to sleep in the nest for up to six nights after fledging, although this was clearly not always the case as at least four broods did not return after fledging.

While attending the nest, the male occasionally gives a burry, hard but quiet *tetch*, apparently as a kind of contact call. On one occasion, at the nest in the old bread oven in 2010, a brisk, anxious, slightly sparrow-like *tsswis* was repeated rapidly but irregularly by the male when a dog went near to the entrance to the cavity (NJC); this was evidently an alarm call. These two calls appear to be the first reported for the species.

Figure 2.26: Post-fledging juvenile White-tailed Swallows spend their first few days in the vicinity of the nest, often perching on *Acacia* fences whilst being fed (Andrew Bladon).

2.2.6 Sex identification and juvenile plumage

Tail colour

As originally established by Benson (1942), males can be told from females by the greater extent and brighter colour of the white on their tails. The amount of white in the tail is shaped by the extension of greyish-black fringes on individual rectrices (Figure 2.27). However, in the field, individuals with less conspicuously white tails may also be juveniles. Late-stage nestlings and recently fledged juveniles were found to have broad greyish-black fringes to their rectrices, producing a much darker overall appearance of their tails even than females. In particular, the innermost tail feathers (R1) are completely greyish-black without any white. The other five pairs of rectrices have substantial white on their inner vanes while their outer vanes and tips are greyish-black. On the outermost rectrix (R6) the white is reduced to a smaller spot on the inner vane (Figure 2.27). This can make the separation of juvenile White-tailed and Ethiopian Swallows in flight difficult.

Young birds studied in 2014 showed a marked difference in the development of white in the tail from day 16 onwards, and this was also noticeable in the juvenile skins. This could be individual variation, but might also reflect the sex of the birds.

Tail length

Sexes and age classes differ in tail length (Turner and Rose, 1989) and furcation. In adult males in NHMUK, the tails are longer than in adult females (mean = 60.4mm and 53.5mm, *n* = 4 and 1 respectively, male range = 59.0–61.5mm) owing to the extension of the outer rectrices, which leads to more pronounced furcation (mean = 23.1mm and 14.0mm, male range = 21.0–26.0mm). Pearl-breasted Swallows show a similar sex difference in tail length (Benson, 1949) and range of lengths (Maclean, 1993). Size differences between the sexes in White-tailed Swallows are visible in the field, with male outer rectrices protruding beyond the tips of the folded wing, while in females these are shorter than the wing-tips (Figure 2.28). Tails of juveniles are even shorter than those of females (46.3mm, *n* = 3) but do not seem to differ between the sexes.

General coloration

While the different tail patterns are visible at reasonable distances in flying birds, we found it nearly impossible to distinguish the sexes by overall coloration. Redman et al.

(2009) stated that females are duller than males, a fact confirmed only under exceptionally favourable conditions, e.g. when pairs are seen at close range sitting next to each other (Figure 2.28). It is too slight a difference to be useful in the field.

On the other hand, juveniles can be told from adults in the field by their dull brownish head colour clearly contrasting with the glossy bluish-black of the back (Figure 2.29), such that juvenile White-tailed Swallows could be mistaken for Grey-rumped Swallows *Pseudhirundo griseopyga*. As with the tail coloration, there is marked individual variation in the extent of the gloss in juveniles, in particular in the wings, which might be related to sex. In adults the head is the same glossy bluish-black as the back and wings. Thus ‘immature browner’ (Redman et al., 2009) seems to apply only to the head and wings, as other differences in plumage gloss are hardly visible in the field.

Figure 2.27: Variation in tail shape and coloration with age and sex of the White-tailed Swallow. *A*) Male, showing more white in the tail and longer outer rectrices. *B*) Variation in tail feather pattern between individual inner rectrices of different males. *C*) Female, lacking streamers and with less white than the male, particularly in the inner rectrices. *D*) Juvenile, similar to female with slightly smaller white patches and still shorter outer feathers (Stefanie Rick and Till Töpfer).

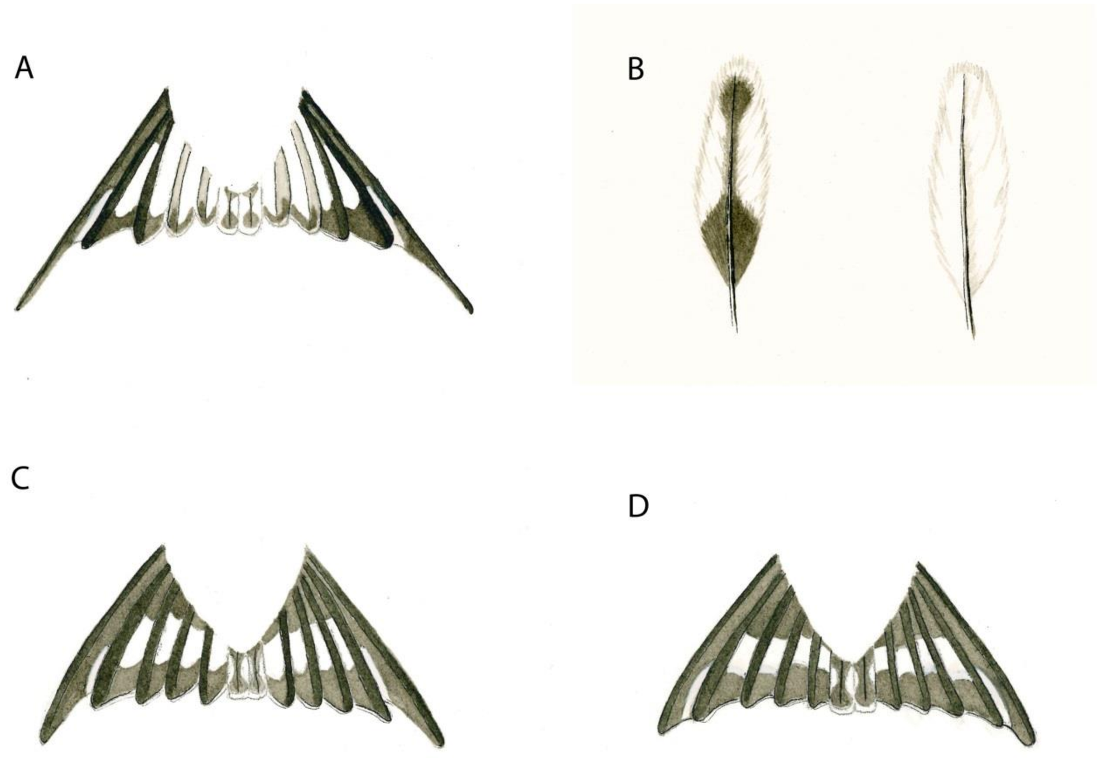


Figure 2.28: A comparison of *A*) adult male and *B*) adult female White-tailed Swallow plumage (Kai Gedeon).

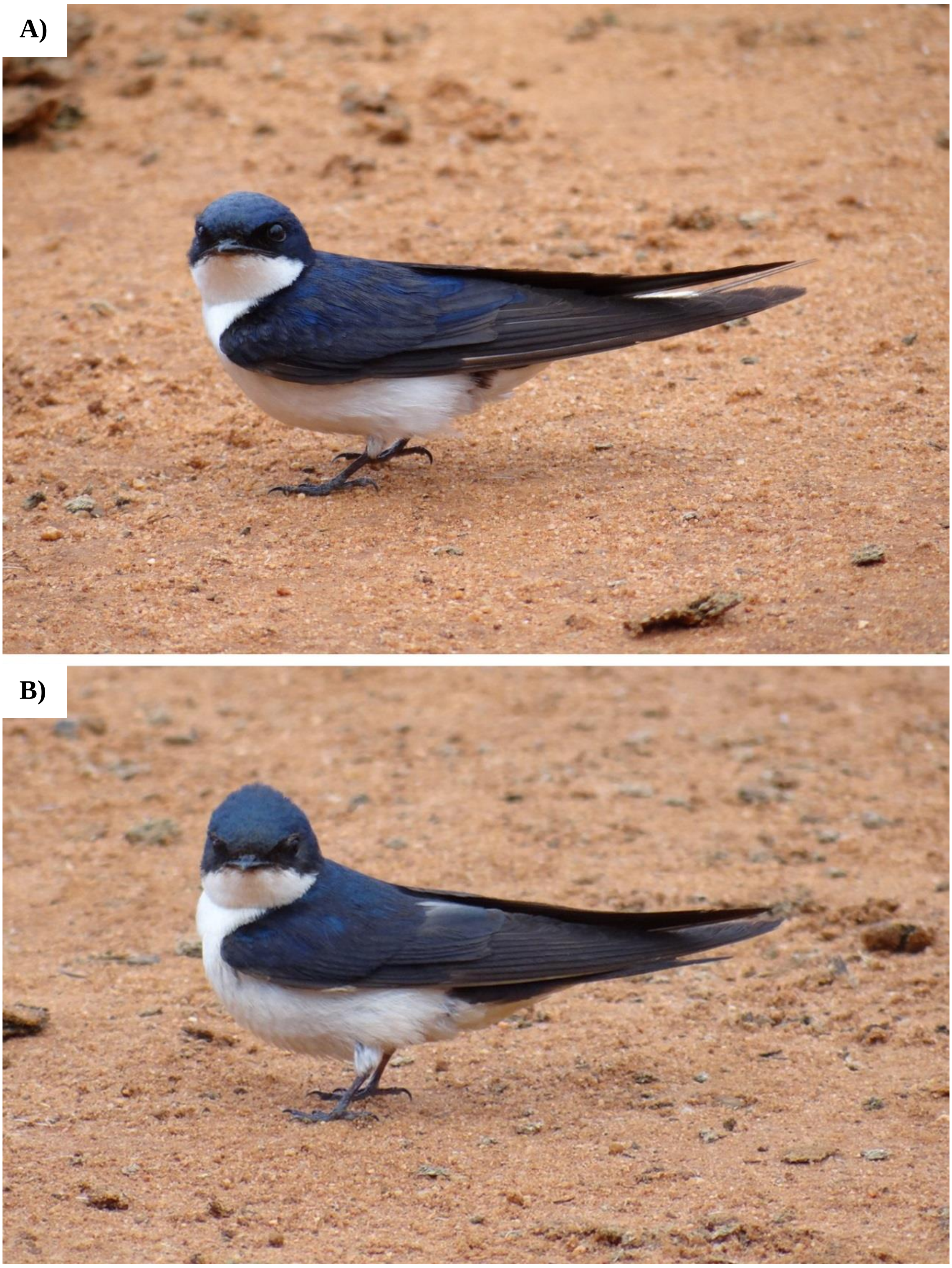
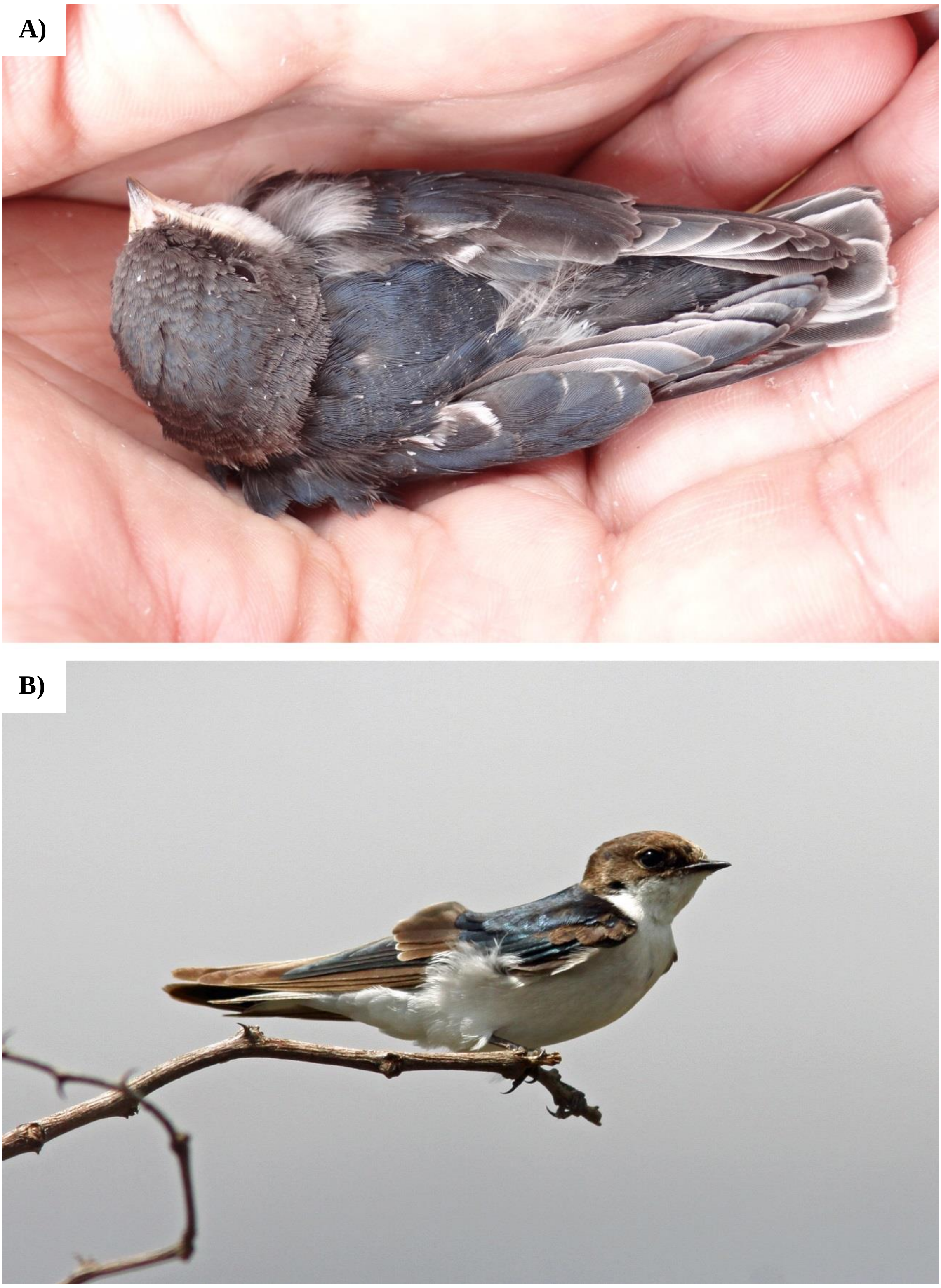


Figure 2.29: White-tailed Swallow *A*) nestling and *B*) juvenile, with browner head and wings than the adult (*cf*. Figure 2.28). Tail feathers of young birds have whitish fringes; the white windows on the inner vanes of tail feathers 2–6 are concealed by overlying feathers (Kai Gedeon and Paul Donald).



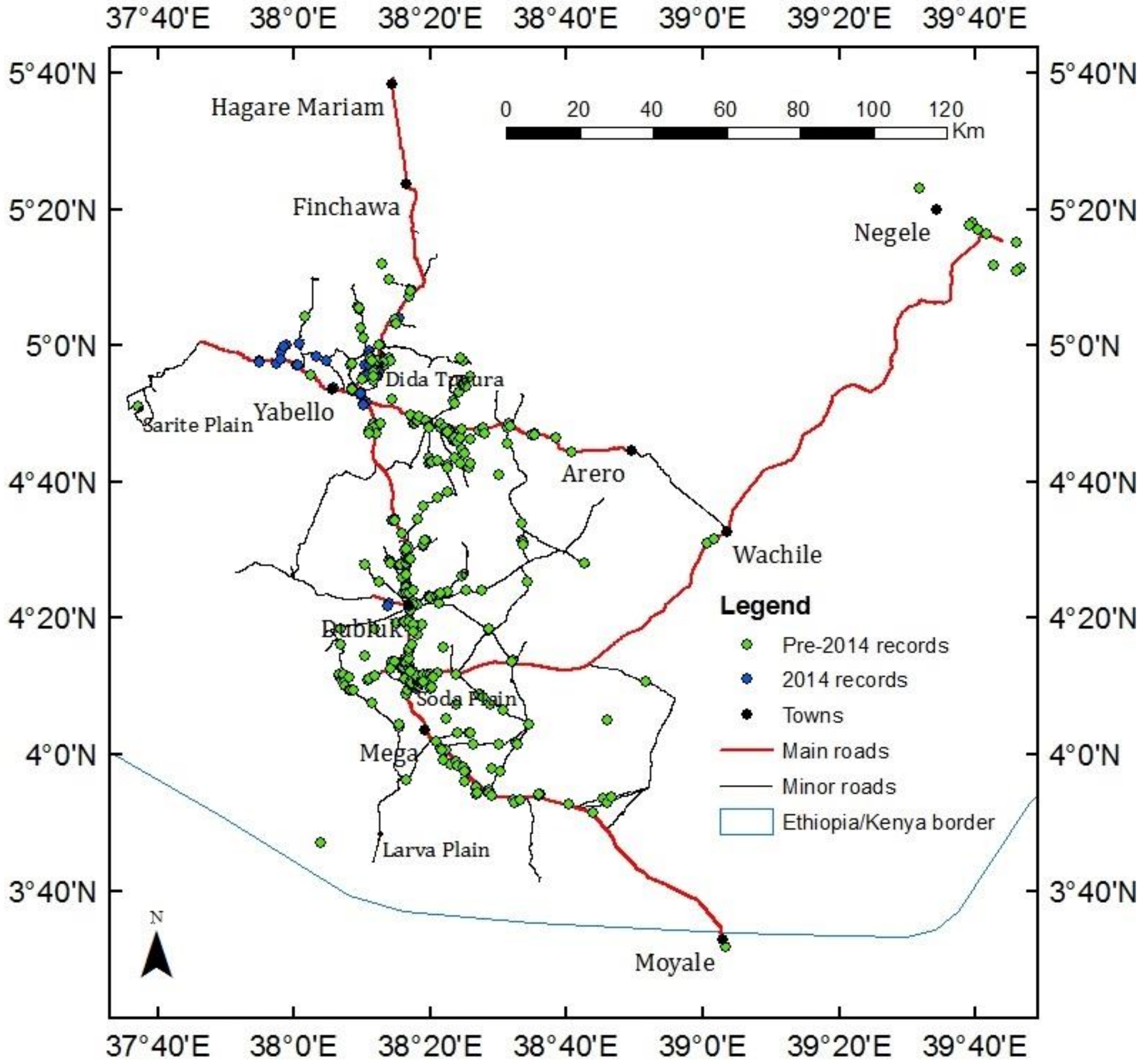
2.2.7 Sociability

The White-tailed Swallow is most frequently observed alone or in pairs, although groups of up to eight have previously been reported (Ash and Atkins, 2009). While nesting, pairs are easy to come by around the nest site, the frequency of visits suggesting they forage mostly around the village and its associated livestock. Elsewhere, single birds and pairs may be encountered at any time, but like the Pearl-breasted Swallow they are inconspicuous (Schmidt, 1959), and typically disappear as quickly as they appear. They favour open grassland and less dense *Acacia* woodland, particularly areas frequented by cattle herds or wild grazers. They are seen less commonly over *Commiphora*-dominated bushland, and do not occur amongst the denser broad-leaved *Combretum–Terminalia* woodland, which contrasts with the broader range of habitats reported for the Pearl-breasted Swallow (Mellanby et al., 2008; Turner, 2004).

A number of sightings have also been made of larger, probably post-breeding flocks, which seem to contain a high proportion of immatures, and presumably occur in response to insect swarms on which the birds forage. Two favoured sites are the Borana cattle ranch at Dida Tuyura, 15km north-east of Yabello, and Soda Plain immediately north of the Mega massif (Figure 2.30). Both sites offer an open landscape with larger *Acacia* trees and frequent grazing herds. Flocks of up to 10–20 White-tailed Swallows were seen at both of these sites on a number of occasions in the last hour or so before sunset during May and June 2013 and 2014. On one evening a mixed flock of White-tailed, Ethiopian and Barn Swallows was seen at Dida Tuyura. These birds fed over open ground at 3–15m, with up to 20 birds at a time resting in the shade of the canopy of a couple of large trees. The numbers of each species were impossible to determine, but the total number of birds was at least 50. A similar, though smaller, mixed flock was also seen on the morning of 14th April 2014 on Dida Yabello plain.

However, flocking in these and other locations is not confined to evenings. A large flock of around 50 White-tailed Swallows, conceivably more, was present on a hot sunny afternoon on 3rd June 2010 on Soda Plain, hawking insects 5–20m above the ground and perching temporarily in the shaded outer subcanopy of a couple of trees, on the opposite side from the sun. The trees held up to 10 birds at any point, a high proportion of them juveniles (NJC). On the morning of 17th November 2012, another flock of around 50 White-tailed Swallows was seen perhaps 30m high over open grassland on the main road south of Dubluk, shortly before the village of Madacho. Within ten minutes they had all disappeared.

Figure 2.30: All White-tailed Swallow records up to 2014 with available or derivable GPS co-ordinates. In 2014 the species was observed regularly west of Yabello for the first time.



2.2.8 Further sightings from the Liben Plain

The occurrence of the White-tailed Swallow on the Liben Plain, south-east of the town of Negele, was first reported by Gabremichael et al. (2009) (Figure 2.30). Since then, a number of other records have been made, summarised here. A bird was seen on a transect across the western end of the Liben Plain on 23rd May 2009 (MG). In February 2010, MW observed birds in an area of cleared scrub and ungrazed grassland in the south-east scrub/grass ecotone of the Liben Plain, and at least five birds were seen at the same site on 5th June 2010 (MW, PFD, NJC). A single bird was seen a few miles north of Negele on the road to Kibre Mengist, again in 2010 (SR). On 22nd November 2012, PFD, YD and REG had two sightings of a single bird on opposite sides of the Liben Plain. On 3rd July 2013, YD observed two birds in the south-east of the plain, close to the area where they were seen in 2010. Finally a bird was reported in the area on 3rd December 2014 (E. Williams in *Bull. ABC* **22**: 104). Birds have also been seen on one occasion just west of the town of Wachile and at nearby Melka Guba (MG), halfway along the road from Mega to Negele.

The frequency of sightings from the Liben Plain, covering all but one year from 2005 to 2014 and across eight months (October–February and May–July), show that the species occurs regularly in the area. It is unclear, however, whether these birds represent a resident breeding population (seven immatures were seen on 31st October 2006: Gabremichael et al. 2009) or if there is some movement between the core range and the plain. Solitary sightings from beyond other range edges at Sarite Plain (Syvertsen and Dellelegn, 1991), Larva Plain (Ash and Atkins, 2009) and near Moyale (Thouless, 1996) suggest that some wandering occurs, which is perhaps unsurprising for a hirundine (Figure 2.30). The records from Wachile may be the first evidence of birds moving between Yabello/Mega and Negele, or an indication that in fact the species is found continuously between the two sites but remains undetected owing to a low density of birds and the lack of search time invested.

2.2.9 Conservation

Traditional Borana huts clearly provide an important nesting site for the White-tailed Swallow, which appears not to utilise larger, more modern buildings, unlike the Pearl-breasted Swallow (Maclean, 1993). This may be due to displacement by larger hirundines (Harrison et al., 1997), but it certainly cannot be attributed to a lack of tolerance of human disturbance, which may affect other species (Turner and Rose, 1989). Across the range the maintenance of traditional houses, with thatched roofs and loose door assemblages, is clearly important for breeding success. Community engagement is also important with respect to recognition of the birds. Mistaken identification of the birds as bats can lead to nest destruction, so initiatives by the National Park authority to raise awareness of the birds may serve to assist conservation efforts.

3 INTRODUCTION TO THE STUDY REGION AND GENERAL METHODS

"Your Borana name is Roba, because you come when it rains."

In this chapter I present an introduction to the ecology of the study region, the Borana rangelands of southern Ethiopia, alongside general methods for preparatory work and analyses relevant to multiple later chapters, predominantly Chapters 4 and 6. Where necessary, reference is made between this and later chapters to guide the reader between methods and results.

3.1 The Study Region

3.1.1 Location

The Ethiopian Bush-crow *Zavattariornis stresemanni* and White-tailed Swallow *Hirundo megaensis* are endemic to the Borana Zone, in the Oromiya region of southern Ethiopia (Figure 2.1 andFigure 3.1) (Collar and Stuart, 1985). The Borana rangelands, within the Borana Zone, lie at an altitude of 1,430-2,000m (Tilahun et al., 1996), between the higher foothills of the eastern Rift Valley to the north, and the lower plains through the Kenyan border to the south. The rangelands consist of dry, semi-arid *Commiphora* scrubland and open *Acacia* woodland at lower altitudes, with broadleaf species such as *Juniperus* and *Olea* becoming more common in the higher areas

(Mellanby et al., 2008; Tilahun et al., 1996), such as the hills west of Yabello and north of Mega. The vegetation is typical of much of the Horn of Africa (Friis et al., 2011). The areas around both Yabello and Neghelle receive two annual rainy seasons, the first between April and May, and the second, shorter and less intense, in October. Mean annual rainfall is around 700mm, while temperatures range from a 13^{o}C to 25^{o}C (mean 19^{o}C) (Tilahun et al., 1996).

3.1.2 Protected Area Status

The Bush-crow's and Swallow's ranges are to the east of the Rift Valley, bounded by the towns of Yabello to the north-west, Mega to the south, and Arero (Metagefersa) to the east (Donald et al., 2012). Yabello and Mega lie on the main road running between Addis Ababa and Nairobi, which provides the main infrastructure through the region.

The Yabello Wildlife Sanctuary, east of the main road and north of Yabello (38^{o}25'E, 04^{o}55'N), was set up to protect the Swayne's Hartebeest *Alcelaphus buselaphus swaynei*, although few have been found there since 1970 (EWNHS, 2001). The wider Borana Zone, generally south of the Sanctuary, is also designated as a Controlled Hunting Area (Ash and Atkins, 2009). The reserve is presently best known for harbouring the Bush-crow and Swallow, along with 25 mammal species (EWNHS, 2001) including Burchell's Zebra *Equus quagga burchellii*, Gerenuk *Litocranius walleri* and Grant's Gazelle *Nanger granti*, and at least 210 bird species, of which 63 are unique to the Somali-Masai biome (Ethiopian Wildlife Conservation Authority, 2016; EWNHS, 2001). Recently, another global endemic has been added to the species list, with the rediscovery of the Black-fronted Francolin *Pternistis atrifrons* near to Mega (Töpfer et al., 2014).

The Southern Ethiopian Highlands are classified by BirdLife International as an Endemic Bird Area (Stattersfield et al., 1998) owing to the presence of five (now six) restricted range species: the Liben Lark *Heteromifrafa sidamoensis*, Prince Ruspoli's Turaco *Turaco ruspolii*, Nechisar Nightjar *Caprimulgus solala*, as well as the Bush-crow, White-tailed Swallow, and Black-fronted Francolin. Two species from the Jubba and Shabeelle Valleys EBA, African White-winged Dove *Streptopelia reichenowi* and Juba Weaver *Ploceus dicrocephalus*, also occur within the Borana Zone (Ash and Atkins, 2009).

In 2014, the Yabello Wildlife Sanctuary was officially upgraded to the Borana National Park, and its boundaries extended to incorporate a number of other important, though disconnected, sites; including Soda Plain just north of Mega, and Sarite Plain to the west along the road to Consu (Ethiopian Wildlife Conservation Authority, 2016).

3.1.3 Human Impacts

The Borana are traditionally pastoralists, grazing herds of cattle across the rangelands and moving them in response to the rains (Bassi, 2002; Cossins and Upton, 1987). Owing to the unpredictability of the rainfall, and the relative frequency of droughts, the Borana '*gaadaa*' management system was used to ensure that areas were grazed systematically, and that some land was left as an insurance against periods of drought. The importance of water in the region can be seen in the ceremonies surrounding the '*tuulaa*' (or singing) wells, dug deep into the ground at sites across the region to ensure a continual supply of ground water for both people and cattle (Bassi, 2002).

The traditional rangeland management by the Borana creates the habitat structure (Tefera et al., 2007a) which appears to be favoured by both Bush-crows and Swallows: open short grassland with isolated tall trees for nesting (Donald et al., 2012), or park-like *Acacia-Commiphora* woodland (Gedeon, 2006; Mellanby et al., 2008). This landscape is probably similar to those modified by wild ungulates and elephants prior to pastoralism (Vera, 2000).

The human population of the region has grown steadily, in part due to natural population growth, but also because of displacement of people from elsewhere in the country throughout the last century, and the associated expansion of the main towns, particularly Yabello (Bassi, 2002; Solomon et al., 2007). This has led to increased pressure on the land for both grazing and tillage, the latter having been increased in an attempt to diversify and stabilise pastoral livelihoods (Elias et al., 2015; Solomon et al., 2007). Both towns (Bassi, 2002) and crops (Solomon et al., 2007) have predominantly taken over more fertile and wetter areas traditionally reserved for drought periods, reducing the resilience of traditional pastoral livelihoods to extreme events (Elias et al., 2015).

Land cover changes across the rangelands over the last 20-30 years have been severe, with a decline in grassland cover, and an increase in woodland, bushland, cultivated land and settlements (Abate and Angassa, 2016). The increase in livestock has led to over-grazing, which diminishes the grass layer of the soil, leaving more water available for woody plants which are normally outcompeted, and allowing them to take over (Tefera et al., 2007a). Confounded by Government-enforced fire-suppression since 1974, this has led to an increase in bush-density within the Yabello Wildlife Sanctuary (Dalle et al., 2006; Solomon et al., 2007; Tefera et al., 2007a) which may have triggered Bush-crow population declines in the past (Borghesio and Giannetti, 2005). These changes have also led to a decline in the condition of the traditional rangelands (Solomon et al., 2007; Tefera et al., 2007b) and are detrimental to local livelihoods (Dalle et al., 2006), threatening the already poor soil quality (Solomon et al., 2007; Tefera et al., 2007c), limited water resources (Bassi, 2002) and per capita cash returns (Cossins and Upton, 1987). This does at least offer hope that conservation efforts for the Bush-crow and Swallow may go hand-in-hand with development opportunities for local people, as development projects in the region often focus on scrub clearance to open up more land for grazing once again (*pers. obs.*).

3.1.4 Sympatric species

Within the range of the Ethiopian Bush-crow, there are a number of sympatric species commonly found in similar habitat. These include the White-crowned Starling *Lamprotornis albicapillus,* Superb Starling *Lamprotornis superbus*, Northern Red-billed Hornbill *Tockus erythrorhynchus,* White-headed Buffalo Weaver *Dinemellia dinemelli,* Red-billed Buffalo Weaver *Bubalornis niger* and d'Arnaud's Barbet *Trachyphonus darnaudii* (Bladon et al., 2016; Gedeon, 2006; Redman et al., 2009). Of these, the two starlings exhibit a number of ecological similarities to the Bush-crow, favouring open *Acacia* woodland habitat, and feeding predominantly on the ground in small family groups (Redman et al., 2009). Within the Bush-crow's range, the three species are commonly found foraging together (Dellelegn, 1993), and join forces to mob raptors and snakes (Bladon et al., 2016). The two starling species therefore make ideal control species for comparison with the Bush-crow, occupying similar habitat but having much larger geographic ranges (Ash and Atkins, 2009).

3.2 Study sites and data collected

The Bush-crow's range has been described by a distribution model, based on interpolated climate data and remotely-sensed habitat data, with the primary effect being its restriction to an area with lower mean annual temperatures (Donald et al., 2012). To begin my study, I wanted to investigate whether a similar effect of temperature and habitat could be detected in the field. I conducted bird and habitat transects across the Bush-crow's range, to estimate Bush-crow and White-tailed Swallow abundance at different sites, which could be compared with local habitat and temperature patterns (Chapters 4 and 6). The methods used for collecting and processing this data, prior to detailed statistical analysis, are described in the following sections, as they are common to both Chapters 4 and 6.

3.2.1 Selection of transect sites

Triangular transects

Transect sites were chosen using data on Bush-crow occurrence reported in Donald et al. (2012). These data recorded Bush-crow occurrence (bird or nest records) in 0.0833x0.0833 decimal degree squares. Four of the 81 occupied squares did not contain a known road (Paul Donald, *pers. comm.*), and these were not considered for surveying. A further 23 squares just outside of the Bush-crow's known range were chosen, using a combination of road availability, proximity to the climate envelope described by Donald et al. (2012) and suitable vegetation. This gave 100 selected transect squares, whose order was then randomised.

Each square was divided into 0.01x0.01 decimal degree cells, and a cell chosen at random in each square. The chosen points were checked for their distance from roads. For logistical ease, 80 points were allowed to be within one kilometre of a road, but 20 selected were more than one kilometre away from any road, to control for any effect of roads on the birds or their habitat (Mellanby et al., 2008). Once 20 selected points in the random square order were away from roads, points which fell more than one kilometre from a road were moved to the nearest cell within a kilometre of a road, within their own square.

In the field, some sites proved inaccessible by road or track. Sites which could be approached to within five kilometres by car were accessed on foot, but sites further away were discarded or moved to a more accessible location. When sites were inaccessible on foot (because of deep river valleys) they were moved to the nearest accessible point to the original location. Owing to a combination of accessibility and time constraints, a total of 61 bird and habitat transects from the 100 sites were completed (with 57 sites having both sets of data; Figure 3.1).

Triangular transects were walked from each selected point, constructed on site by walking one kilometre along a bearing perpendicular to and away from the nearest road. Where this was not possible (e.g. due to a river valley crossing the route), a path running parallel and to the right of the obstruction was chosen. Equilateral triangles were created by adding 120° to the previous bearing, and thus walking a three-kilometre transect in total.

In addition to the above sites, a further six were chosen in specific locations. I conducted three transects on Soda Plain and two east of Dida Hara whilst trialling methods in November 2012, and a single transect at Arbora in 2014 following the discovery of Bush-crows there (Bladon et al., 2016). The results from these transects were comparable enough to be included in my analyses.

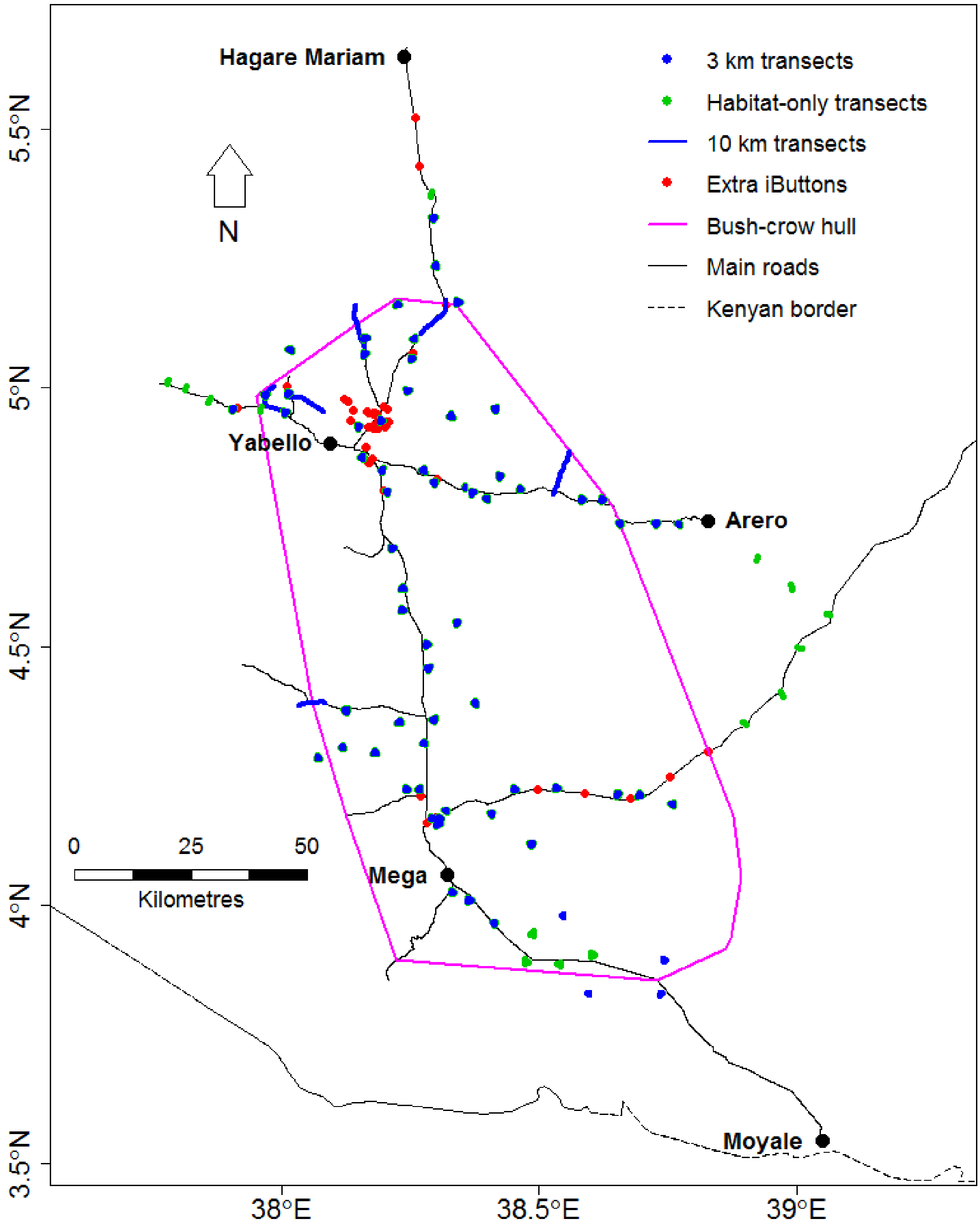
“Habitat-only” transects

To better compare habitat parameters inside and outside of the Bush-crow’s range, I conducted one-kilometre habitat transects (Section 3.4) at sites further outside of the Bush-crow’s known range. To do this in a time efficient manner, these sites were chosen at ten kilometre intervals along roads to the west (towards Consu, four sites), north (towards Finchawa, one site) and east (from Soda and Arero towards Wachile, six sites) (Figure 3.1). I did not conduct bird transects at these sites, as I had prior knowledge that Bush-crows would not be found there. This assumption was upheld by the lack of any evidence for Bush-crow presence on, or anywhere near to, any of these transects.

“Edge-of-range” transects

In 2015, a further six transects were conducted by Simon Busuttil, following my methods. Rather than being three-kilometre triangles, these transects were ten kilometres long (although in one case this was reduced to six kilometres) and designed to sample changes across the edge of the Bush-crow’s range. The locations of these transects were chosen to capture areas where the edge of the Bush-crow’s range was reasonably well known, and there was little apparent variation in habitat along the length of the transect. Necessarily, therefore, these sites ran close to roads (Figure 3.1).

Figure 3.1: Map of study sites, showing the locations where 3-km triangular transects (blue dots), 1-km habitat-only transects (green dots), and 10-km edge-of-range transects (blue lines) were conducted. Red dots show the locations where additional iButton temperature loggers were left at other study sites. The pink line represents the convex hull drawn around the Bush-crow's known range (Donald *et al.*, 2012).



3.3 Bird data

3.3.1 Data collection

At each site, a bird transect was conducted. Along bird transects all sightings of Ethiopian Bush-crows or their nests, White-crowned Starlings or their nests, and White-tailed Swallows were recorded, except for the 2012 and 2015 transects when White-crowned Starling nests were not recorded. Records included distance from the transect (measured using a laser range-finder), the angle between the transect line and the bird or nest when first detected (measured using a compass), the angle up to nests and the top of the tree containing them (measured using a clinometer), and any association between birds and nests. The perpendicular distance between each record and the transect line was calculated later. The movement of birds was noted, so that if they were seen again later in the transect, it was recorded as a double count. Where a small group was initially seen, followed by a larger one suspected to contain some of the same individuals, the second group was recorded with the number of extra individuals noted.

Triangular transects were completed on 19th and 20th November 2012 (five sites), between 27th March and 8th June 2013 (61 sites) and on 12th June 2014 (one site). “Edge-of-range” transects were completed between 13th and 22nd April 2015. All except two triangular and two “edge-of-range” transects were completed during dry weather. On the other occasions, when rain became heavy, the transect was paused while it passed, on the assumption that any birds present were also likely to stop moving and become less visible during the rain.

3.3.2 Data processing

To generate site-based abundance estimates for analysis of the effects of temperature and habitat on Bush-crow and Swallow distributions (Chapters 4 and 6), I used DISTANCE sampling (Buckland et al., 2001) to estimate the probability of detecting each of my five recorded objects on the birds transects (Bush-crow nests, Bush-crow groups, White-crowned Starling groups, White-crowned Starling nests and White-tailed Swallow groups). These detection functions were used to estimate the effective area surveyed, and therefore the density of birds and nests at each site.

Data selection

Double-count records for birds were removed from the raw data, as detection probability must be based on the first detection of a group (Buckland et al., 2001). The detection distances for each object were then divided into distance bins, and a histogram of frequency against distance was plotted. Bins of three different widths, resulting in three different histograms, were produced for each object. The three histograms were compared to find the first distance at which the frequency of detection dropped to zero in all three plots. This was taken to indicate a natural break in the data, and was chosen as the truncation distance for the object. Data truncation is recommended to avoid outliers at large distances causing unrealistic models to be fitted (Buckland et al., 2001, p. 48). The chosen truncation distances are shown in Table 3.1.

Covariates

Detection probability of each object can be affected by a number of covariates, and these in turn affect density estimates at each site (Buckland et al., 2004, p. 31). My transect data were collected by one of two observers, and one of five guides from the Borana National Park. The ability of different observers and guides to detect birds and nests may vary, but observer and guide were constant across a transect. The local tree density could have a strong impact on detection probability, so this was calculated from my habitat data as the mean density across the six habitat sample points on each triangular transect, or the three habitat sample points along the leg of the "edge-of-range" transect from which the observation was made (see Section 3.4). The group size and detection method (seen or heard), could also affect detection probability. These values are unique to each observation. Detection method was not tested for White-crowned Starlings or White-tailed Swallows, owing to the small number of observations detected by sound. The covariates tested for each object are shown in Table 3.1.

For initial analysis, any observation with any of the putative covariates for that object missing was removed from the data to allow all possible models to be fitted. Once the final model had been selected (see below), any observations missing covariates which were not included in the final model were replaced, and the final model was refitted to this, slightly larger, dataset.

Table 3.1: Truncation distance, initial and final sample sizes, covariates tested and models used for detection function fitting for each of five model objects (Bush-crows, Bush-crow nests, White-crowned Starlings, White-crowned Starling nests, and White-tailed Swallows.

Object	Truncation distance / m	Initial sample size	Final sample size	Covariates tested	Model form
Bush-crow nests	350	398	392	Tree density Observer Guide	Hazard-rate No adjustment
Bush-crow groups	170	78	70	Tree density Group size Observer Guide Detection method	Hazard-rate No adjustment
White-crowned Starling groups	110	55	52	Tree density Group size Observer Guide	Hazard-rate No adjustment
White-crowned Starling nests	140	55	49	Tree density Observer Guide	Half-normal No adjustment
White-tailed Swallow groups	40	29	25	Tree density Group size Observer Guide	Hazard-rate No adjustment

Truncation distance: *the perpendicular distance of an object from the line of the transect, within which observations were included (Buckland et al., 2001).* ***Initial sample size:*** *the total number of independent observations from all transects.* ***Final sample size:*** *the number of observations included in the final DISTANCE analysis, once observations beyond the truncation distance, and those missing selected habitat covariates, had been removed.* ***Covariates:*** *parameters tested.* ***Model form:*** *the key function and adjustment terms used in the final model.*

Testing assumptions

DISTANCE sampling assumes that transects are completed instantaneously, or as fast as realistically possible. The speed with which the transect is completed will affect the density estimates obtained, as slower transects increase the likelihood of coming across moving objects, such as birds (Buckland et al., 2001, p. 12). There was no difference in the speed at which transects were conducted by the two observers, so the data from all transects were comparable.

Detection model fitting

The following procedure was carried out for each of the five objects. Two basic forms of detection function, which assume that the decline in probability of detection with distance from the transect follows either a half-normal or a hazard-rate distribution, were fitted. Each detection function was fitted without any adjustment terms, and with two different adjustment terms; cosine and hermite polynomial adjustments for half-normal functions, and cosine and simple polynomial adjustments for hazard-rate functions. These combinations are recommended by Buckland et al. (2001, pp. 47-48). Adjustment terms were scaled by the scale parameter, so that the covariates (where included) could only affect the scale of the detection function. This is recommended by Buckland et al. (2001, pp. 37-38).

The order in which covariates are added to a model affects the variation attributed to each one, therefore forward stepwise selection was used initially (Thomas et al., 2009). Each model structure (half-normal and hazard-rate, with and without each adjustment term) was fitted with no covariates, and with each of the covariates independently. Model selection (see below) was carried out to find the best model and, if this model included a covariate, all model structures were then fitted with each remaining covariate added to the first. This process was repeated until the best model did not contain any new covariates, and thus was the best overall model.

To test the results of the forward stepwise selection procedure, the four objects for which covariates were selected were re-modelled. All possible combinations of covariates were fitted to each model with both half-normal and hazard-rate key functions, but no adjustment terms. Model selection (see below) was carried out to find the best model, and the result compared to that from the forward stepwise procedure.

Model selection

Within each suite of models, those which failed to fit were removed. Those which did fit were tested using three Goodness-of-Fit tests: a chi-squared test of the likelihood that the fitted model is the true model; a Kolmogorov-Smirnov test, which tests the largest deviation of the fitted cumulative detection function from the data; and an unweighted Cramer-von Mises test, which tests deviation of the cumulative detection function from the data across their entire range (Buckland et al., 2004, pp. 387–388). Models which failed all three of these tests ($P < 0.05$) were removed (Buckland et al., 2004). The normal Q-Q plots of all remaining models were then inspected by eye, and any which failed to approximate normality were rejected. Particular attention was paid to the behaviour close to the origin, as it is this area which most strongly affects the successful estimation of detection probability by the function (Buckland et al., 2004, p. 387). The detection functions of the remaining models were then inspected by eye, and any with irregular shapes (e.g. increases in detection probability with distance, negative detection probabilities) were rejected. Finally, the AIC_c of the remaining models were compared, and the lowest AIC_c selected as the best model. AIC_c was favoured over AIC, as it is more robust for smaller sample sizes (Buckland et al., 2001, p. 70).

For the first process, forward stepwise selection then continued until the minimum AIC_c was given by the model with no extra covariates added, indicating that this was the best model. If necessary, this model was refitted with observations included which had data missing for covariates not used in the final model, in order to maximise model fit.

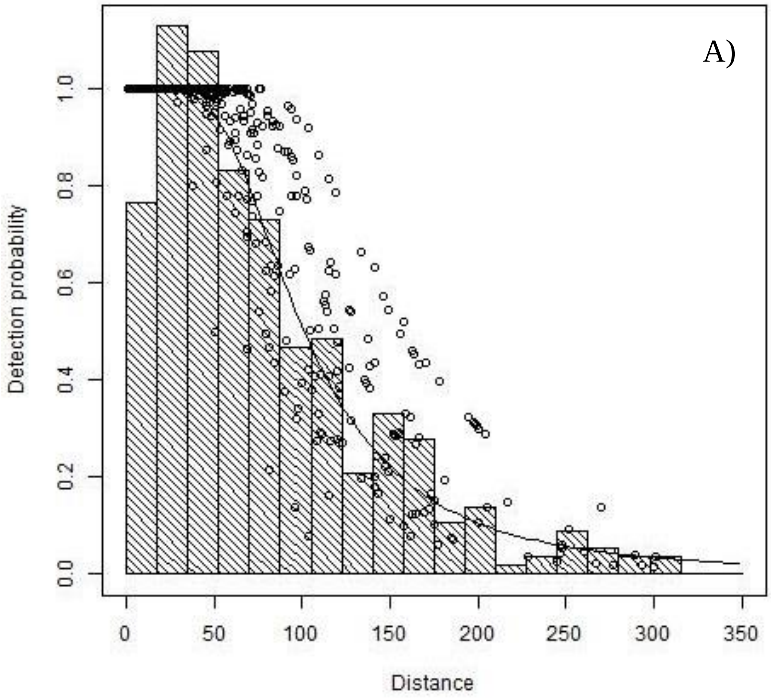
For the second, comparative process, selection by AIC_c provided the final model, and this was compared with the results from the forward stepwise procedure. In all cases, the models selected by the two processes were the same.

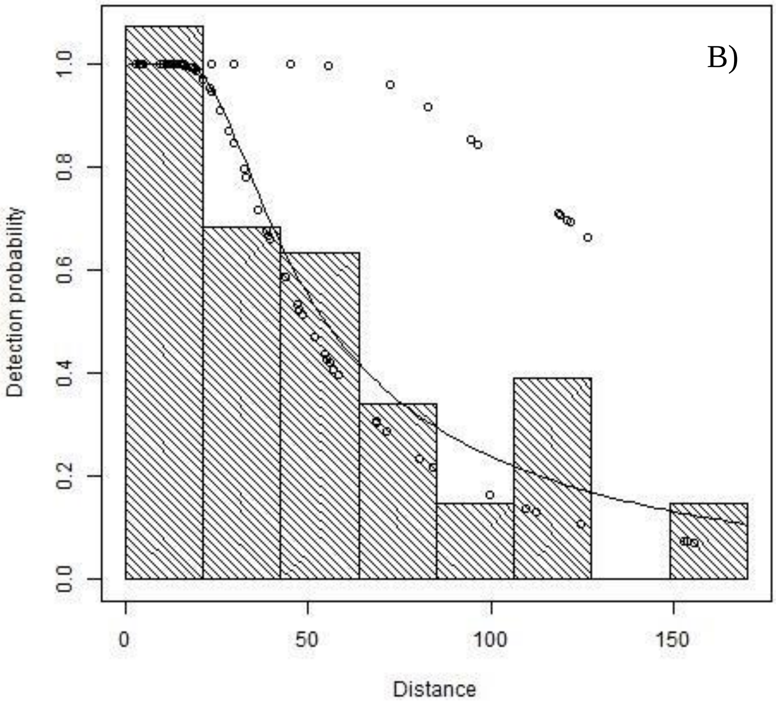
Chosen models

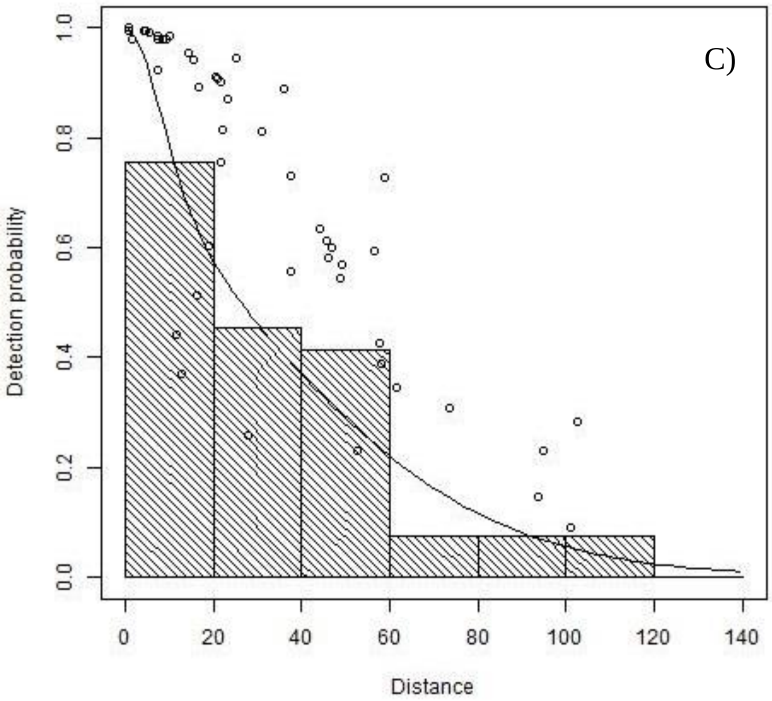
The final detection model for Bush-crow nests contained tree density and the identity of the guide as covariates, with a hazard-rate key term (Table 3.1; Figure 3.2 *A*). In the models of Bush-crow groups, group size was a significant covariate once the identity of the observer had been added. However its effect was negative, i.e. larger groups have a lower detection probability, which does not make biological sense. Therefore this model was ignored and the next best model, which was within 2 AIC_c points of the previous model, was selected. This was the single covariate model with only observer identity, and a hazard-rate key term (Table 3.1; Figure 3.2 *B*).

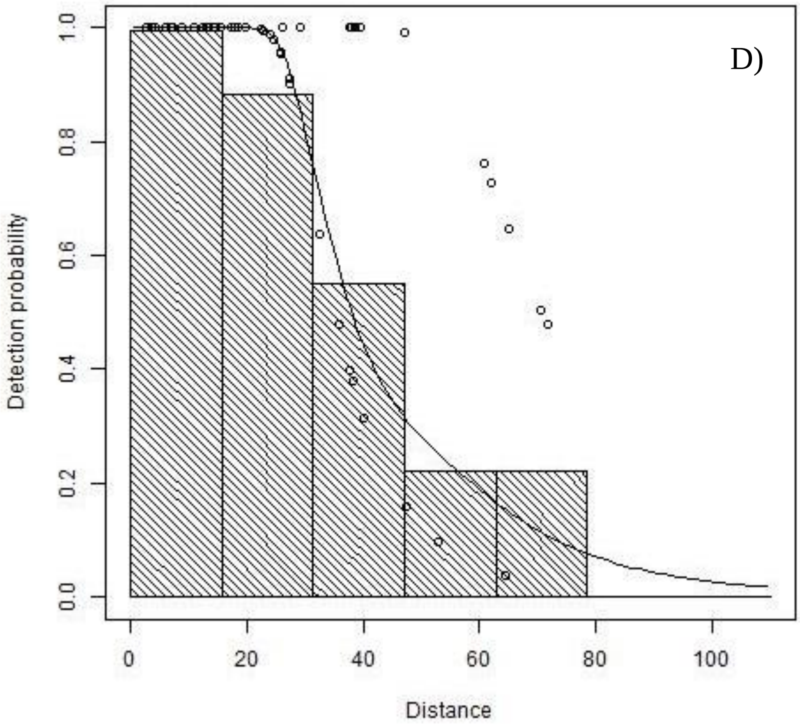
The final model for White-crowned Starling nests contained the identity of the guide and tree density as covariates, with a half-normal key term (Table 3.1; Figure 3.2 *C*). The final model for White-crowned Starling groups contained observer identity as the only covariate, with a hazard-rate key term (Table 3.1; Figure 3.2 *D*).

Figure 3.2: Final fitted detection functions for *A*) Bush-crow nests, *B*) Bush-crow groups, *C*) White-crowned Starling nests and *D*) White-crowned Starling groups. Histograms show the distribution of nest/group records in distance bands from the transect line. Points show the predicted probability of detection of each nest/group given its distance from the transect line. Curves show the fitted detection probabilities against distance from the transect line. Fitted covariates were tree density and guide for both species' nests, and observer for both species' groups.









White-tailed Swallow

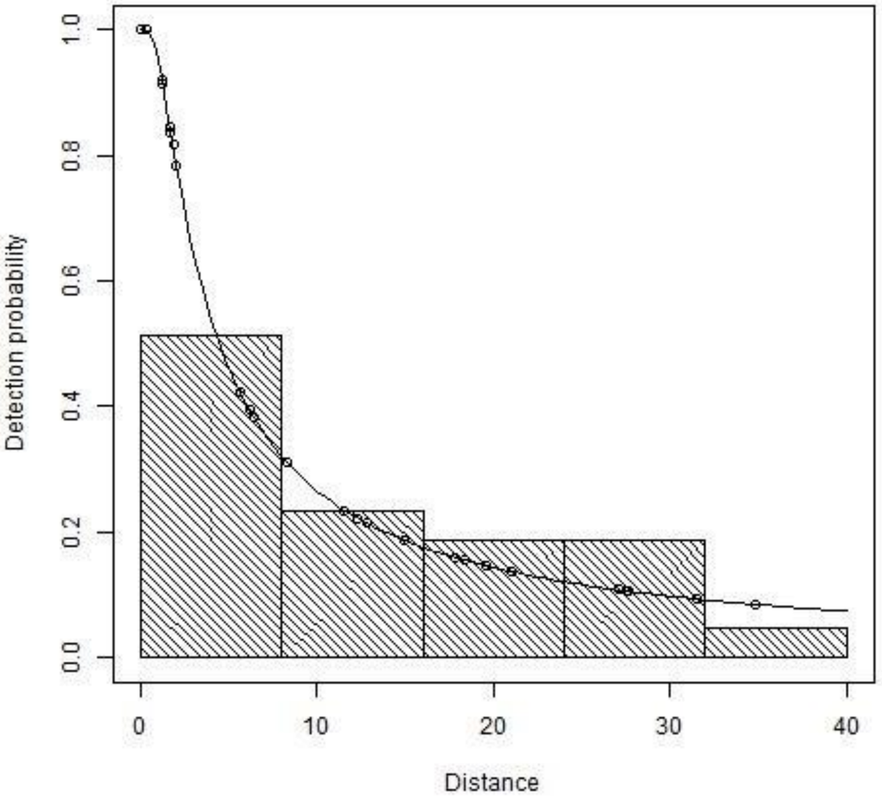
Initially, I truncated the distance from the transect line of Swallow records included in the DISTANCE analysis at 150m. The detection function was modelled in relation to covariates. Only two models were retained by the selection criteria. The best model included group size as a covariate, but many of the detection probabilities even close to the transect line were very low (<0.1), which suggests either that covariates should not be included, or that truncation distance should be decreased (Buckland et al., 2004, p. 47). In addition, the effect of group size was found to be negative, i.e. larger groups have a lower detection probability, which is counterintuitive.

To overcome these issues, the models were refitted with truncation distance reduced to 80m. This time a model with no covariates was selected, but the model still had most detection probabilities below 0.2, suggesting that the truncation distance should be further reduced (Buckland et al., 2004, p. 47). The next best model, within 1 AIC_c point, had a much better shape to the detection function, with higher detection probabilities near to the transect line, but included group size as a covariate, again with a negative effect. The third best model included the identity of the guide as a covariate, but the large number of factor levels for guide meant that it had no degrees of freedom left to perform the chi-squared test. Factor level reduction was attempted, but did not release enough degrees of freedom.

I decided, therefore, that the use of covariates with the small White-tailed Swallow dataset was not justified, and instead looked for the best fitting model from a range of different truncation distances with no covariates. Truncation distances of 40, 50, 60, 70 and 80 metres were tested. The only models kept by the selection process were those with a hazard-rate key function, and no adjustment terms for each truncation distance. AIC_c cannot be used to compare models with different truncation distances, as this changes the data being used. The normal Q-Q plots for the five models were very similar, but the detection probabilities dropped with increasing truncation distance, therefore the 40-m truncation was chosen. No further truncation was tried, as this would have drastically reduced the already small sample size.

The addition of covariates to this 40-m model was tried but the best model, with tree density as a covariate, once again had very low detection probabilities, and no degrees of freedom left for testing. The next best model, within two AIC_c points of the first, was the previous model with no covariates, and this was therefore selected as the final model (Table 3.1; Figure 3.3).

Figure 3.3: Final fitted detection function for White-tailed Swallow groups, with a 40-m truncation distance and no covariates. The histogram shows the distribution of Swallow group records in distance bands from the transect line. Points show the predicted probability of detection of each group given its distance from the transect line. The curve shows the fitted detection probability against distance from the transect line.



Effective area surveyed

Since triangular transects had been used at some sites, it was not possible to output site-specific density estimates directly from DISTANCE. I therefore calculated the effective area surveyed (EAS) and density at each site as follows.

The effective area surveyed (EAS) for each object was calculated for each one-kilometre transect leg. For each object, the half effective strip width (HESW) for each observation was predicted using the relevant DISTANCE model. Since all three birds had either a single factorial covariate or no covariates, simple application of the HESW for the relevant factor level to each site with no observations was used. For both nest types, which had tree density and guide as covariates, a linear model was fitted:

$$HESW \sim Tree\ density * Guide$$

This model was then used to predict the HESW at sites with no nest observations. In all cases, the effective area surveyed (EAS) for each leg was then calculated using one of four equations.

- For each interior leg of the 10-km "edge-of-range" transects:

$$EAS = 2 * HESW * Leg\ length$$

- For each terminal leg of the 10-km transects, including the area surveyed around the terminal point:

$$EAS = (2 * HESW * Leg\ length) + \left(\frac{1}{2} * \pi * HESW^2\right)$$

- For the single solitary 1-km straight transect, including the area surveyed around each terminal point:

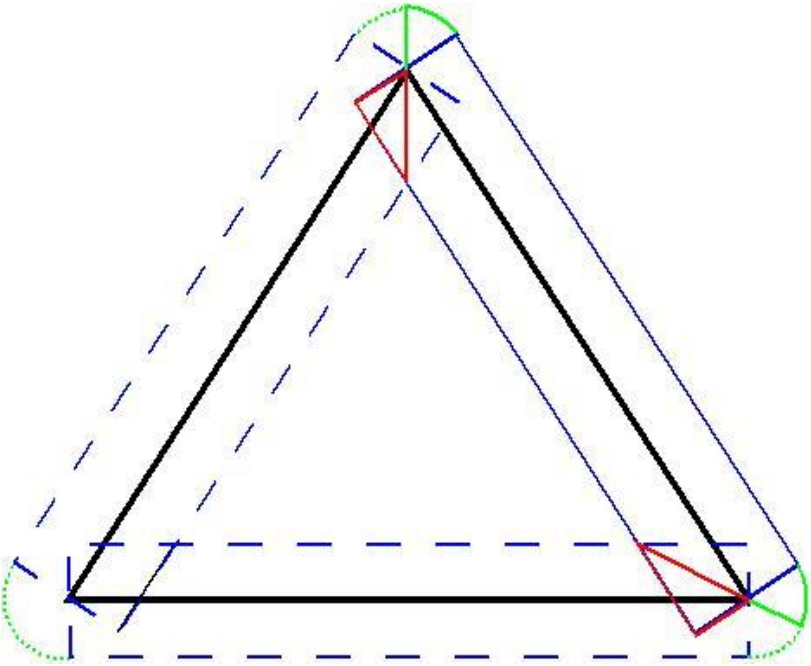
$$EAS = (2 * HESW * Leg\ length) + (\pi * HESW^2)$$

- For each leg of the 3-km triangular transects:

$$EAS = (2 * HESW * Leg\ length) + \left(\frac{1}{3} * \pi * HESW^2\right) - (HESW^2 * tan(60))$$

where $(2 * HESW * Leg\ length)$ gives the area surveyed as though the transect was a solitary one-kilometre straight line, $\left(\frac{1}{3} * \pi * HESW^2\right)$ accounts for the extra area surveyed on the outside of the corners of the triangle closest to that leg, and $(HESW^2 * \tan(60))$ subtracts the overlap with neighbouring legs which occurs on the inside of the corners of the triangle (Figure 3.4). The total area surveyed on each triangular transect was then calculated by summing the areas surveyed on each of the individual legs.

Figure 3.4: The effective area surveyed on each leg of a triangular transect.



Black: *the transect route.* ***Blue:*** *the area surveyed along each leg of the transect assuming it is an independent line* $(\mathbf{2} * \boldsymbol{HESW} * \boldsymbol{Leg\ length})$. ***Green:*** *the additional area surveyed by turning on each corner of the transect* $\left(\frac{\mathbf{1}}{\mathbf{3}} * \boldsymbol{\pi} * \boldsymbol{HESW}^{\mathbf{2}}\right)$. ***Red:*** *the overlap between legs on the inside of each corner* $(\boldsymbol{HESW}^{\mathbf{2}} * \boldsymbol{tan}(\mathbf{60}))$. ***Solid lines:*** *focal leg areas (on the right-hand side).* ***Dashed lines:*** *adjoining leg areas.*

<u>Density calculation</u>

Using the area calculations, the density of each bird or nest on each three kilometre transect, and on each one kilometre leg of an “edge-of-range” transect, was estimated. I estimated densities over different scales for the two types of transect because Bush-crow density would obviously vary along the full length of a 10km transect moving from inside to outside of the Bush-crow’s range, and therefore a transect-long average density would be meaningless.

Observations were assigned to the transect leg which they were nearest to, by using the distance and bearing to the object, and the co-ordinates of the point on the transect at which it was recorded, to calculate the actual co-ordinates of the bird or nest. In most cases this was the same as the leg from which it was recorded, but a few records were allocated to different legs. This did not affect density estimation for three kilometre transects, but did affect it for the independent legs of the 10km transect. This applied to five Bush-crow nests, two Bush-crow groups, and two White-crowned Starling groups.

Additionally, double count data needed to be treated differently here. For detection function fitting, the first detection of any group was retained and all later detections discarded, in order to get accurate detection probabilities and remove the effect of earlier detection on the probability of later detection of the same group. For density estimation the largest recorded group size for each group was retained, and all smaller group sizes discarded. This was done to obtain more accurate estimates for group size, and density of both groups and individuals. This applied to all three bird species, but not to either nest type, as there were no double count data for the latter.

The data for each object were subset to observations within the truncation distance, and the total number of birds and groups, or nests, seen on each transect or leg was calculated. The total counts and the area surveyed were used to calculate the mean group size and the bird and group density per square kilometre in each transect and leg for bird species, and density per square kilometre for Bush-crow and White-crowned Starling nests. Density estimates could not be calculated for White-tailed Swallows, as they move too quickly compared to the movement of the observer along the transect, and therefore violate the ‘snapshot’ assumption of DISTANCE sampling, where objects are ‘frozen’ at a point in time (Buckland et al., 2001, p. 12). A summary of estimated densities for each object across all sites is shown in Table 3.2.

Table 3.2: Summary of estimated densities and group sizes of Bush-crows, White-crowned Starlings and White-tailed Swallows across all sites.

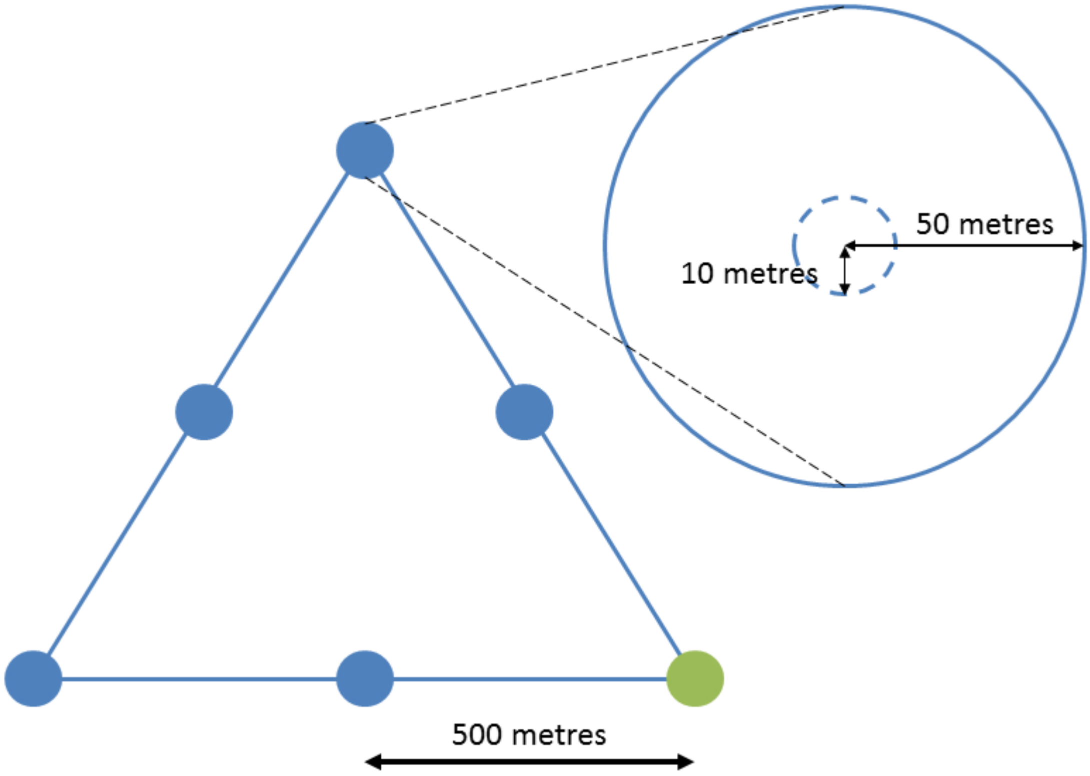
		Density / km^{-2}		Group size	
Species	**Type**	**Mean ± SD**	**Maximum**	**Mean ± SD**	**Maximum**
Ethiopian Bush-crow	Nests	14.28 ± 14.48	73.92	-	-
	Groups	5.71 ± 3.00	13.91	2.74 ± 1.98	8
	Individuals	16.31 ± 17.05	72.35		
White-crowned Starling	Nests	11.01 ± 9.59	40.52	-	-
	Groups	10.86 ± 9.19	34.56	2.79 ± 3.79	18
	Individuals	23.46 ± 25.39	100.67		
White-tailed Swallow	-	-	-	1.93 ± 1.16	5

3.4 Habitat data

3.4.1 Data collection

Habitat surveys were conducted separately to bird surveys along the route of each transect. Data were collected either at the start, along the walked route, or at sample points along the transects (Figure 3.5).

Figure 3.5: Diagram of a triangular habitat transect. The blue line represents the route of the transect, along which dung counts were tallied. Every 500m, at the blue circles, trees were identified and bushes counted within a 50m radius, ground cover was sampled within a 10m radius, and all visible villages were counted. At the starting point, in green, a soil sample was taken and an iButton temperature logger was placed (see text, and Section 3.5.1).



Soil water content affects invertebrate abundance (Sutherland and Green, 2004), and it has been suggested that Bush-crows favour areas of loosely packed soil for foraging (Gedeon, 2006). At the start of each transect a 51.1cm^3 cylindrical soil core (2.55cm diameter, 10cm deep) was taken using a steel corer. The sample was weighed fresh, air dried, and weighed again, using a small electronic balance (Sutherland and Green, 2004). These values were used to calculate soil wetness ($Wet\ weight/Dry\ weight$) and bulk density ($Wet\ weight/Volume$).

Trees provide Bush-crows with nesting sites (Gedeon, 2006), and they show a preference for *Acacia* and *Commiphora* woodland (Mellanby et al., 2008). They forage on the ground amongst vegetation (Gedeon, 2006; Ross et al., 2009). Every 500m along the transect route (i.e. at each vertex of the triangle, and halfway along each leg), within a 50m radius circle, all trees (>10cm diameter at breast height) were identified to species and measured, bushes (<10cm diameter at breast height) were counted, ground cover was estimated using the Domin scale (Table 3.3) for bare ground, grass and herbs in each of ten random quadrats within a 10m radius, and average grass length (<5cm, 5-10cm, >10cm) was estimated by eye in each quadrat. The advantage of the Domin scale is that it allows for more accurate recording of low density presence within the quadrat.

Bush-crows associate with people and forage amongst herds of livestock and their dung (Gedeon, 2006). Villages visible from each sample point were recorded with an estimate of the number of buildings and their distance from the point. Along the whole transect the number of dung piles was tallied within a two metre wide strip, and categorised as cow, goat or sheep, equid, camel or other.

Table 3.3: The Domin scale, used for assessing bare ground, grass and herb cover within quadrats at habitat sample points (see text).

Percent cover	Domin Score	Description
0	0	None
0	+	1 individual, no measurable cover
< 4	1	Few individuals
< 4	2	Several individuals
< 4	3	Many individuals
4 – 10	4	-
11 – 25	5	-
26 – 33	6	-
34 – 50	7	-
51 – 75	8	-
76 – 90	9	-
91 – 100	10	-

3.4.2 Data processing

Prior to conducting analyses of the effects of temperature and habitat on Bush-crow abundance, it was necessary to compute a number of meaningful variables from the recorded habitat data.

Point-level data

Tree survey data were used to calculate tree density (count of trees divided by area surveyed) and average tree height at each survey point. The density of trees in the genera *Acacia* or *Commiphora* was also calculated separately, along with bush density.

The mean Domin score (Table 3.3) for three categories of ground cover (bare ground, grass and herbs) was calculated across the ten quadrats at each point, along with the mean grass length from across the quadrats in which some grass had been recorded.

The number of villages and the number of houses seen within 500m of a point, as well as the distance to the nearest village, were calculated.

Transect leg-level data

Point-level data were summarised over each of the transect legs (three points per leg) to obtain mean tree density, mean tree height, mean density of *Acacia* and *Commiphora*, mean bush density, mean ground cover Domin scores and mean grass length. For villages, the data were further summarised to “Distance to nearest village” and “Presence of a village within one kilometre”.

Dung counts were divided into three categories; cow dung, goat or sheep dung, and cow, equid or camel dung. For each category, the density on each transect leg (count, divided by the product of leg length and survey strip width) was calculated.

As soil samples were only taken at one point per three-kilometre transect, data from them were applied to all three legs of the whole transect. Soil wetness was calculated as $Wet\ weight\ /\ Dry\ weight$, and bulk density as $Wet\ weight\ /\ Volume$.

Distribution of tree heights

Bush-crow nests are often built in the crown of tall *Acacia* trees, but the reason for this is unclear. Recently, nests have also been found at the top of high man-made structures (Bladon et al., 2016). To investigate whether nest height was influenced by temperature, whilst controlling for the availability of trees in the area, I calculated the cumulative probability of tree height on each transect, and found the percentile in which each nest fell.

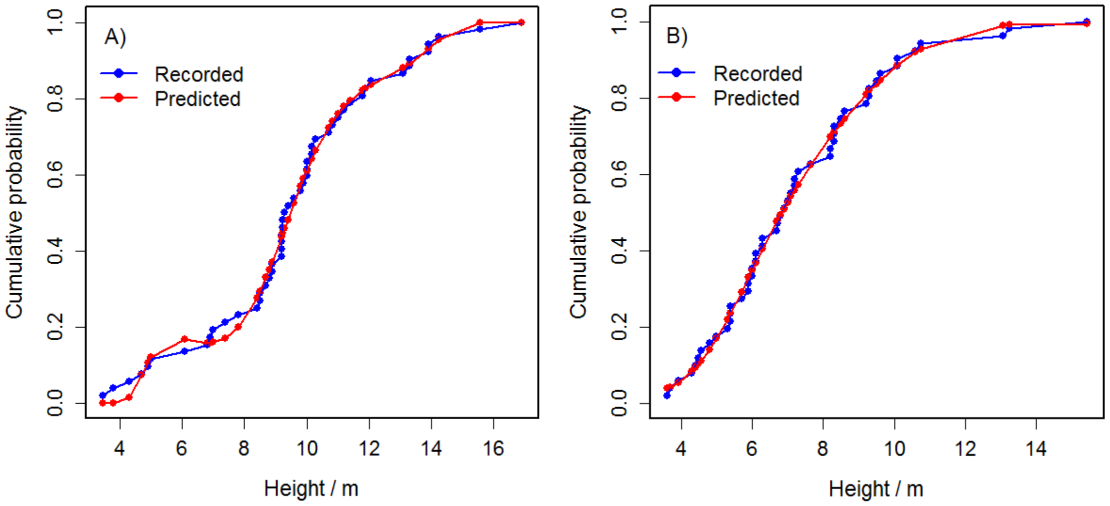
To select the best model form, tree height data from all transects were modelled against their simple cumulative probability, using both the complementary log-log distribution and the complementary log-logistic distribution, each with one through to five expansion terms. All of the log-log models fitted the data better than any of the log-logistic models, and so the log-log distribution was chosen for further use. The process below was repeated using transect (six points around a triangle) and leg (three points along a 1km leg) as units.

Tree heights from the sample points were combined with the heights of any trees recorded with nests in them, and the cumulative probability was modelled against height. Models with one through to five expansion terms were fitted to each dataset, and minimum AIC was used to select the best model for each leg.

Cumulative probability should not decline with height, so plots of the raw data and the model prediction for the selected model on each leg were inspected to check for problems with the model fit. Ten models which predicted declines in cumulative probability had to be removed (e.g. Figure 3.6 *A*, around 7 metres), and the next best AIC model chosen for that leg. This process was repeated until each transect leg had a valid fitted model (e.g. Figure 3.6 *B*).

The fitted models were used to calculate the percentile of tree height distribution on the relevant transect leg in which each nest, and the tree in which it was built, was found. The mean percentile for Bush-crow nests, White-crowned Starling nests, and the trees containing each of them, was then computed for each transect leg on which nests had been seen, and this was used as the dependent variable for later analyses (Chapter 4).

Figure 3.6: Examples of *A)* over-fitted and *B)* selected models of cumulative probability of tree heights. Blue dots show ordered heights of trees recorded on the transect leg, red dots show the predicted cumulative probability of tree heights from complementary log-log models of their distribution. *A)* shows an over-fitted model, where cumulative probability declines at 7m. *B)* shows a well-fitted final model, with no decline in cumulative probability.



3.5 Temperature data

3.5.1 Data collection

At each triangular and habitat-only transect site an iButton Thermochron® (Maxim Integrated, DS1921G-F5), set to record hourly temperatures, was placed in a shaded position between chest and head height in a tree, within 100m of the starting point. On the few occasions where no trees were available, they were instead placed in low bushes. To detect temperature variations along the length of the "edge-of-range" transects, iButtons were placed every 500m along the route. iButtons were wrapped in a layer of clingfilm to protect them from rain.

To extend the network of temperature loggers across the region, iButtons were also left in other areas where I worked regularly. These included one or two (depending on the proximity of a transect site) near to each Bush-crow behavioural study site (Chapter 5), one near to every White-tailed Swallow and Ethiopian Swallow nesting location (Chapter 7), and at ten-kilometre intervals along the roads north (Yabello to Finchawa, four sites) and east (Soda to Wachile, six sites). These latter sites were contiguous with the locations where I also conducted one-kilometre habitat transects outside of the Bush-crow's range (Section 3.2.1; Figure 3.1).

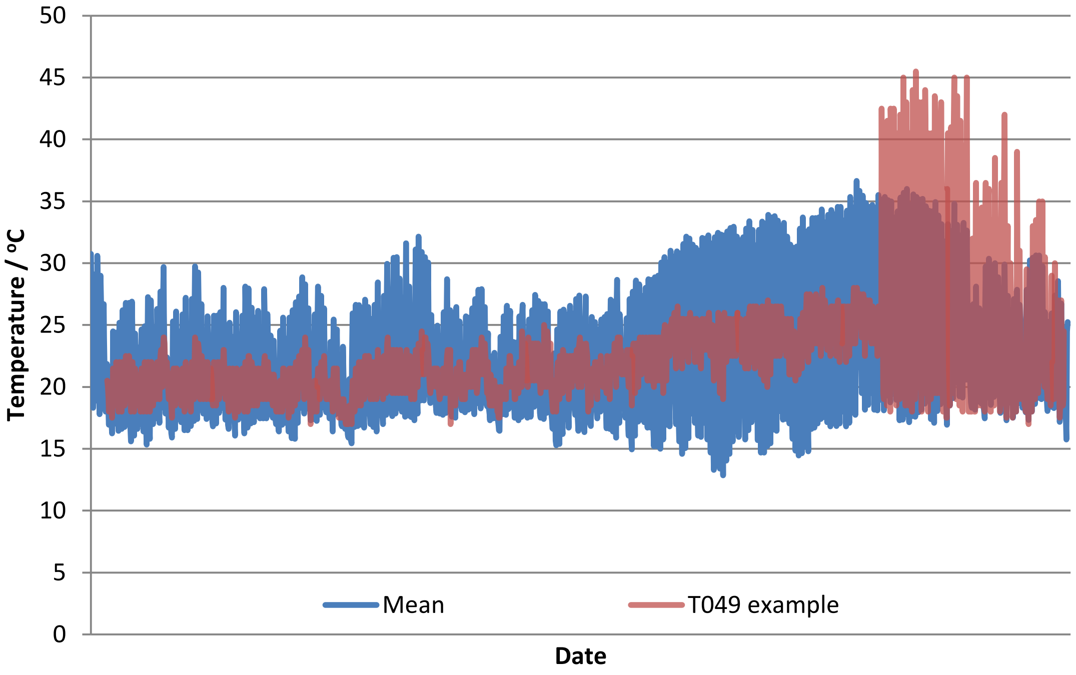
Across the network of 226 sites, iButtons were left out continuously from 25th March 2013 to 1st May 2015. Not every site had an iButton recording on every day during this time, but there was significant overlap in recording times between all sites and dates. For periods of field work (25th March to 9th June 2013, 7th April to 24th June 2014, 9th April to 1st May 2015), iButtons recorded hourly temperatures, but in order to preserve memory for the entire year, those left out between field seasons recorded temperatures every four hours. 3pm was most commonly the hottest time of the day, so I set the four-hour recording slots as 3am, 7am, 11am, 3pm, 7pm and 11pm.

3.5.2 Data processing

Upon collection of the iButton units (Maxim Integrated, DS1921G-F5), most were found to have stayed in place, but some were recovered from the ground nearby. Data from units left in place were used to generate a plot of mean temperatures, and this was compared by eye to the plot from each unit which had fallen, looking for obvious changes in the relative temperature or range of temperatures recorded by the fallen unit when compared to the mean. In most cases, this yielded an obvious time when the unit had been disturbed from its position (e.g. Figure 3.7) and the data were then truncated to the midnight before this time. In the few cases where no obvious change occurred in the pattern of the data relative to the mean, the data were retained, as the disturbance was deemed not to have affected the recordings.

To correct for variations in temperature arising from the use of different units, iButtons were set recording in batches under controlled conditions. A minimum of two units was used to overlap between any two batches, allowing all units to be compared. A series of generalised linear models were fitted with the general formula $Value \sim DateTime + Unit\ ID$ and a range of transformations and error structures. The model with a Gamma error structure gave the lowest residual deviance and the highest r^2 value, so the average predicted temperature from this model was calculated for each unit. The difference between each unit's average predicted temperature and the lowest predicted temperature across all units represents the "correction factor" which was subtracted from each recorded value to standardise field temperatures recorded on different units.

Figure 3.7: Variation in mean temperature across all sites (blue) and at a single site (red) throughout the year. The single site shows a clear change in the temperature recording pattern relative to the mean temperature, showing where the iButton has changed position.



3.5.3 Calculating temperature metrics

A range of possible temperature values (means, maximums, thresholds) could potentially be investigated with respect to Bush-crow and White-tailed Swallow abundance. I undertook initial investigations of my temperature data to explore these possible values, and computed a number of metrics used in analyses of abundance (Chapters 4 and 6).

Temperature data from all units across the entire period were collated, and corrected for the effect of the unit (Section 3.5.2). Meaningful biological effects of temperature are more likely to occur at temperature extremes (Cunningham et al., 2013a), therefore I obtained temperature metrics which reflect the absolute value of extreme events, such as temperature maxima, or the regularity with which extreme temperatures occur, such as the number of days where certain temperature thresholds are exceeded.

Temperature maxima

Since the out-of-season data were collected at four hour intervals, computing a maximum daily temperature was less meaningful for these days. I therefore used my during-season data to compare the temperature at 3pm with the maximum recorded temperature, to see whether the 3pm temperature acted as a reasonable proxy. The maximum temperature was on average 1.46^{o}C warmer (±1.96 SD) than the temperature at 3pm (n = 4,264), and the Pearson correlation between the temperatures was 0.84, so I decided that 3pm temperature probably was a reasonable proxy for maximum temperature. I additionally ran analyses using the 11am and 3pm data in order to compare results, and because there were occasions when the 11am temperature was higher than the 3pm temperature.

I fitted two-way ANOVAs to each dataset ($Temperature \sim Date\ +\ Site$). As the aim was to generate predicted values for each site on each date and "Site effects" for use in later models, rather than hypothesis testing, alternative models with different error structures or transformations were not tried.

I used the fitted models to predict daily 3pm, and 11am and 3pm, temperature values across all sites, and these were summarised to mean 3pm temperature and mean 11am and 3pm temperature at each site across the recording periods. These "site effects" were used in models of Bush-crow and Swallow occurrence and density (Chapters 4 and 6).

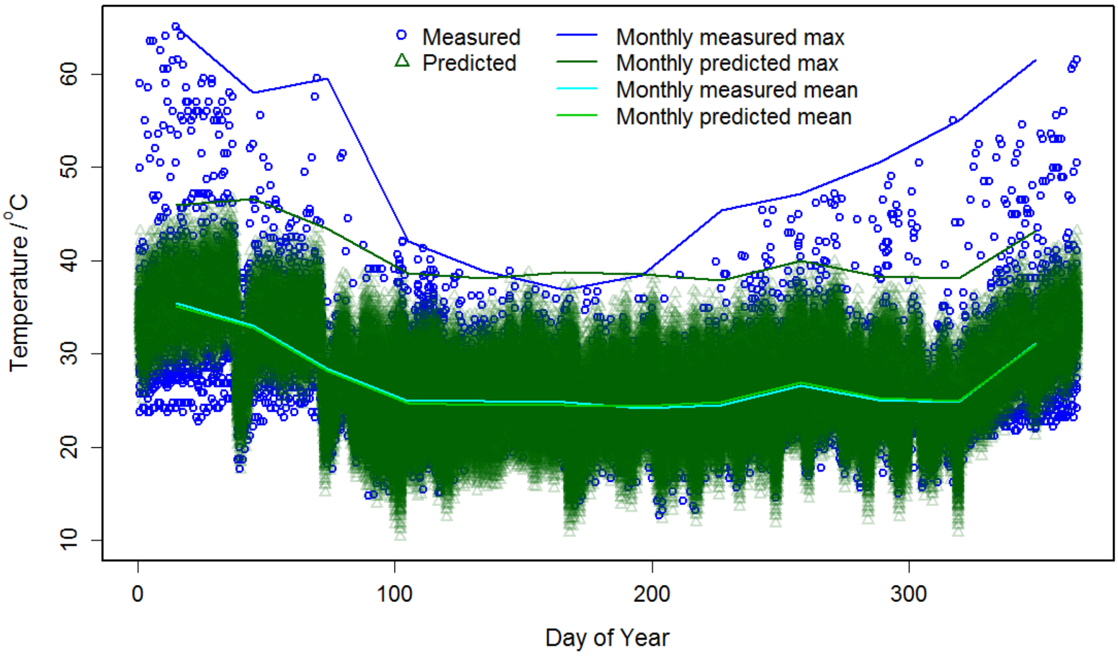
I used the 3pm temperature dataset to check for differences between my recorded temperature data, and the values predicted by the model. Plots of the two datasets showed that the predicted values masked some inter-seasonal variation in the recorded values. Whilst the monthly mean values arising from each dataset barely differed, there was a marked difference in the monthly maximum temperatures, especially between August and March, where the model did not capture the full variation in the data (Figure 3.8). Maximum temperatures are more likely to impact the Bush-crows and Swallows than any mean value, so this loss of variation could be important (Cunningham et al., 2013a). I therefore conducted analyses by season, to better capture this variation (see below).

Temperature thresholds

Previous studies of the effects of temperature on birds have found non-linear responses, where critical threshold temperatures adversely affect species (Cunningham et al., 2013b; du Plessis et al., 2012). To investigate this effect, I converted daily 11am and 3pm temperatures to a binary response; for each degree of temperature rise from 11°C to 65°C, assigning 1 where the temperature exceeded the threshold, 0 where it did not.

I fitted logistic ANOVAs to the dataset for each threshold ($Exceedence \sim Date + Site$), again using data from both 11am and 3pm, and 3pm only. I used these models to predict the probability that the temperature exceeded each threshold on each day at each site. To obtain a single "site effect", I then found the mean probability for each site across all days.

Figure 3.8: 3pm temperatures throughout the year (1 = 1st Jan). Points show measured (blue) and predicted (green) values for individual sites on each day of the year. Lines show the monthly mean and maximum temperatures for the measured (blue) and predicted (green) values. Predicted values are plotted semi-transparent, to show the range of the measured values around them.

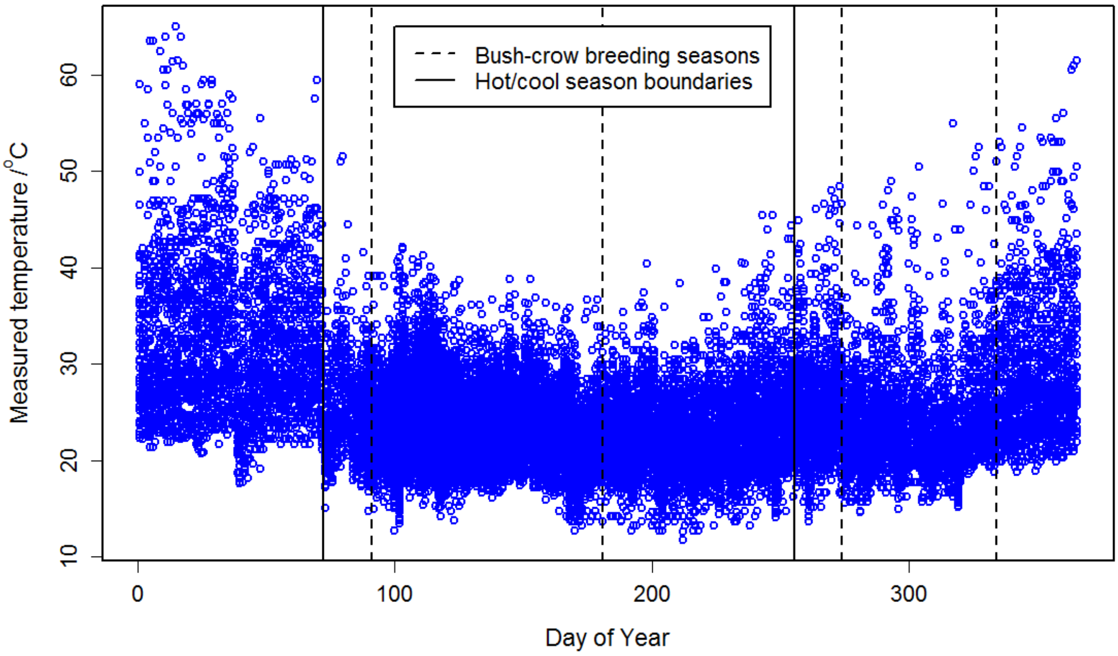


Seasonal temperature variation

There was a marked variation in recorded temperatures across the year which was not captured by the original models (Figure 3.8), so I split the year into two parts, a hot season and a cool season, and repeated the analyses described above in each season. As I did not leave temperature loggers at all sites between my field seasons, the hot season sample was smaller than the cold season, and its size could vary with the placement of the season boundaries as some loggers fell out of trees and had their data truncated part way through recording (Section 3.5.2).

To determine the dates at which to define changes between the seasons, I first looked at the raw temperature data. There was a marked decrease in temperatures between 13th and 14th March (days 72 and 73), so this was taken as the beginning of the cool season. Temperatures rose steadily from 30th August, with another increase on 20th September. Using either of these dates as the start of the hot season yielded 31 sites with hot season data. A logical division of six months after the start of the cool season placed the boundary between these two dates. I checked at what point the next site lost data in the hot season (reducing the dataset to 30 sites), and found that this was 12 days after the 6 month divide. This seemed a reasonable number of days to sample that site, so I divided the year into two blocks of six months; 14th March – 12th September as the cool season, and 13th September – 13th March as the hot season (Figure 3.9).

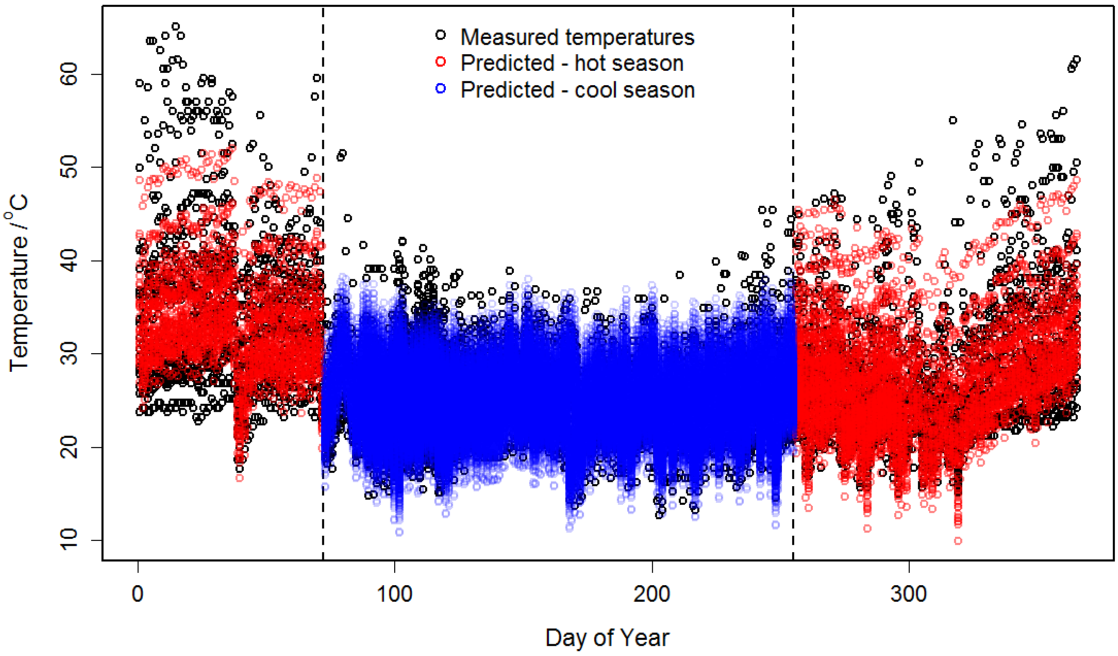
Figure 3.9: Measured 11am and 3pm temperatures used to choose season boundaries. Points show data from individual sites on each day of the year. Dashed lines roughly indicate the beginning and end of the two Bush-crow breeding seasons (April-June, October-November); solid lines show the chosen seasonal boundaries (see text for method); 1 = 1st Jan.



For each dataset (11am and 3pm temperatures, and 3pm temperatures only) I split the data into “hot” and “cool” seasons, subset the “hot” season data to only include those 31 sites where some temperature records were available within the six months, and fitted a two-way ANOVA of $Temperature \sim Date + Site$ to each of the four datasets.

Plotting the predicted values with the raw data showed that the seasonal models did better at representing the higher temperatures in the hot season (Figure 3.10, c.f. Figure 3.8).

Figure 3.10: 3pm temperatures from the seasonal models. Points show measured (black) and predicted cool season (blue) and hot season (red) values from individual sites. Predicted values are plotted semi-transparent, to show the range of the measured values around them. Dashed lines show the season boundaries; 1 = 1st Jan.



Using the threshold data described above, and splitting the data into seasons, I fitted logistic ANOVAs to $Date + Site$ for each threshold in each season. I used these models to predict the probability that the temperature exceeded each threshold on each day at each site, in each season. I then found the mean probability for each site across all days in each season.

3.6 Remote-sensing data

Previous work has shown that the Bush-crow's small range is described by a region of cooler mean annual temperature and lower mean annual rainfall than surrounding areas (Donald et al., 2012). However, mean values are unlikely to be the true biological drivers of the species' range-restriction (Cunningham et al., 2013a), and it is not clear whether these patterns also match the distributions of ecologically similar species, such as the White-crowned and Superb Starlings. I was therefore interested in re-modelling the Bush-crow's distribution against measures of climatic extremes, and comparing the results with those for the two starling species (Chapter 4).

The White-tailed Swallow's global distribution closely matches that of the Ethiopian Bush-crow (Bladon et al., 2015; Mellanby et al., 2008), which raises the intriguing possibility that it may be described by similar aspects of the local climate. To investigate this, I also wanted to fit species distribution models for the White-tailed Swallow (Chapter 6). The common methods used for obtaining climatic and habitat data for these models are described here. To increase comparability between this and previous studies, I restricted the layers to the same area as that used by Donald et al. (2012), extending from 33.17^{o} – 43.67^{o}E, and 1.86^{o} – 6.87^{o}N.

3.6.1 WorldClim climatic data

The WorldClim website contains global climatic variables, averaged from 1950 to 2000, at a range of spatial resolutions (Hijmans et al., 2005). Data layers can be directly downloaded into R (R Core Team, 2016) using the '*getData()*' function in the '*raster*' package (Hijmans et al., 2015). I downloaded the highest resolution data (30 arc-second, or 0.86 km^2 at the equator) for the WorldClim tile (number 27) which incorporated the Yabello region. Although the density of meteorological stations from which the WorldClim data is derived is relatively sparse in the region (Hijmans et al., 2005), and the choice of baseline data can affect projections (Baker et al., 2016), WorldClim data is derived from standardised methods, which are used to generate current, past and future climate layers, and is widely used for species distribution modelling. Following guidance from the results of Donald et al. (2012) and Huntley et al. (2006), I downloaded:

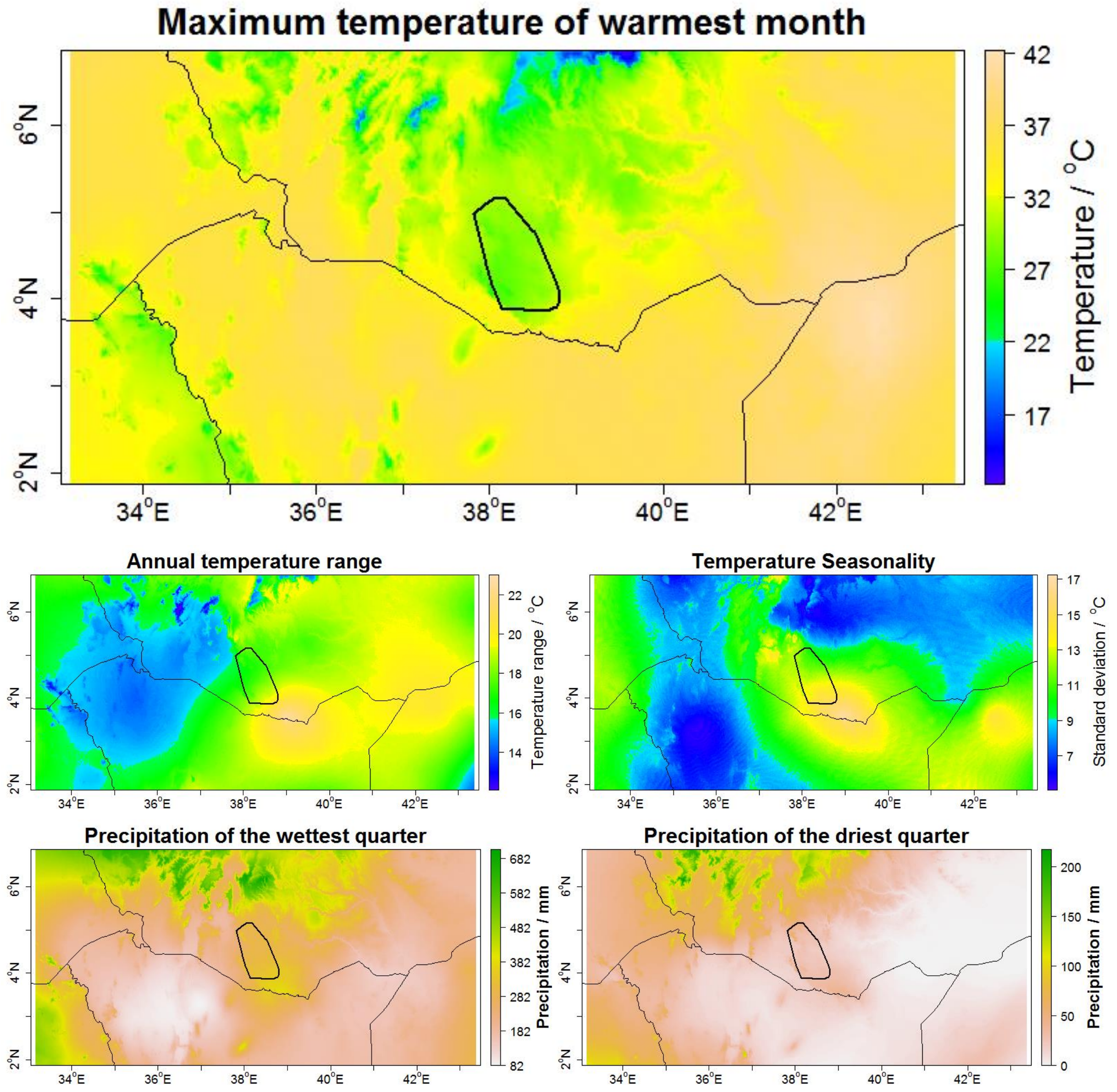
- Monthly maximum temperatures
- Monthly precipitation

- Altitude
- Eight computed bioclimatic variables:
    - Temperature seasonality (standard deviation of monthly temperatures * 100, “$Bio4$”)
    - Maximum temperature of the warmest month (“$Bio5$”)
    - Annual temperature range (maximum temperature of warmest month – minimum temperature of the coldest month, “$Bio7$”)
    - Mean temperature of the wettest quarter (“$Bio8$”)
    - Mean temperature of the warmest quarter (“$Bio10$”)
    - Precipitation seasonality (coefficient of variation of monthly precipitation, “$Bio15$”)
    - Precipitation of the wettest quarter (“$Bio16$”, wet season intensity)
    - Precipitation of the driest quarter (“$Bio17$”, dry season intensity)

Inspection of these variables (Franklin, 2009) across the study region revealed that there was a high collinearity between each of the monthly maximum temperatures, with all pairwise Pearson correlation coefficients greater than |0.93|. Monthly maximum temperatures were also highly correlated with three of the computed temperature layers ($Bio5$, $Bio8$ and $Bio10$), so I retained temperature seasonality and annual temperature range (neither of which were strongly correlated with other temperature metrics) and maximum temperature of the warmest month, as the temperature variables for modelling (Figure 3.11).

Some collinearity was also seen in the monthly precipitation data, although this was less consistent between months. As expected, consecutive dry season months (January–March and June–September) were strongly correlated, as were primary wet season months (April and May with October). I conducted a PCA on the 12 monthly variables, which produced three principal components explaining 59%, 16% and 14% of the variation respectively. I compared these with the available summary metrics for rainfall, and found that the first principal component correlated strongly with precipitation in the wettest and driest quarters. In order to retain clarity in the suite of variables, I decided not to use the monthly PCA results for rainfall, and instead focused on the three downloaded bioclimatic variables (precipitation seasonality and precipitation of the wettest and driest quarters) (Figure 3.11).

Figure 3.11: Bioclimatic variables downloaded from WorldClim (Hijmans et al., 2005) used for modelling. The black polygon indicates the Bush-crow's range.



Maximum temperature of warmest month

Annual temperature range

Temperature Seasonality

Precipitation of the wettest quarter

Precipitation of the driest quarter

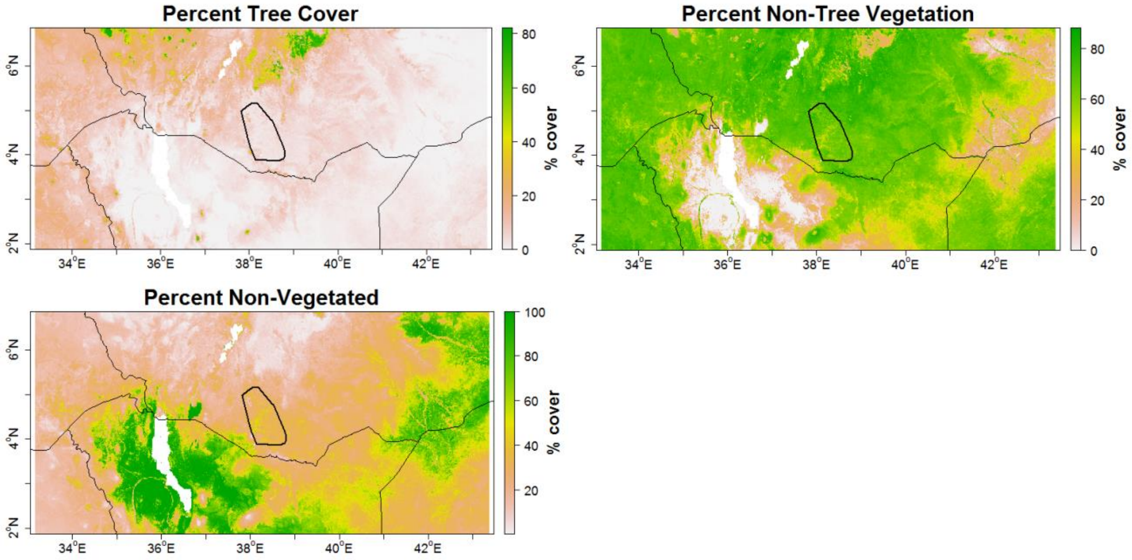
3.6.2 MODIS Vegetation and Temperature data

Data from the North American Space Agency's (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) (NASA, 2016) instruments are available as a number of products calculated from imagery collected daily across the world. The data comes with quality control and/or standard error rates for each pixel (NASA/USGS, 2016), and these were used to process the data and remove pixels with high uncertainty, often caused by the presence of clouds in the image. The vast majority of Bush-crow and Swallow GPS records come from 2005 to early 2015. I used this to restrict my choice of available data on MODIS to 1 January 2005 to 31 December 2014.

Vegetation Cover

The Vegetation Continuous Fields (VCF) product (version 5.1) (Townshend et al., 2011) is available at 250m resolution (MOD44B), and contains annual information on percent tree cover, non-tree vegetation, and non-vegetated surface within each pixel, composed from eight composite images taken throughout the year. Trees provide Bush-crows with nesting sites (Donald et al., 2012; Gedeon, 2006; Mellanby et al., 2008), while the matrix of vegetation and bare ground are important for foraging (Gedeon, 2006), so I downloaded all three available layers for each year. Pairs plots showed that the Pearson correlation coefficient between each pair of years for all three datasets was very high (>|0.8| for all tree cover and non-vegetated pairs, and >|0.7| for all non-tree vegetation pairs), so I calculated the mean value for each of the three coverages across the 10 years (Figure 3.12). Pairs plots on the three means then showed correlations of |0.31| (Tree-NonTree), |0.62| (Tree-NonVeg) and |0.94| (NonTree-NonVeg), so I used only percent tree cover and percent non-tree vegetation for analysis. The VCF layers each contained values identifying the presence of water, so I also averaged across the ten years to produce a water mask to remove lakes from other layers.

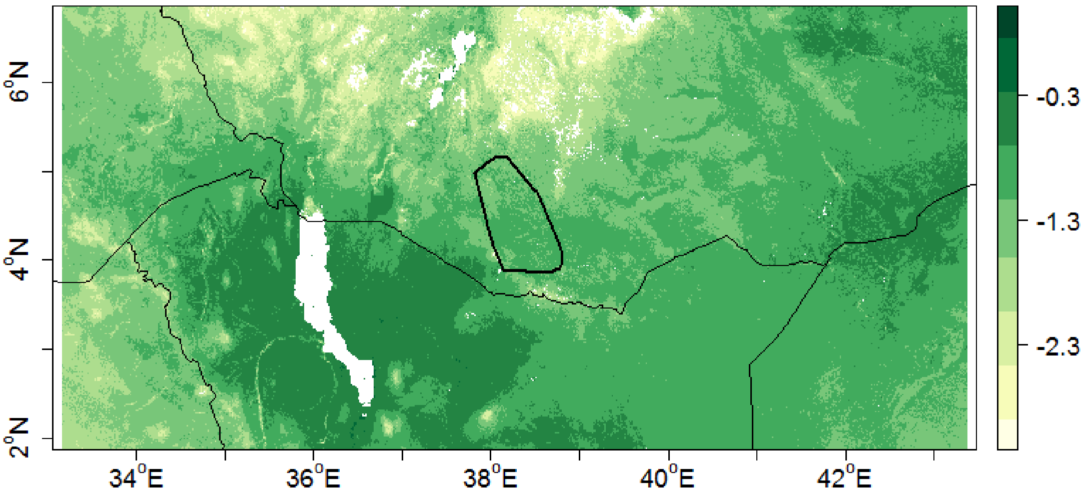
Figure 3.12: Mean tree and vegetation cover calculated from MODIS Vegetation Continuous Fields data from 2005-2014 (Townshend et al., 2011). The black polygon indicates the Bush-crow's range.



Vegetation Indices

Vegetation Indices (version 5) (Didan et al., 2015) are available at 250m resolution (MOD13Q1), with annual data for twenty-three 16-day periods. Donald et al. (2012) used the Normalised Difference Vegetation Index (NDVI) as a measure of habitat variation in their species distribution models, and found that whilst it did not accurately predict Bush-crow occurrence outside of climatic suitability, it did provide information on habitat suitability within the species' range. However, in the field I found that some areas predicted to contain suitable habitat based on NDVI were devoid of Bush-crows and too densely covered with bushes to expect to find birds there. The Enhanced Vegetation Index (EVI) is an improvement on NDVI, as it minimises background variation and maintains sensitivity over dense vegetation. EVI removes residual atmosphere contamination from smoke and thin clouds, creating an overall more accurate image (Didan et al., 2015). I averaged the EVI layers from each 16-day period across the ten years of my study. For each layer, prior to averaging, I used the "Pixel Reliability" layer to check for and remove cloudy pixels. Inspection of the data showed that there was some correlation between consecutive 16-day periods, particularly in the dry seasons. Averaging across the time periods would not correctly reflect the seasonal variation inherent in EVI data, so I conducted a PCA to produce orthogonal layers representing the maximal amount of variation (Figure 3.13).

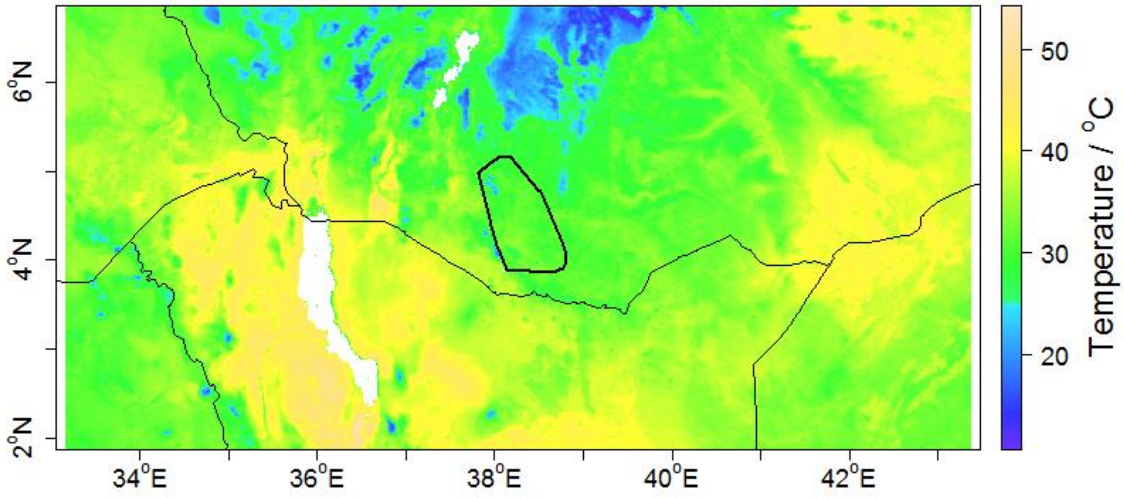
Figure 3.13: The first principal component of EVI score, which explained 84% of the variation in annual EVI data for twenty-three 16-day periods. Data from 2005-2014 (inclusive) was used. The black polygon indicates the Bush-crow's range.



Land Surface Temperatures

Land Surface Temperature (LST) information (version 5) (Wan et al., 2015) is also available from MODIS at 1-km resolution, with annual data for 46 eight-day composites (MOD11A2). I downloaded this data for each year from 2005 to 2014, and used the "Quality Control" layer, included in the download, to check for pixels with high estimation error, and removed those with errors greater than 3 degrees Kelvin. LST values are not produced for cloudy cells, so these did not need to be removed. To reduce the number of layers, I combined each eight-day pair to produce 16-day composites, averaged over ten years, comparable to the EVI layers. Data inspection showed very high correlation between these 16-day composites, so I further averaged each consecutive pair into 32-day composites, but with the first three 16-day periods (which were the most strongly correlated) averaged to produce a single 48-day composite. Correlation between these layers was still high, with the coefficient for all pairs greater than |0.7|, and for all but three greater than |0.8|. I therefore used the original eight-day composites to produce a single, mean LST layer from across the 10 years (Figure 3.14). This was not strongly correlated with the WorldClim temperature data, and so was retained for variable selection (Section 3.6.4).

Figure 3.14: Mean land surface temperature, produced from annual data for 46 eight-day composites. Data from 2005-2014 (inclusive) was used. The black polygon indicates the Bush-crow's range.



3.6.3 African Soil Grids

The ISRIC World Soil Information project compiles global soil data from a variety of sources. For Africa these have been used, together with Africa Soil Information Service (Hengl et al., 2015) ground-truthing samples from much of the continent, to produce 250m resolution data on a number of soil metrics at a range of depths.

Gedeon (2006) suggested that Bush-crows prefer to forage in loosely packed soil, but this was not rigorously tested. A possible indirect mechanism for the Bush-crow's range-restriction is that they are limited by food availability in certain areas, and this could be related to soil type and content. I downloaded the following variables: bulk density (gm^{-3}), percent clay, percent sand, percent silt, soil organic carbon (permilles), and total nitrogen (gkg^{-1}). The higher layers of soil are those most likely to impact the birds, so I obtained data for 0-5cm and 5-15cm depth, except for nitrogen where this was only available as a single layer.

Inspection of the data showed that for each variable, the two layers were nearly identical (Pearson correlation coefficient >|0.98| for each pair), and so I retained only the 0-5cm layer for analysis. However, the percent clay and sand, and the nitrogen and organic carbon contents were also highly correlated (|0.91| and |0.90| respectively) with a few other pairs of coefficients also greater than |0.75|. Bulk density was not correlated with any other variable, and was explicitly considered as a variable with an *a priori* reason for inclusion. I therefore considered bulk density separately, and conducted a PCA on the remaining five variables. Plots of the top two principal components are shown in Figure 3.15, and the raw soil variables are shown in Figure 3.16.

Figure 3.15: First two principal components of five soil layers (percent clay, sand and silt, soil organic carbon and total nitrogen), which explain 63% and 23% of the variation respectively. The black polygon indicates the Bush-crow's range.

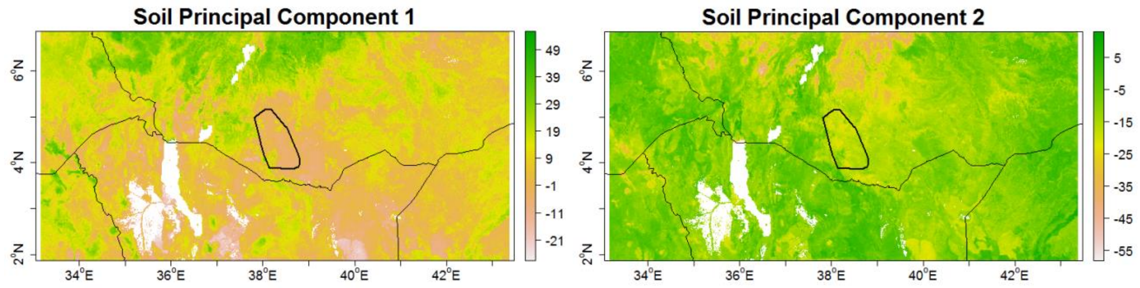
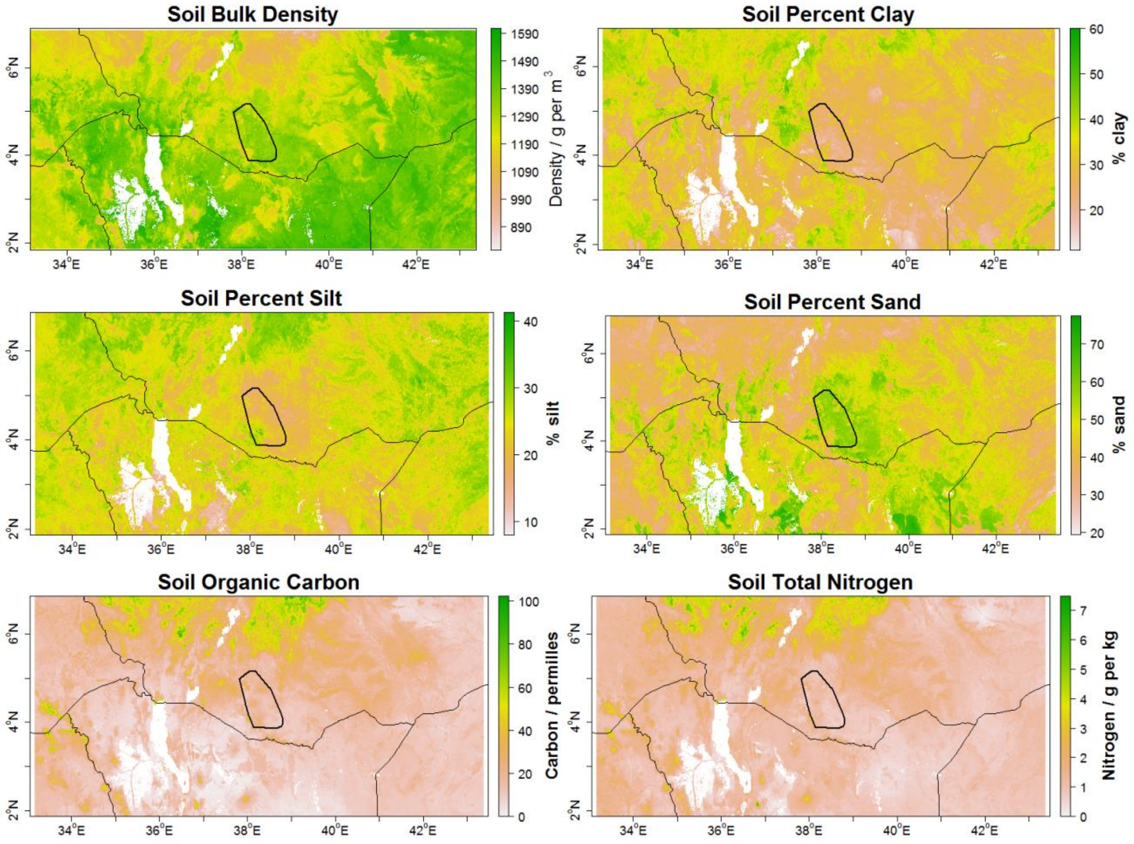


Figure 3.16: Six soil variables downloaded from the Africa Soil Information Service (Hengl et al., 2015). The black polygon indicates the Bush-crow's range.



3.6.4 Variable selection

Taking account of the correlations found above, and selecting principal components such that at least 80% of the variance among input variables was included, I selected a candidate set of 14 variables for use in species distribution modelling (Section 3.7; Chapters 4 and 6):

- Maximum temperature of the warmest month
- Temperature seasonality
- Annual temperature range
- Precipitation seasonality
- Precipitation of the wettest quarter
- Precipitation of the driest quarter
- Altitude
- Percent tree cover
- Percent non-tree vegetation

- EVI principal component 1
- Mean land surface temperature (LST)
- Soil bulk density
- Soil principal component 1
- Soil principal component 2

Comparison of these variables revealed further correlations. Altitude and maximum temperature of the warmest month were highly correlated (Pearson correlation coefficient = |0.96|). Since temperature is more likely to be the direct driver of a species' distribution than altitude, I removed altitude. EVI principal component 1 was correlated with LST (coefficient = |0.86|). Since temperature is already included in the model via three other variables, whereas EVI is not, I removed LST. Precipitation seasonality was correlated with precipitation in the driest quarter (coefficient = |0.84|). Since precipitation seasonality is essentially an effect of precipitation in each of the wettest and driest quarters, both of which are included, I decided to remove seasonality. This left me with 11 variables (three for temperature, two for precipitation, three for land cover and EVI, and three for soil) to use for modelling.

3.7 Species Distribution Modelling

Species distribution modelling was used to describe the climate and habitat associations of the Ethiopian Bush-crow, White-crowned Starling and Superb Starling in Chapter 4, and of the White-tailed Swallow and Pearl-breasted Swallow in Chapter 6. The methods common to both chapters are described here, whilst the selection of each species' presence and absence data is presented in the methods section of the relevant chapter.

3.7.1 Introduction

Species Distribution Models (SDMs) are widely used for predicting the potential ranges of species under current and projected future conditions (Franklin, 2009). Proponents of SDMs emphasise the utility of such models to describe a species' response to environmental variables (Elith et al., 2005; Elith and Leathwick, 2009), and to aid conservation planning for future changes (Pearce-Higgins and Green, 2014). Critics, on the other hand, question the usefulness of the models because they assume the following things, which may not be true. (1) The distribution of the species is in equilibrium with the environmental conditions in which it is found. (2) Species-environment associations indicate cause-and-effect mechanisms between the occurrence of the species and the predictor variable itself or some closely correlated variable for which the variable used is a good proxy. (3) Other processes such as restricted dispersal ability and interspecific interactions have minor effects which can be ignored. (4) Unmeasured environmental variables that really affect the distribution of the species only have minor effects or are well correlated with influential measured variables (Araújo et al., 2005).

Whilst these concerns must be borne in mind when considering the outputs of SDMs, a number of studies have addressed these concerns and provide reassuring results. Araújo et al. (2005) used species-climate data from two separate time periods to fit models using a variety of techniques, and then assessed their ability to predict future ranges. Green et al. (2008) compared the population trends of 42 UK bird species with climate suitability trends simulated using climate envelope models, whilst Gregory et al. (2009) performed a similar analysis across Europe. Stephens et al. (2016) analysed geographic variation in annual climate suitability, according to SDMs, for 525 bird species in Europe and the USA for which annual abundance data was also available. This allowed the differing effects on a species which is favoured by climate change in some places and adversely affected in others to be considered. These studies all demonstrated that range shifts, population trends and changes in abundance are associated with changes in climate, and thus that the climate envelope models are useful in projecting species' actual ranges. Moreover, a comparison of modelling techniques fitted to 226 species from 6 regions of the world found that geographically or environmentally restricted species, such as the Ethiopian Bush-crow and White-tailed Swallow could generally be modelled with greater accuracy, although this did depend on the spatial extent of analysis and type of evaluation (Elith et al., 2006).

3.7.2 Environmental data

Fitting SDMs with a large number of environmental variables can result in spurious correlations arising. To avoid this problem, it is best to define a small number of variables which are likely to be relevant to the species (Pearce-Higgins and Green, 2014). Following inspection of environmental variables considered likely to have an effect on Bush-crow and Swallow occurrence (Section 3.6.4), I was left with 11 variables to use as predictors (Table 3.4).

Variable selection through testing the statistical significance of explanatory variables is not recommended for SDM, as selection rules can lead to a minimally different model being chosen, with the risk of a variable with a true effect being left out (Pearce-Higgins and Green, 2014). Instead, the most likely variables should be selected based on ecological knowledge prior to model fitting (Section 3.6.4). However, I required models with the maximal ability to describe current associations (i.e. with climatic and non-climatic factors (Pearce-Higgins and Green, 2014; Chapters 4 and 6)), and models which could be projected into the future (Chapter 8). I therefore fitted models based on three subsets of the variables in Table 3.4: all variables, climate variables alone, and habitat variables alone.

Table 3.4: Variables used to fit Species Distribution Models.

Variable	Source	Resolution	Time period
Temperature Seasonality (standard deviation * 100)	WorldClim	30 arc-second	Mean, 1950-2000
Maximum temperature of warmest month (^{o}C)	WorldClim	30 arc-second	Mean, 1950-2000
Temperature Annual Range (Max of warmest month – Min of coldest month) (^{o}C)	WorldClim	30 arc-second	Mean, 1950-2000
Precipitation of the wettest quarter (mm)	WorldClim	30 arc-second	Mean, 1950-2000
Precipitation of the driest quarter (mm)	WorldClim	30 arc-second	Mean, 1950-2000
Percent Tree Cover	MODIS	250m	Mean, 2005-2014
Percent Non-Tree Vegetation	MODIS	250m	Mean, 2005-2014
Enhanced Vegetation Index Principal Component 1	MODIS	250m	1st principal component of EVI, across 23 annual 16-day periods, 2005-2014
Bulk density (0-5cm) (kgm^{-3})	African SoilGrids	250m	NA
Soil Principal Component 1	African SoilGrids	250m	NA
Soil Principal Component 2	African SoilGrids	250m	NA

3.7.3 Modelling techniques

The choice of modelling technique is among the largest contributor to variation in SDM output and projection (Buisson et al., 2010; Dormann et al., 2008), therefore assessment of the relative ability of multiple techniques to describe the data is sensible. I used the "*biomod2*" package (Thuiller et al., 2009) in R (R Core Team, 2016) to fit a series of distribution models. "*Biomod2*" allows the use of ten algorithms (Table 3.5) which are described below.

Table 3.5: Model algorithms available in "biomod2" (Thuiller et al., 2009).

Biomod2 name (abbreviation)	Other names (abbreviation)	Data	Type^{+}	References
Surface Range Envelope (SRE)	BIOCLIM	Presence-only	Profile matching	Busby (1991), Lindenmayer et al. (1991)
Generalised Linear Model (GLM)	-	Presence-absence	Statistical, regression	McCullagh and Nelder (1989), Austin et al. (1983)
Generalised Additive Model (GAM)	-	Presence-absence	Statistical, regression	Hastie and Tibshirani (1990), Yee and Mitchell (1991)
Multiple Adaptive Regression Splines (MARS)	-	Presence-absence	Statistical, regression	Friedman (1991)
Flexible Discriminant Analysis (FDA)	Mixture Discriminant Analysis (MDA)	Presence-absence	Statistical	Hastie et al. (1994)
Classification Tree Analysis (CTA)*	Decision Tree Analysis (DT), Regression Tree Analysis (RTA)*	Presence-absence	Machine learning	Breiman et al. (1984)
Artificial Neural Networks (ANN)	-	Presence-absence	Machine learning	Ripley (1996)
Generalised Boosting Model (GBM)	Boosted Regression Trees (BRTs)	Presence-absence	Machine learning	Ridgeway (1999)
Random Forest (RF)	-	Presence-absence	Machine learning	Breiman (2001), Prasad et al. (2006)
Maximum Entropy (MaxEnt)	-	Presence-background	Machine learning	Phillips et al. (2006)

$^{+}$ ***Type** is based on classification in Elith et al. (2006) and Franklin (2009).*

**Although the name CTA is used in "biomod2", this function actually conducts a Decision Tree-based method, which can be either "Classification" or "Regression" (i.e. CTA or RTA) depending on whether the response variable is categorical or continuous, respectively (see text). Most commonly, SDM uses a categorical response, species presence or absence.*

Surface Range Envelope (SRE, or BIOCLIM) (Busby, 1991) is a profile-matching method, which summarises the distribution of presence points with respect to environmental variables, without reference to absence or background points. It defines the multi-dimensional environmental space of a species in terms of minimum and maximum tolerances across the range, without allowing for regions of absence (Elith et al., 2006; Franklin, 2009). Prediction to new areas is conducted by identifying points where the environmental conditions fall within the limits of those known from the occurrence profile (Lindenmayer et al., 1991).

Generalised Linear Models (GLMs) (Austin et al., 1983; McCullagh and Nelder, 1989) are a large group of statistical models which can be fitted to presence-absence, occupancy probability and abundance response variables with a range of predictors. They assume that an algebraic parametric function represents the mean value of the dependent variable (probability of occurrence or population density) in terms of the independent variables, with deviations from the expected mean occurring. The use of different error terms allows for differences in the distribution of deviations from the fitted mean values, and the inclusion of a link function accounts for different forms of the relationship between the dependent and independent variables. GLMs with curvilinear link functions are particularly useful for modelling ecological data, which often do not conform to the assumptions of ordinary least squares linear regression and other simple GLMs (Franklin, 2009). In SDMs with presence-absence data, GLMs are usually fitted via logistic regression and maximum likelihood estimation, with model selection usually conducted by a backwards stepwise procedure. GLMs allow for models of varying complexity to be fitted, but do not allow for non-linear models (Elith et al., 2006).

Generalised Additive Models (GAMs) (Hastie and Tibshirani, 1990) are similar to GLMs, except that they use non-parametric smoothing functions to fit non-linear relationships between the predictor and response variables (Elith et al., 2006), and thus allow the data to determine the shape of the response curves in a more flexible way (Yee and Mitchell, 1991). GAMs are particularly useful for visualising relationships in the data. In some cases, the shape of the GAM may suggest a form of link function for a GLM. A number of comparative studies have found that GAMs outperform GLMs in explanatory SDM (e.g. Randin et al., 2006). However, the additive nature of GAMs makes it difficult to incorporate interaction terms, and like GLMs they can be difficult to fit to large datasets, meaning that they may not always be able to build realistic enough models (Franklin, 2009). Moreover, GAMs often do not make accurate predictions outside of the ranges of the explanatory variables upon which they were built (Pearce-Higgins and Green, 2014; Randin et al., 2006).

Flexible Discriminant Analysis (FDA) (Hastie et al., 1994) divides the distribution of each predictor variable into a series of sub-classes, each with a Gaussian distribution, determined by the variation in the training data. These sub-classes are classified to describe the distribution density of the environmental variables (Virkkala et al., 2010), by minimising the overlap between the Gaussian distributions of predictors for the presence and absence points.

Decision Trees (DT) (Breiman et al., 1984) search all of the potential splits that could be applied to each of the predictor variables, and select the one which maximises homogeneity, or minimises variance or deviance, within the two resulting groups of data. The process is repeated to continue splitting each subgroup (recursive binary partitioning) to produce a “decision tree”, termed a regression tree for a continuous response, or a classification tree for a categorical response (such as species occurrence). Splitting is normally stopped when the partitioning fails to increase subgroup homogeneity above a defined threshold, or when the resulting groups contain a defined minimum number of data points (Franklin, 2009). The maximal tree is then pruned via cross-validation to remove splits which add the least to subgroup homogeneity, which eliminates over-fitting. The process makes no assumptions about the relationships between response and predictor variables, and deals with multi-level categorical predictor variables and thresholds in the data in a natural way, but because of this may struggle to accurately characterise truly linear relationships, and can require larger datasets in order to detect patterns (Franklin, 2009). They are also sensitive to small changes in the data (Prasad et al., 2006), and offer poor predictive performance (Elith et al., 2008). When used for explanation, single decision trees are easier to interpret than ensembles of trees (see below) (Prasad et al., 2006). When used for prediction, the output of a classification tree is analogous to the probability of an event occurring predicted by GLM or GAM, which is a useful property for SDM (Franklin, 2009).

Multiple Adaptive Regression Splines (MARS) (Friedman, 1991) offers a hybrid between regression techniques (such as GLMs and GAMs) and partitioning methods (such as DT). The algorithm searches for inflection points (knots) within the predictors, and fits localised regression models to each section between knots, generating continuous, smooth functions. Fitting proceeds until a maximum model size is reached, after which pruning removes functions which contribute little to the model. MARS is computationally faster than GAMs, and allows for greater flexibility than traditional GLM methods (such as the ability to specify interaction terms over only part of the environmental range and the ability to handle large numbers of predictor variables), whilst creating a smoother output than DT. However, outputs can be biased by local variations in the data, which leads to a loss of predictive power when extrapolating to new environments (Elith et al., 2006; Franklin, 2009; Prasad et al., 2006).

Generalised Boosting Models (GBM, or Boosted Regression Trees, BRT) (Ridgeway, 1999) build on the DT process by growing multiple trees (30-80). For each successive tree, the training data are re-weighted to favour selection of samples which were misclassified by the previous model. This overcomes the inaccuracies of a single model, and allows more complex responses to be modelled. Complexity is measured by the number of trees in the boosted model. Maximal trees are not pruned but their predictions are averaged, which reduces the variance of the output error and increases the stability of the resulting model to outliers or changes in the data (Elith et al., 2006; Prasad et al., 2006). BRTs benefit from the advantages of tree-based methods, such as accommodating missing data and outliers, and fitting non-linear relationships and interaction effects, whilst overcoming the tendency for over-fitting (Franklin, 2009) and poor predictive performance of single trees (Elith et al., 2008). However, the ease of interpretation of the effects and thresholds in predictor variables associated with single trees is lost in ensemble methods (Elith et al., 2006; Franklin, 2009; Prasad et al., 2006), although partial dependence plots for each predictor allow graphical representation (Elith et al., 2008), and the relative importance of predictors can be measured by how many times each variable is selected across models (Franklin, 2009).

The Random Forests (RF) (Breiman, 2001) algorithm is a further extension of BRT, where each tree is grown using a subset of the data, and each split in each tree is chosen from a random subset of the available predictor variables. This generates diversity among trees, and therefore robustness of the model to changes in the data, whilst averaging across unpruned trees reduces model variance. Samples not used in fitting each tree can be used to calculate error rates and variable importance. To reduce bias generated by sampling predictor variables, a much larger number of trees (500-2000) are grown than in BRT algorithms (Prasad et al., 2006).

Maximum Entropy (MaxEnt) (Phillips et al., 2006) is a method for making predictions from incomplete information; an unknown probability distribution is best estimated as the distribution with maximum entropy, subject to constraints imposed by the information available. The information is a set of real-valued features, whose empirical average over a set of sample points is expected to match the values elsewhere in the distribution. No assumptions are made about what is not known. The unknown probability distribution is proportional to the probability of occurrence at each site (Elith et al., 2006). MaxEnt was developed for use with presence-only data and to work with small, undesigned samples, but can be used with true or pseudo-absence data like other methods (Franklin, 2009).

Artificial Neural Networks (ANN) (Ripley, 1996) derive composite features from linear combinations of the predictor variables, and model the response as a non-linear function of those features. Like Decision Trees, they apply hierarchical partitions to the data. They overcome empty areas of the environmental space in a way that parametric functions cannot. ANNs are not easily interpretable, although tools have been developed to offer contributions of predictors, analogous to coefficients in regression (Franklin, 2009). Training neural networks can be tricky as one must make a number of decisions prior to the fitting process, so experience is required to use them effectively. It is not clear whether this difficulty is partially responsible for the weaker performance of ANNs found by some comparative studies (Dormann et al., 2008; Franklin, 2009).

The choice of modelling technique can have a substantial effect on the predictions made by SDMs (Dormann et al., 2008; Lawler et al., 2006), so I investigated this effect on my study species by utilising most of the modelling techniques available in "*biomod2*" (Thuiller et al., 2009). In the interests of computation time and output size, I omitted three techniques which, based on the literature, seemed unlikely to improve the results. These were: "SRE" (BIOCLIM) due to its consistently weaker performance (Elith et al., 2006); "ANN" (Advanced Neural Networks) due to their cumbersome nature and disconnection from biological mechanisms (Franklin, 2009); and "CTA" (Decision Trees), as both BRT and RF provide demonstrable prediction improvements on the single decision tree modelling process (Franklin, 2009; Prasad et al., 2006). Given previous findings (Elith et al., 2006; Elith and Graham, 2009; Lawler et al., 2006;

Marmion et al., 2009; Prasad et al., 2006), my expectation was that the machine-learning (MaxEnt) and ensemble tree methods (BRT, RF) would perform best (Elith et al., 2006; Franklin, 2009; Guisan et al., 2007) and have the strongest predictive capacity (Prasad et al., 2006).

3.7.4 Model evaluation

There are a number of available measures of model performance, but the most widely used is the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot (Hanley and McNeil, 1982; Pearce-Higgins and Green, 2014). AUC is favoured because it is independent of the threshold chosen to convert continuous probabilities of occurrence into binary presence-absence scores, which makes it beneficial for comparing between different model fitting techniques (Franklin, 2009). It is commonly abbreviated to AUC, but in "*biomod2*" (Thuiller et al., 2009) it is referred to as ROC. AUC can range from 0.5 (random predictions) to 1.0 (perfect prediction), with values greater than 0.9 considered as high, and those greater than 0.7 considered useful (Swets, 1988).

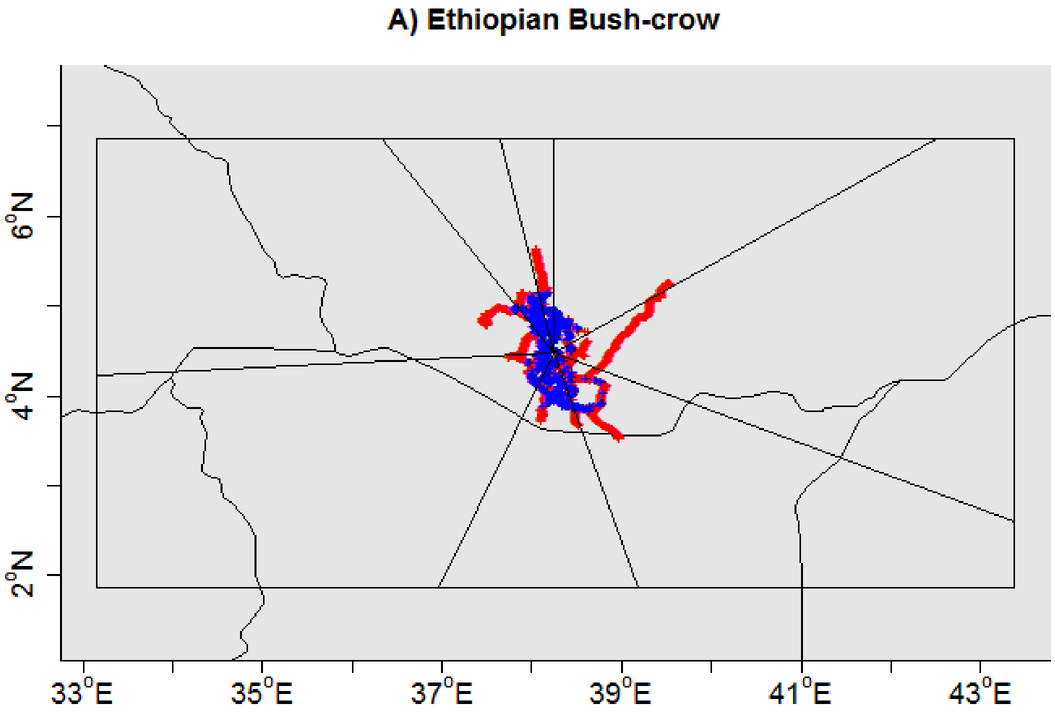
The Bush-crow and Swallow data used for modelling (Chapters 4 and 6) were not representative of the species' true prevalence in the environment, because the samples were biased to areas where the birds are known to occur. The choice of model performance metric therefore needs to be insensitive to species prevalence (Franklin, 2009). There is some debate over whether AUC is truly independent of species prevalence, as AUC values tend to be low for species with very low prevalence, or whether some observed trends are in fact due to differences in species ecology (Huntley et al., 2007; Manel et al., 2001).

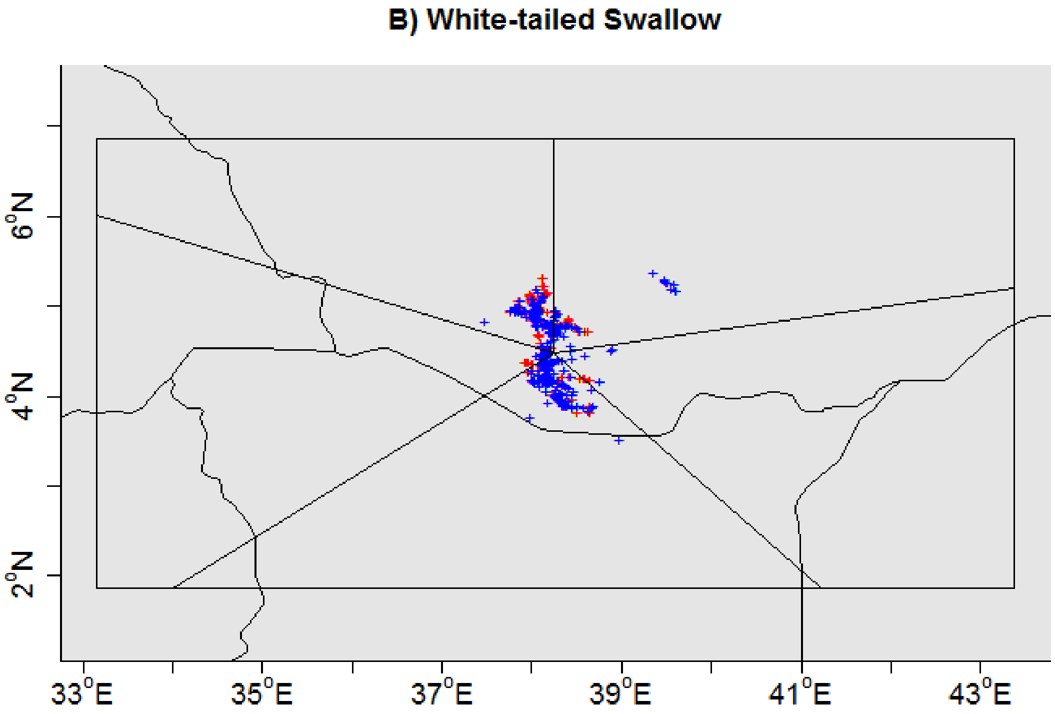
In order to generate robust estimates of prediction success, testing or validation data, which are independent of the training or calibration data used to build the model, must be used to evaluate model accuracy (Fielding and Bell, 1997). Ideally, testing data should come from an independent sample, such as using planned survey data to verify models built using incidental records from unplanned surveys and museum records (Elith et al., 2006). However, such independent samples are often not available, and a number of other techniques exist to partition data into training and testing samples, such as bootstrapping (sampling with replacement), k-fold partitioning (k – 1 partitions pooled for testing) and jack-knifing (n – 1 partitions used for training) (Fielding and

Bell, 1997). In all cases there is a trade-off between the merits of having a large training sample (increased model accuracy) and a large testing set (reduced variance in error estimate) (Fielding and Bell, 1997). Repeated partitioning and model fitting can be used to overcome this, by averaging over multiple estimates of accuracy (Dormann et al., 2008; Fielding and Bell, 1997). This is normally done by randomly assigning points to the training and testing sets for each run. However, this method does not account for spatial autocorrelation, and inflates estimates of model fit (Pearce-Higgins and Green, 2014). Huntley et al. (2007) used a jack-knife approach, whereby models were fitted to data from *k*-1 geographically determined map ‘panels’, and the values for each cell predicted using the model which was not trained over that cell. Jack-knifing necessarily produces lower AUC values than full model fitting, but more accurately reflects model performance as it greatly reduces the problem of spatial autocorrelation. There is a trade-off between larger panels, which remove more spatial autocorrelation, and smaller ones, which enable model fitting for species with limited geographic distributions (Pearce-Higgins and Green, 2014). Huntley et al. (2008) found that the most marked difference between jack-knifing and full model performance was seen for range-restricted species, due to the high proportion of presence locations which are omitted in a single panel.

In order to get a spread of presence, true- and pseudo-absence points (the latter were not used for model testing) within each panel, I divided the study region using spokes radiating from the centre of the Bush-crow’s range (Figure 3.17). The range centre was calculated by scoring each 0.05 degree cell across the range by whether or not it contained a Bush-crow or Bush-crow nest record, and calculating the geodesic centroid of the presence cells. Cell sizes of 0.01, 0.05 and 0.1 degrees were tried, along with a centroid based on all presence records. The centroids from 0.01 degree cells and all records were skewed by the higher density of records around Dida Hara (where much previous work has been conducted (Donald et al., 2012; Gedeon, 2006) and along the main road, while the 0.1 degree centroid moved south-east of most records, due to the small number of records scattered over a larger area there. The centroid based on 0.05 degree cells was therefore preferred.

Figure 3.17: Geographic segments used for *k*-fold cross-validation of models fitted to *A*) Ethiopian Bush-crow and *B*) White-tailed Swallow data. Presence locations are shown in blue, true absences are shown in red.





Beginning at due north, I split the range into eight segments for the Bush-crow, and five for White-tailed Swallow, choosing boundaries which spread the total number of points (presence, true- and pseudo-absence) evenly between the segments. The disadvantage of this approach is that the centre of the panel, where the spokes meet, suffers from spatial autocorrelation, but given the species' limited ranges, splitting into rectangular panels would result in too few observations in most panels for modelling to be robust (Huntley et al., 2008). Fewer segments were required for White-tailed Swallows, because the greatly reduced number of true absence points made it harder to ensure that each segment contained some points for testing.

Models were built on k-1 segments, and used to predict occurrence in the k^{th} segment. Predictions from each modelling algorithm were compiled across segments, and used to compute a single AUC score for each algorithm under the k-fold jack-knifing approach. These scores were compared to assess the ability of each technique under each set of environmental predictors (climate-only, habitat-only, and all).

Fielding and Bell (1997) recommend that if a predictive model is required, then once estimates of accuracy have been obtained via partitioning, all data should be used to estimate model parameters. I re-fitted each model algorithm to the full bird datasets with each set of environmental variables, and compared the AUC scores with those produced by jack-knifing.

3.7.5 Variable importance and response plots

To investigate the importance of each variable to the model, I re-fitted the best models for each species to the k-fold data, in each run leaving out one of the predictor variables. For each removed predictor variable, I calculated the k-fold probability of occurrence for each presence and true absence location. I used these probabilities of occurrence to estimate the model AUC with each variable removed. These scores were subtracted from the AUC of the maximum model to give delta AUC. The higher the value of delta AUC, the more important the variable is to the full model. Delta AUC for the climate-only and habitat-only models was also calculated.

The response of probability of occurrence to each predictor variable (when all others are held constant), can be estimated for each model, and output as evaluation strips (Elith et al., 2005). This is useful for interpreting the biological effect of each predictor on the species of interest, and can be used in conjunction with range projection maps for interpreting each model. Bird species in the Sierra Nevada, whose century-long range shifts match climatic changes, respond most strongly to the climate variable to which climate envelope models suggested they were most sensitive (Tingley et al., 2009).

3.7.6 Model projections

Assessment of the spatial predictions of different modelling techniques is an important part of model comparison, and Franklin (2009) recommends that before conducting ensemble modelling, the spatial overlap of alternative SDMs should be assessed. I used the seven fitted algorithms, and the three different environmental raster stacks used to build them, to map the predicted current distribution of each species according to each algorithm. The results are presented in Chapters 4 and 6.

4 THE DISTRIBUTION AND LOCAL DENSITY OF THE ETHIOPIAN BUSH-CROW

"I thought that red men couldn't survive outside of the city."

4.1 Introduction

The restricted range of the Ethiopian Bush-crow (Collar and Stuart, 1985) has puzzled ornithologists ever since its discovery in 1938 (Moltoni, 1938). Its limitation to a seemingly unremarkable area of *Acacia* woodland and thorn-scrub in southern Ethiopia, despite the ubiquity of this habitat in the region, could not seemingly be explained by habitat variation (Donald et al., 2012). It was only in 2012 that Donald et al. (2012) provided the first indication of the explanation for the Bush-crow's tiny global range, by modelling its distribution in relation to climatic variables. They found that the species' range was accurately described by a climatic envelope based on mean annual temperature, temperature seasonality, and annual precipitation. However, they did not investigate the effects of maximum temperatures or annual variation in rainfall on the Bush-crow's distribution. Huntley et al. (2006) fitted species distribution models for birds in Europe and Africa, using mean temperatures of the warmest and coldest months as proxies for temperature extremes, and estimates of the length and intensity of wet and dry seasons in Africa, reasoning that these are more likely constraints on species' ranges than mean values. They found that models using temperature extremes consistently outperformed those using annual temperature metrics.

Temperature could affect Bush-crow distribution in a number of ways. It may directly determine presence at or absence from a site, if there is a threshold beyond which populations are unable to persist (Frumkin et al., 1986; Furness, 1988). Alternatively, or in addition, there might be a more gradual effect in which population density or mean group size is reduced in warmer areas which are less thermally suitable (Forrester et al., 1998). There could also be effects of temperature on aspects of behaviour, such as the height at which nests are built.

Bush-crows' nests, built at the top of *Acacia* trees or on tall manmade structures (Benson, 1942; Bladon et al., 2016), provide a thermally stable nesting environment (Töpfer and Gedeon, 2012), potentially buffering the contents against high temperatures. Temperatures tend to decline with height above the ground (Stone and Carlson, 1979), and it is possible that building nests as high as possible is a behavioural response to reduce thermal stress on adults, eggs or nestlings.

If the Bush-crow's small global range is determined by some aspect of local climate, then it would be expected that wider geographic ranges of sympatric and ecologically similar species, such as the White-crowned Starling *Lamprotornis albicapillus* or Superb Starling *Lamprotornis superbus* (Bladon et al., 2016; Dellelegn, 1993; Redman et al., 2009), would not be described by the same climatic features as the Bush-crow's range.

Here, I re-examine factors affecting the distribution of the Ethiopian Bush-crow at two spatial scales. I investigate the effects of temperature and habitat on local Bush-crow population density and group size, within, at the edge of, and outside the species' range. I compare these relationships with those for the White-crowned Starling. I then model the factors affecting the Bush-crow's global distribution using measures of climatic extremes and a wider range of habitat variables than Donald et al. (2012). By fitting similar climate-only models to the distributions of the White-crowned Starling and Superb Starling, I directly compare the effects of temperature and precipitation on the range limits of three ecologically similar species, to assess the importance of temperature in limiting the Bush-crow's distribution.

4.2 Methods

I investigated whether local temperature patterns matched the presence/absence of Bush-crows (Section 4.2.1), modelled the effect of temperature on Bush-crow and White-crowned Starling bird and nest presence, density and group size (Section 4.2.2), modelled the effects of habitat on Bush-crow presence and density (Section 4.2.3) and fitted a suite of species distribution models (SDMs) for the Bush-crow, White-crowned Starling and Superb Starling (Section 4.2.4).

4.2.1 Preliminary investigation of temperature patterns

Using data from my network of iButton temperature loggers (Section 3.4.2), I investigated whether local temperature patterns correlated with Bush-crow occurrence.

Temperatures at sites where Bush-crows are present and absent

I split the sites where I had recorded local temperature data based on the presence or absence of Bush-crows or their nests nearby. For most sites, this information came from my bird transects, but additional ‘presence’ sites occurred where I had conducted Bush-crow behavioural studies (Chapter 5), and ‘absence’ sites where I had conducted habitat-only transects outside of the Bush-crow’s range. I spent sufficient time at these sites to have detected birds or nests had they been present. There remained some study sites near to my White-tailed and Ethiopian Swallow study nests where the presence or absence of Bush-crows was unknown.

Having divided the year into “hot” and “cool” seasons, and fitted linear and logistic regressions of temperatures and temperature threshold exceedance within each season (Section 3.4.2), I compared the predicted values from these models between Bush-crow presence and absence sites.

I calculated the mean predicted temperature at each site in each season and compared presence and absence sites using t-tests in the cool season, and Wilcoxon tests in the hot season (as the hot season data were not normally distributed).

Temperature thresholds

Rather than responding to maximum temperatures, birds might be affected by the frequency of extreme weather events (Cunningham et al., 2013a). I therefore investigated how the difference in threshold exceedance between presence and absence sites varied with temperature. I calculated the number of days at each site that exceeded each 1°C threshold from 10°C to 70°C and calculated the difference between the mean number of days at presence and absence sites. I then calculated the mean probability of each site exceeding each threshold in the hot and cool seasons (Section 3.5.3), and again found the difference between presence and absence sites for each threshold temperature.

4.2.2 Effects of temperature on local occurrence and density

To investigate the effects of temperature on Bush-crow and White-crowned Starling abundance, I used the data on bird and nest presence and density, group size and nest heights calculated in Sections 3.3 and 3.4. I investigated the effects of different temperature metrics (calculated in Section 3.5.3) on these responses. Temperature variables used were mean predicted 3pm and 11am+3pm temperatures across the whole year, and separately for the hot and cool seasons, and the mean probability of 3pm and 11am+3pm temperatures exceeding temperature thresholds across the whole year, and in each season. Based on the apparent differences between presence and absence sites at different temperature thresholds, I decided to use thresholds spaced 2°C apart from 24–30°C, giving a total of 30 explanatory variables. I treated each 3-km triangular transect or each 1-km leg of an “edge-of-range” transect as an independent datum.

As fewer temperature loggers were deployed when bird fieldwork was not in progress (Section 3.5.3), it was only possible to obtain temperature predictions for the hot season from 31 sites. Of these, only some had birds or nests recorded at them, which further reduced the sample of sites with nest height or group size and temperature data in the hot season. Therefore, to avoid fitting models to too few data, I did not use hot season explanatory variables for models of presence-only site density, nest height or group size, leaving 20 temperature variables for these models.

Multiple testing correction

Conducting multiple statistical tests leads to an increased chance of making type I errors when assessing significance (Benjamini and Hochberg, 1995; Verhoeven et al., 2005). One approach to deal with this is the use of a Bonferroni-type correction such as sequential Bonferroni adjustments (Hochberg, 1988; Holm, 1979), which control the familywise error rate (FWER), i.e. the chance of falsely rejecting the null hypothesis at least once. However, in order to control the FWER as the number of models increases, such corrections necessarily inflate the type II error rate (Verhoeven et al., 2005) (falsely accepting the null hypothesis), thereby decreasing the power of the test to detect truly significant results (Benjamini and Yekutieli, 2001; Verhoeven et al., 2005). Additionally, a sequential Bonferroni approach does not take into account the number of significant tests, which can be an important aspect of interpretation (Moran, 2003), albeit of more value when the variables being tested are independent (García, 2003). Conversely, when variables are highly correlated, the significance threshold required may be increased, even when a large number of tests are performed (García, 2003).

Benjamini and Hochberg (1995) proposed an alternative correction, which is less conservative with respect to type I errors, whilst allowing a reduction in the type II error rate, and is thus intermediate between uncorrected and Bonferroni testing (Genovese and Wasserman, 2002). The False Discovery Rate (FDR) controls the proportion of results which are deemed significant that are in fact type I errors (Verhoeven et al., 2005), and is particularly useful when analysing large multiple-test tables in which several or many null hypotheses are rejected (García, 2003). It also has the same control as FWER methods when all null hypotheses are true (García, 2003; Verhoeven et al., 2005).

Numerous additions and adjustments to the FDR have been proposed: the False Non-Discovery Rate which complements the FDR with proportion of non-rejections of the null hypothesis which are incorrect (Genovese and Wasserman, 2002); the positive False Discovery Rate (pFDR) which utilises information on the rate of false discoveries and requires that at least one test is called significant (Storey, 2003; Storey and Tibshirani, 2003), and the associated q-value (the minimum pFDR at which a feature can be called significant) which arises from fixing the rejection region and estimating the error rate, and offers a measure of significance in terms of the FDR rather than the false positive rate (a standard P-value) (Storey, 2002; Storey and Tibshirani, 2003); the decisive False Discovery Rate which arises from a decision-theoretic framework (Bickel, 2004a, 2004b); and Bayesian methods such as the local False Discovery Rate, e.g. (Bickel, 2013).

The use of pFDR control and the calculation of q-values are straightforward and provide powerful methods for allowing for multiple testing (Storey, 2002). However, the results only hold for independent tests, or those exhibiting weak dependence (Storey and Tibshirani, 2003). As all of my temperature variables are derived from the same data, they are not independent, and therefore pFDR and q-values would not be robust. The

FDR control procedure outlined by Benjamini and Hochberg controls the FDR both when all tests are independent (Benjamini and Hochberg, 1995) and when tests are positively correlated (Benjamini and Yekutieli, 2001). When further examining the behaviour of Benjamini and Hochberg's procedure, Genovese and Wasserman (2002) found that it is the optimal distribution-free method to use.

I therefore used the original FDR control procedure to correct for multiple testing for each response variable: in each case all models (m) were fitted, and their P-values ranked in ascending order $P_{(1)} \leq P_{(2)} \leq \cdots \leq P_{(m)}$. $H_{(i)}$ corresponds to the null hypothesis for $P_{(i)}$. k was taken as the largest i for which $P_{(i)} \leq \frac{\alpha}{m}\, i$ (where $\alpha = 0.05$), and all null hypotheses $H_{(1)} \ldots H_{(k)}$ were rejected (Benjamini and Hochberg, 1995).

Model forms

I fitted logistic regressions to the presence-absence data for each species or nest, with a logit link and binomial error, and each temperature variable in turn as the predictor. I used data from all sites, both inside and outside of the range.

For bird, bird group and nest density on each transect, I fitted Poisson regressions with a log-link, and with the natural logarithm of area surveyed (in kilometres squared) for each object (calculated in Section 3.3.2) as an offset. The models were tested for over-dispersion using the '*dispersiontest*' function in the "*AER*" package (Kleiber and Zeileis, 2008) in R (R Core Team, 2016). A one-tailed test was used as it is more conservative when testing for over-dispersion, and over-dispersion is both more likely (based on initial data inspection) and more troublesome where it occurs than under-dispersion is. Models which were over-dispersed were re-fitted using a quasi-Poisson model (Venables and Ripley, 2013). Models were fitted to data from all sites, and to data from only sites where the species in question had been recorded (presence-only models).

Mean group size on each transect where birds were recorded was modelled using ordinary least squares regression with normal error and an identity link.

To directly compare differences between species, I fitted the presence, density and group size models to Bush-crow and White-crowned Starling data combined, with species as a categorical explanatory variable. In these models, FDR control was used to test the significance of the interaction term and each single term during backwards stepwise selection.

Lapse rate and nest height

I investigated the effect of height above the ground on ambient air temperature (Lapse rate) by attaching iButtons to a pole at one-metre intervals from 0.4–9.35 metres (the final unit only 95cm above the penultimate due to the height of the pole). Each iButton was sheltered by a Stevenson screen made from a Tupperware box, painted white to reduce heat absorption and with holes drilled around the bottom half to allow air flow whilst providing weather protection. All boxes were attached to the same side of the pole, which was erected vertically and left in constant sun at Dida Tuyura, a site with good Bush-crow habitat with a large number of nests, for five days from 9th to 14th April 2015, with iButtons recording temperature every 15 minutes.

I fitted a series of ordinary least squares regressions with mean temperature across the five days as the dependent variable and time of day, height and their interaction as independent variables. Time of day was fitted as a factor. To deal with unequal variance and non-normal errors found in the data, I used the Box-Cox function in the '*MASS*' package (Ripley et al., 2013) in R (R Core Team, 2016) to suggest transformations, and the result was used to transform the response variable and fit an alternative power-link function. Deletion of terms in the favoured model was tested using an *F*-test.

Using the transect data described above, I regressed the mean height above the ground of Bush-crow and White-crowned Starling nests, as a percentile of the distribution of local tree heights (Section 3.4.2), against temperature using ordinary least squares regression with identity link and normal errors. I fitted separate models for each species and also a combined model with a species by temperature interaction included.

I calculated individual nest heights as a percentile of the distribution of local tree heights (Section 3.4.2), and fitted a random effects model with temperature, location and nest type (Bush-crow or White-crowned Starling) as explanatory variables. Two temperature terms, mean 3pm temperature and mean 11am and 3pm temperature, and two location terms, distance from the edge of the range and percent distance from the centre to the edge of the range, were each fitted separately, giving four maximal model structures. Transect ID (a single triangular transect or 1-km leg of an "edge-of-range" transect) was included as a random effect.

4.2.3 Effects of habitat on local occurrence and density

The methods for collecting and processing habitat data are described in Section 3.4. To model the effect of habitat on Bush-crow occurrence and density, I restricted the data to sites which fell within the Bush-crow's range, as defined by the convex hull (Donald et al., 2012). For the "edge-of-range" transects, where more fine scale information was available, I found the 1-km leg most distant from the Bush-crow range centre on which Bush-crows or their nests had been recorded, and assigned all legs closer to the centre than this as inside, and all legs outside of this as outside. Soil samples were not collected on the "edge-of-range" transects, so the data were subdivided into two sets for modelling:

1) All sites (199 1-km transect legs) with no soil data
2) Only the triangular transects (167 1-km transect legs) with soil data

Within these datasets, other variables were missing from a few sites (e.g. temperature data from 12 legs across the range; all habitat data from 6 legs in the south of the range; dung data from one leg on a long transect), but these were not deemed significant enough to warrant splitting the data further. Instead, I excluded these sites from the relevant models.

I fitted generalised linear mixed models to datasets 1) and 2), under the Laplace approximation using the '*glmer*' function in the R package "*lme4*" (Bates et al., 2014). Transect ID was fitted as a random intercept in each model. Presence of birds or nests was modelled as a binomial response with a logit-link, and density of birds, groups or nests was modelled as a Poisson response with a log-link, and the natural logarithm of the area surveyed (calculated in Section 3.3.2) as an offset. Each model included a temperature variable (see below), distance to the edge of the range, distance to a road and habitat as independent variables. I tested Poisson models for over-dispersion.

For each response variable, I used the temperature variable which produced the lowest P-value from the models in Section 4.2.2, excluding hot season variables due to the low number of sites. I estimated distance to the edge of the range as the distance from the middle of each transect leg to the nearest edge of the convex hull surrounding all Bush-crow bird and nest records (Bladon et al., 2016; Donald et al., 2012). Minimum distance to a main road was the closest distance between the transect route and a main road (defined as tarmacked or topped with smooth gravel, and receiving regular traffic from local buses). The full list of predictor variables, along with the expected effect of each based on the current literature and my own observations, is given in Table 4.1.

Table 4.1: Habitat variables considered for modelling, with their expected effects on Bush-crow abundance based on literature and my own observations.

Variable	Reason	Reference	Expected trend
Temperature	Range has cooler climate	Donald et al., 2012	Negative
Distance to edge of range	Expect core to provide better habitat	Brown, 1984	Positive
Minimum distance to a main road	Disturbance near roads	Borghesio and Giannetti, 2005	Positive
Tree density + (Tree density)^2	Availability of nest sites, but prefer open landscape	Gedeon, 2006; Mellanby et al., 2008; pers. obs.	Optimum peak (negative)
Acacia-Commiphora density + (Acacia-Commiphora density)^2	Availability of nest sites, but prefer open landscape	Mellanby et al., 2008	Optimum peak (negative)
Average tree height	Availability of nest sites in higher trees	Benson, 1942; Gedeon, 2006	Positive
Bush density + Bush density^2	Foraging opportunities, but prefer open landscape	Gedeon, 2006; pers. obs.	Optimum peak (negative)
Presence of a village within 1km	Foraging opportunities	Gedeon, 2006	Positive
Dung density (Goat) + (Dung density (Goat))^2	Proxy for stocking density: associates with livestock, but overgrazing a problem	Gedeon, 2006	Optimum peak (negative)
Dung density (Cow, equid and camel)	Source of food	Gedeon, 2006	Positive
Soil wetness	Insect abundance	Sutherland and Green, 2004	Positive
Soil bulk density	Prefer loosely packed soil	Gedeon, 2006	Negative
Percent bare ground + (Percent bare ground)^2	Access to foraging areas, lack of foraging areas	Pers. obs.	Optimum peak (negative)
Percent grass cover	Foraging opportunities	Pers. obs.	Positive
Grass length + (Grass length)^2	Foraging opportunities, too tall to walk through	Pers. obs.	Optimum peak (negative)

Because different predictor variables were of different magnitudes, I centered (mean subtracted from each value) and scaled (centered values divided by the standard deviation) each continuous variable prior to model fitting.

I tested co-correlation between independent variables, and found that three pairs had a correlation greater than |0.5| (Table 4.2). I decided that the correlation between ground cover variables was low enough to not be of concern, but only fitted tree density, and not *Acacia-Commiphora* density, in the models.

Table 4.2: Correlations greater than |0.5| between pairs of independent habitat variables considered for inclusion in the maximal models.

Predictor 1	Predictor 2	Correlation (all sites)	Correlation (triangular sites)
Tree density	Acacia-Commiphora density	0.941	0.944
Percent bare ground	Percent grass cover	-0.532	-0.507
Percent bare ground	Grass length	-0.523	-0.545

Model fitting procedure

For each model, I fitted the maximal model structure, with no interactions, and used backwards stepwise elimination to obtain the minimum adequate model, testing the removal of each term using likelihood-ratio tests (Crawley, 2005). I tested minimal models by first removing each remaining term to check for significant increases in residual deviance, and then by adding back in each previously removed term to check that decreases in deviance were not significant. I used the "*MuMIn*" package (Barton, 2015; Nakagawa and Schielzeth, 2013) to obtain r^2 values for each minimal model.

I used each minimum adequate model to predict the probability of occurrence and density of Bush-crows and nests at all sites, inside and outside the range and I plotted these against distance from the edge of the range. If habitat suitability limits the Bush-crow's distribution, there should be a clear decline in predicted occurrence and density outside of the range.

4.2.4 Effects of temperature and habitat on global distribution

I used the species distribution modelling (SDM) methods described in Section 3.7 to fit models for the Ethiopian Bush-crow, White-crowned Starling and Superb Starling. Bush-crow models were fitted with climate-only, habitat-only, and climate and habitat environmental variables, whilst starling models were fitted with climate variables alone.

A weakness of the previously published SDM for the Ethiopian Bush-crow was that it did not use any true absence data, but relied solely on pseudo-absences, which were locations selected at random by the Maximum Entropy (MaxEnt) algorithm (Donald et al., 2012). For my SDM for the Bush-crow, I used both presence and absence data. For presence, I used all GPS bird and nest records from 2005–2015, including previous records collected by Kai Gedeon, Claire Spottiswoode, Paul Donald and Richard Mellanby and colleagues (Mellanby et al., 2008), my casual records of Bush-crows and nests and all georeferenced locations of Bush-crows and their nests recorded on my transects. To define Bush-crow absences, I took the mid-point of any 1-km transect leg on which neither birds nor nests were recorded. In addition, Donald et al. (2012) drove a high proportion of the road network in and around the Bush-crow's range, moving at a constant speed and recording any nests or birds they came across. Given the conspicuousness of Bush-crow nests and their high detectability from a moving vehicle, it is reasonable to assume that stretches of these road routes with no records of birds or nests represent true Bush-crow absences. I divided the road network driven into 1-km segments, and took the mid-point of each segment without a bird or nest record within 1km of the route as an absence point. This resulted in 2,921 presence and 1,905 true absence points. Because the Bush-crow is only found in a very small area, and the true absence points are distributed in and around this area, the range of values of the environmental variables for these points was limited. This limited range might reduce the extent to which the models could be used reliably to make predictions for other areas (Randin et al., 2006). To increase the range of values used for model building, I took a random sample of 3,095 additional pseudo-absence points, to give a total of 5,000 absence points after being added to the 1,905 true absences from field surveys. I took these pseudo-absences at random from a tile stretching from 33.17^{o}–43.67^{o}E and 1.86^{o}–6.87^{o}N (the extent of Figure 3.11–Figure 3.15), with the constraint that these points had to be at least 10km from any presence location.

For the White-crowned and Superb Starlings, I used species range data from BirdLife International (BirdLife International and NatureServe, 2015), which was available as range polygons (Figure 4.1). I converted these to rasters with the same 30 arc-second resolution as the climate data from WorldClim (Hijmans et al., 2005). I randomly sampled 5,000 cells from within each species' range polygon as presence locations, and 10,000 cells from outside of a 100km buffer around each species' polygon as absence locations. I chose the extent of the background sample area to be significantly larger than the respective species' polygon so that it encompassed a range of climatic variables beyond those within the polygon. I divided each starling species' range into eight segments in a similar way as for the Bush-crow (c.f. Figure 3.1). For the Bush-crow, I chose segments which minimised the variance in the number of presence locations, but because the starling presence locations were randomly sampled, I instead minimised the variance in the number of presence cells within each segment, with the segments constrained to originate from each corner of the chosen geographic extent (Figure 4.1).

4.3 Results

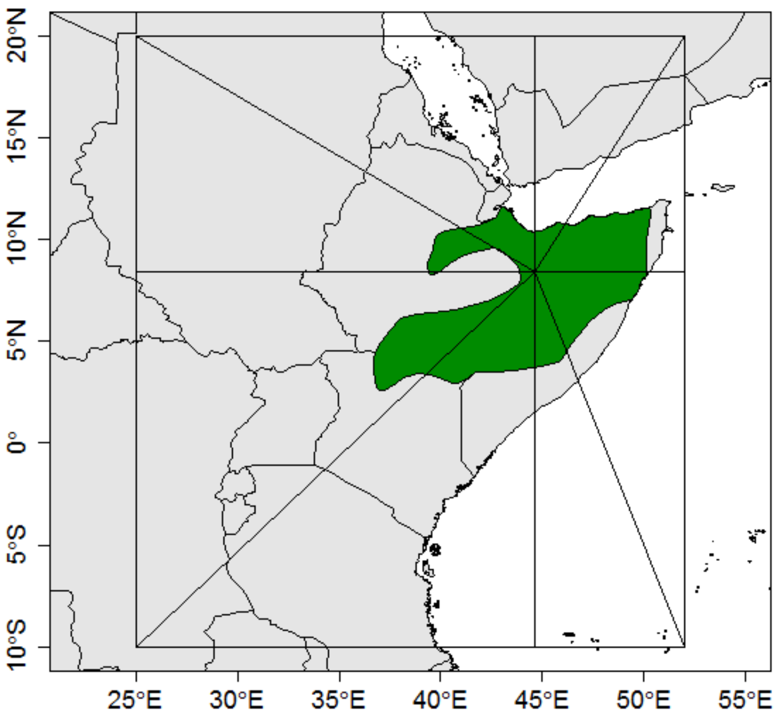
4.3.1 Preliminary investigation of temperature patterns

Temperatures at sites where Bush-crows are present and absent

Neither Bush-crows nor their nests were present in sites with the highest recorded temperatures, and most of the presence sites with the highest temperatures in the breeding seasons (April–June and October–November) had nests, but not birds, recorded. Such sites were often close to the edges of the Bush-crow's range, and it is possible that birds are only found in these areas in cooler years (Figure 4.2).

The predicted values from models fitted by season suggested that temperatures were generally higher at Bush-crow absence than presence sites during the hot season, but not during the cool season (Figure 4.3). However, although the mean temperature at the presence sites was always lower than at the absence sites, the difference was not significant for either season or dataset (Table 4.3).

Figure 4.1: BirdLife International range maps for *A*) the White-crowned Starling and *B*) the Superb Starling, overlaid with the geographic segments used for *k*-fold model fitting. Green shows the area of occupation of each species.


A) White-crowned Starling

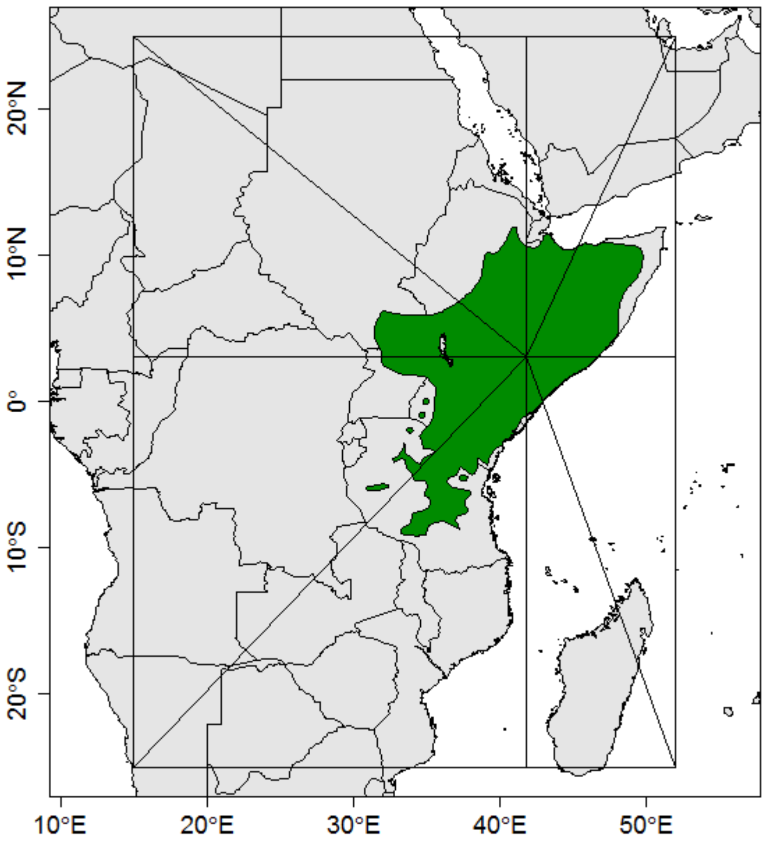

B) Superb Starling

Figure 4.2: Measured 3pm temperatures throughout the year from sites where Bush-crows or their nests were recorded as present and absent. Points show temperature data from individual sites on each day. *A)* Presence is any site where either Bush-crow birds or nests were recorded. Lines show the monthly maximum temperature recorded across all presence and absence sites. *B)* Presence is split to sites where birds were recorded (blue), and sites where only nests, but no birds, were seen (green). The green rings highlight areas, within the breeding seasons, where these "nest only" sites stand out as warmer than any other "presence" site. Dashed lines roughly indicate the Bush-crow's breeding season.

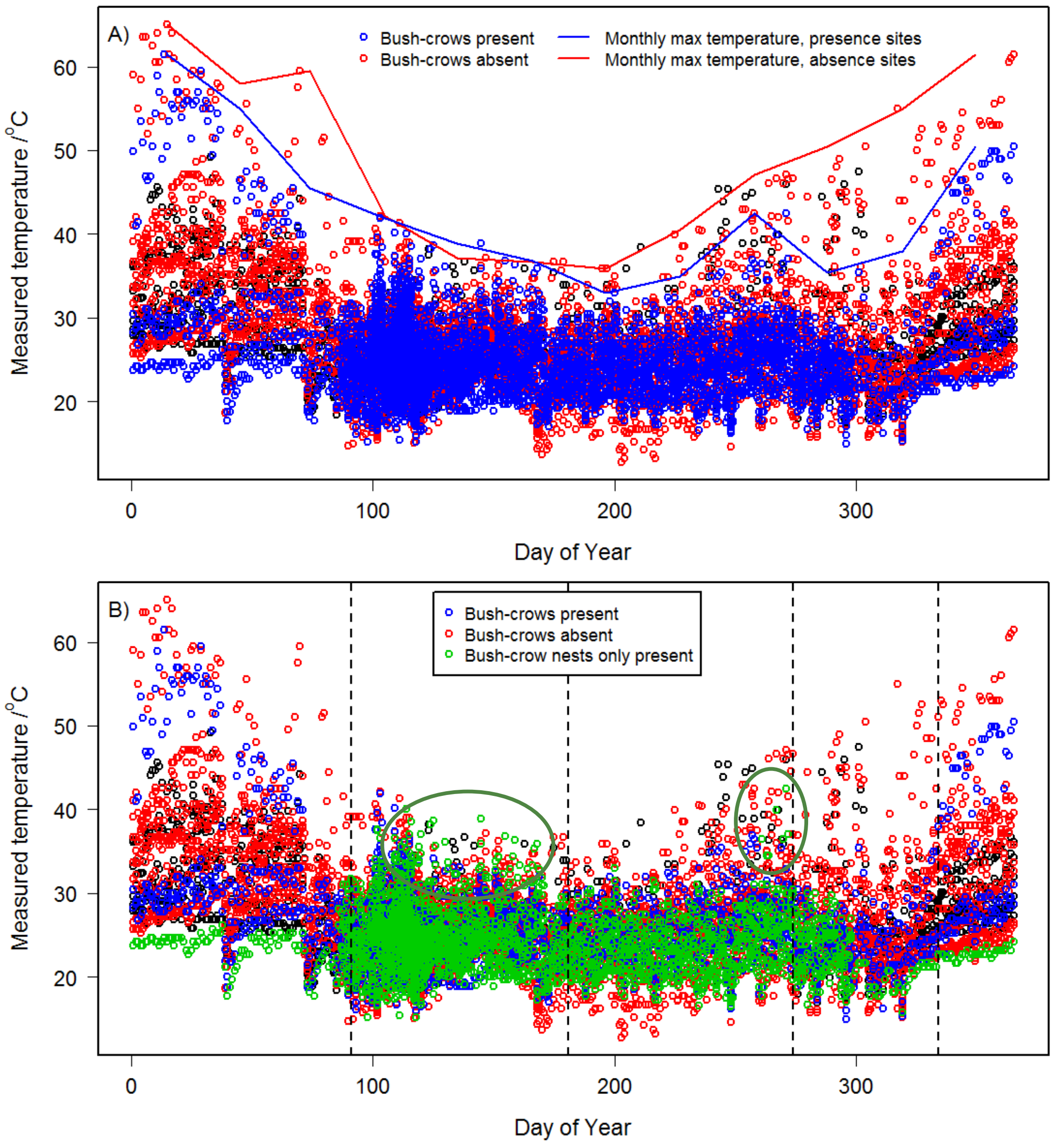


Figure 4.3: Predicted 3pm temperatures from separate models of Temperature ~ Date + Site, fitted to data from the cool season (between the dashed lines) and the hot season (outside the dashed lines). Points show predictions for individual sites on each day, divided visually into sites where Bush-crows or their nests were recorded as present (blue) and absent (red).

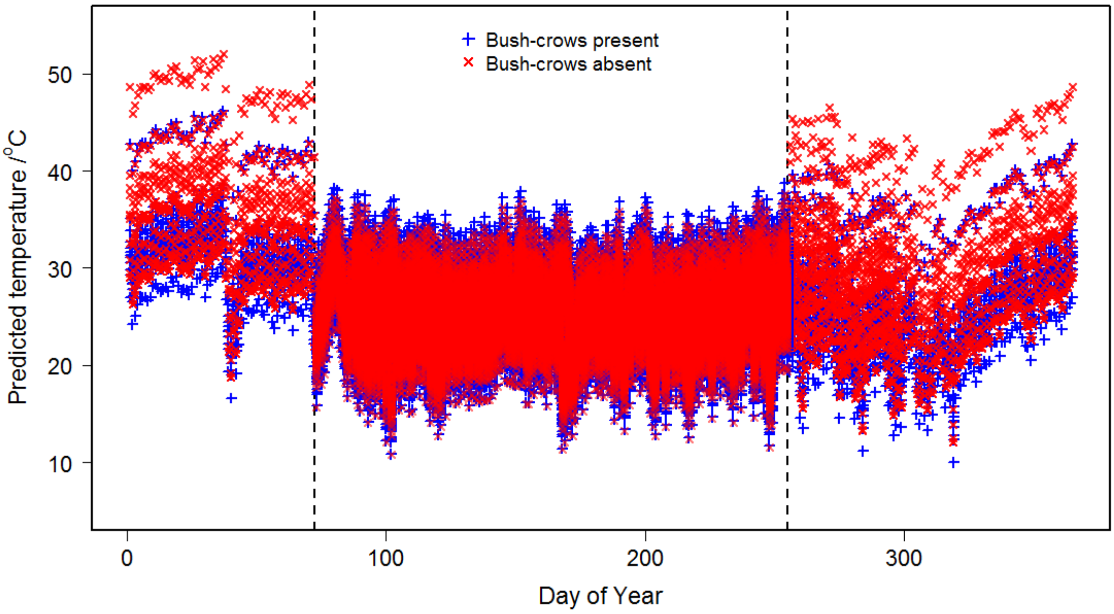


Table 4.3: Tests of differences in temperature between Bush-crow presence and absence sites in each season. Although all presence site means were lower than those for the corresponding absence site, no differences were significant.

Dataset	**Mean temperature ± S.D.**		**Test**	**Stat**	**DF**	**P-value**
	Presence sites	**Absence sites**				
3pm hot	27.2 ± 3.9	30.6 ± 5.8	Wilcoxon	104	-	0.168
3pm cold	25.0 ± 2.9	25.1 ± 2.4	Student's t	0.34	179	0.734
11am+3pm hot	25.5 ± 3.4	28.8 ± 5.4	Wilcoxon	108	-	0.110
11am+3pm cold	23.3 ± 2.4	23.6 ± 2.1	Student's t	0.85	179	0.395

Temperature thresholds

The largest difference, of 4.0 days, between Bush-crow presence and absence sites in the number of days per month at which a temperature threshold was exceeded occurred at 25.5^{o}C (Figure 4.4). The greatest difference between presence and absence sites in the probability of temperatures exceeding given thresholds in the hot season was 0.25, which occurred at 29.0^{o}C. This was substantially higher than the differences in either the cool season, or the full year's data (Figure 4.5).

Figure 4.4: The difference between Bush-crow presence and absence sites in the mean number of days per month (from March 2013–May 2015) which exceeded temperature thresholds from 10 to 70°C.

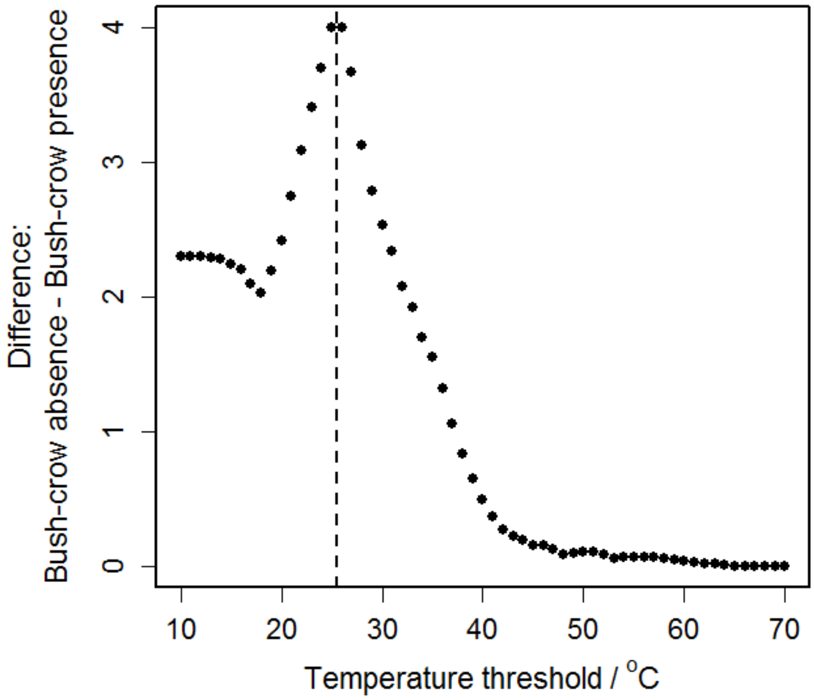
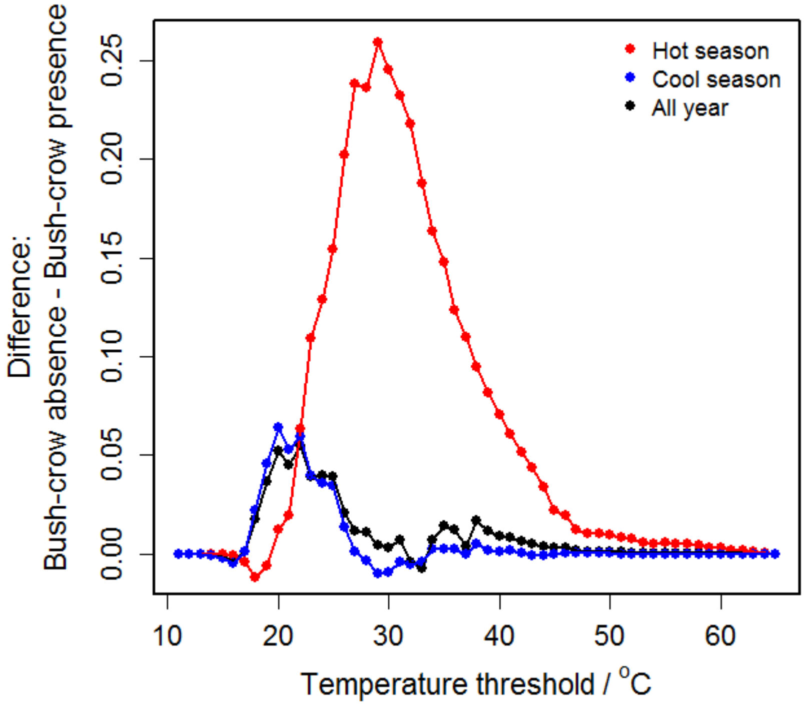


Figure 4.5: Difference between Bush-crow presence and absence sites in the mean predicted probability of 11am or 3pm temperature exceeding each temperature in the hot season (red), cool season (blue), and over the entire year (black).



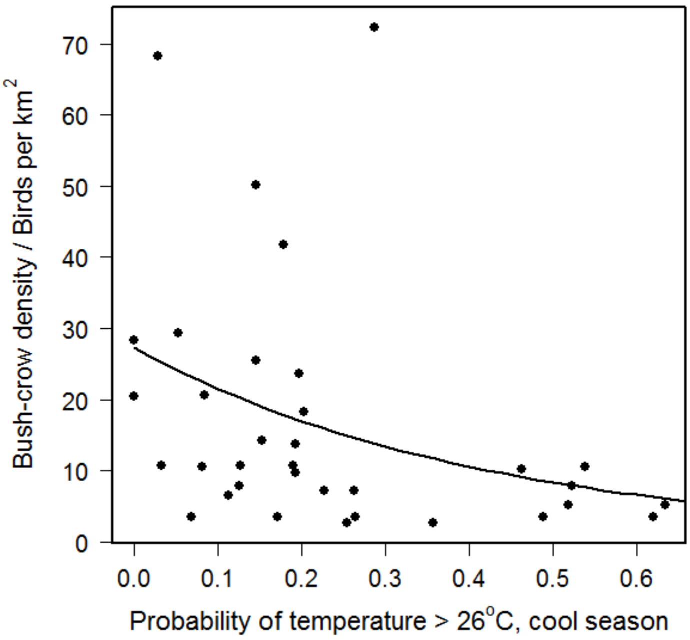
4.3.2 Effects of temperature on local occurrence and density

Across sites both inside and outside of the Bush-crow's range, there was no effect of temperature on the presence/absence of either Bush-crows or White-crowned Starlings, or either species' nests, even before results were corrected for multiple testing. The effect of species approached significance in the two-species model, with Bush-crows found at more sites than White-crowned Starlings (deviance = 3.79, d.f. = 1, P = 0.051).

There was a negative effect of cool season exceedance of 24^{o}C across all sites on Bush-crow bird density (deviance = 41.21, d.f. = 1, P = 0.038), but this effect was not retained following correction for multiple testing. There were no significant effects on White-crowned Starling bird density across all sites.

At presence sites alone, the probability of exceedance of the 26^{o}C threshold for 11am or 3pm temperature in the cool season had a negative effect on Bush-crow bird density (deviance = 27.87, d.f. = 1, P < 0.001) (Figure 4.6). Four further models (with mean 3pm temperature and exceedance of 28 ^{o}C and 30^{o}C thresholds as explanatory variables) were also significant before multiple testing adjustments (deviance range = 26.92–31.34, d.f. = 1, P-value range = 0.027–0.047), but were not retained by FDR control.

Figure 4.6: The response of Bush-crow density at sites where the birds were present to the probability of 11am or 3pm temperatures exceeding 26^{o}C in the cool season. Points show data from individual transects. The line shows the predicted density from the Poisson model.



There was a significant temperature by species interaction in three of the bird density (F range = 4.10–4.90, d.f. = 1, P-value range = 0.028–0.045) and four of the group density (F range = 4.07–5.34, d.f. = 1, P-value range = 0.021–0.045) models fitted to combined data for both species across all sites. However, none of these interactions were retained following FDR control. These models suggested that White-crowned Starling bird and group density may increase, while Bush-crow bird and group density may decrease, with the frequency of exceedance of 24^{o}C and 26^{o}C temperature thresholds in the cool season and across the whole year (Figure 4.7).

The probability of 3pm temperatures exceeding 24^{o}C in the hot season had a different effect on the bird density of the two species at presence-only sites, with White-crowned Starling density declining more rapidly than Bush-crows (deviance = 13.74, d.f. = 1, P = 0.0002; Figure 4.8). This effect was retained by FDR control. There was an additional effect in the model with probability of 11am or 3pm temperatures exceeding 28^{o}C across the entire year, where Bush-crow density was negatively affected but Starling density increased with temperature (F = 4.08, d.f. = 1, P = 0.049), but this was not retained by FDR control.

White-crowned Starling groups occurred at a higher density than Bush-crow groups across presence-only sites (respective means 11.3 and 5.9 groups per km^{2}, deviance = 10.06, d.f. = 1, P = 0.0015). Two models, with the probability of temperatures exceeding 24^{o}C at 11am or 3pm in the cool season and across the entire year as independent variables, found a significant interaction between species and temperature, again with Bush-crow group density declining and Starling group density increasing, but neither was retained by FDR control (deviance = 5.20, d.f. = 1, P = 0.022 and deviance = 4.48, d.f. = 1, P = 0.035 respectively; Figure 4.9).

Seven models with group size as the dependent variable, and with the probability of temperatures exceeding 26–30^{o}C at 3pm alone and 11am or 3pm, across the whole year and in the cool season as independent variables, all found a significant interaction between species and temperature, even after correction for multiple testing (deviance range = 55.61–64.65, d.f. = 1, P-value range = 0.005–0.011). A further seven models also had significant effects which were not retained. Bush-crow group size declined with temperature, whilst White-crowned Starling group size increased (Figure 4.10).

Figure 4.7: The response of Bush-crow (blue) and White-crowned Starling (green) *A*) bird density and *B*) group density across all sites to the probability of 11am or 3pm temperatures exceeding *A*) 26°C and *B*) 24°C in the cool season. Points show data from individual transects. The lines show the predicted densities from the Poisson models with an interaction between temperature and species.

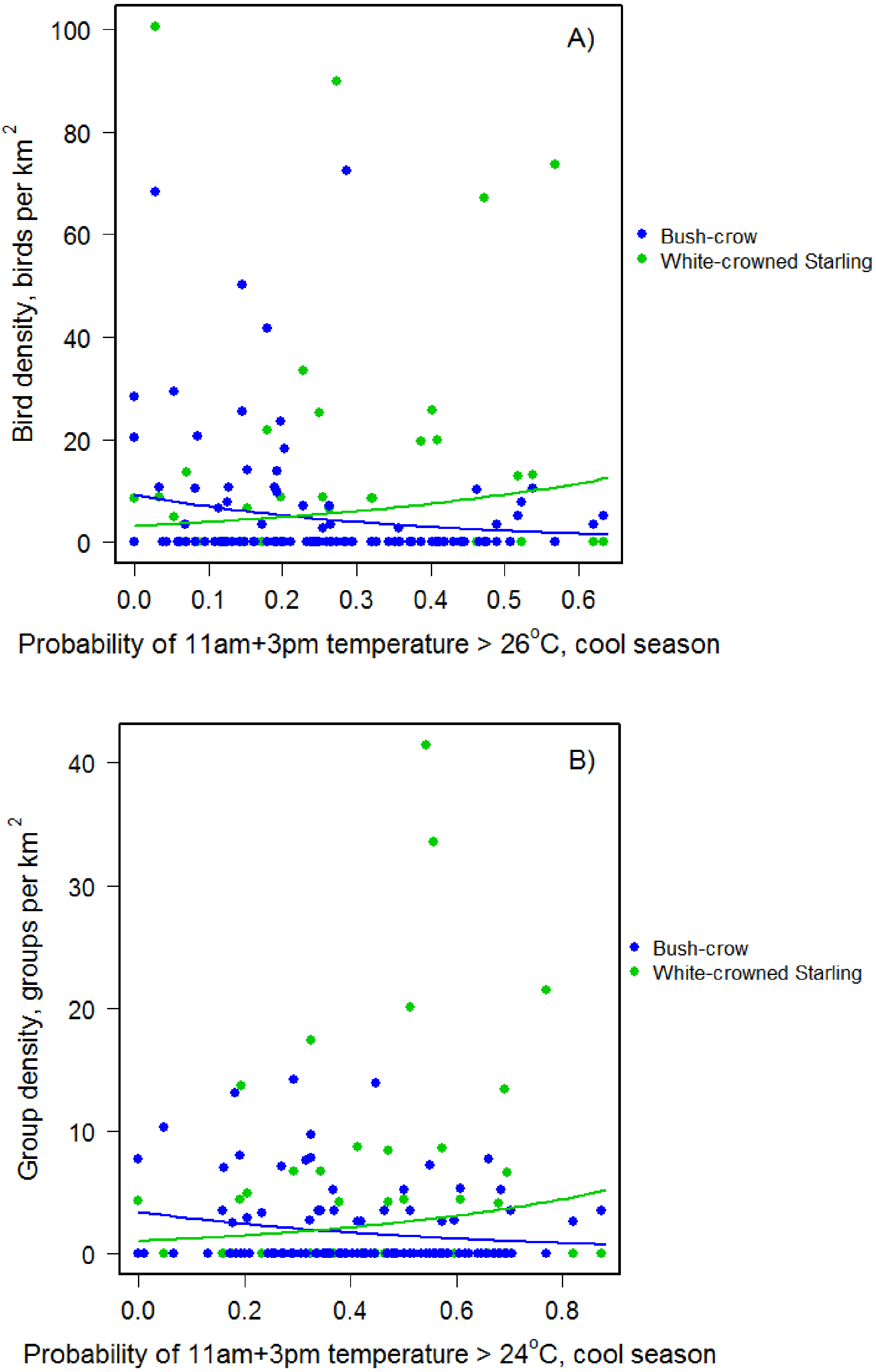


Figure 4.8: The response of Bush-crow (blue) and White-crowned Starling (green) density at sites where the birds were present to probability of 3pm temperatures exceeding 24°C in the hot season. Points show data from individual transects. The lines show the predicted densities from the Poisson model with an interaction between temperature and species.

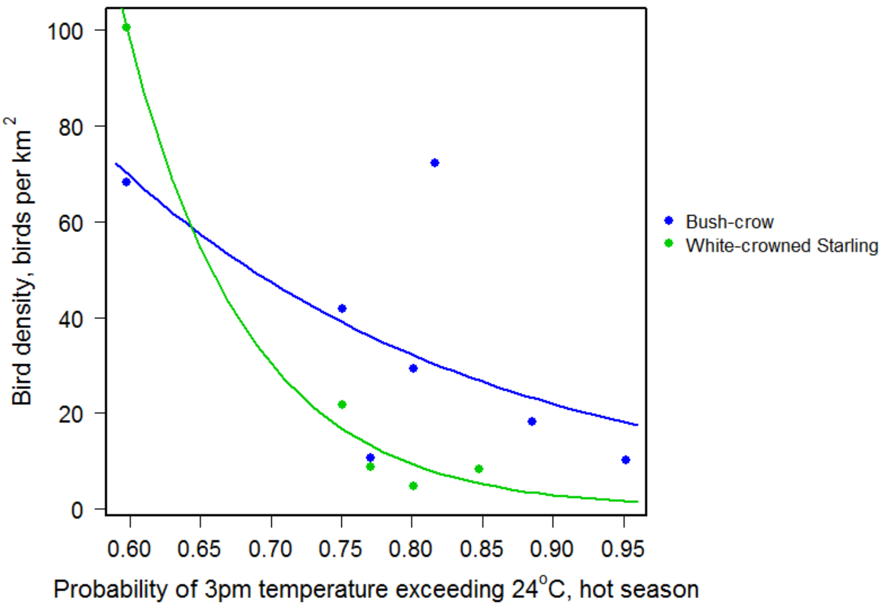


Figure 4.9: The response of Bush-crow (blue) and White-crowned Starling (green) group density at sites where the birds were present to the probability of 11am or 3pm temperatures exceeding 24°C in the cool season. Points show data from individual transects. The lines show the predicted densities from the Poisson model with an interaction between temperature and species.

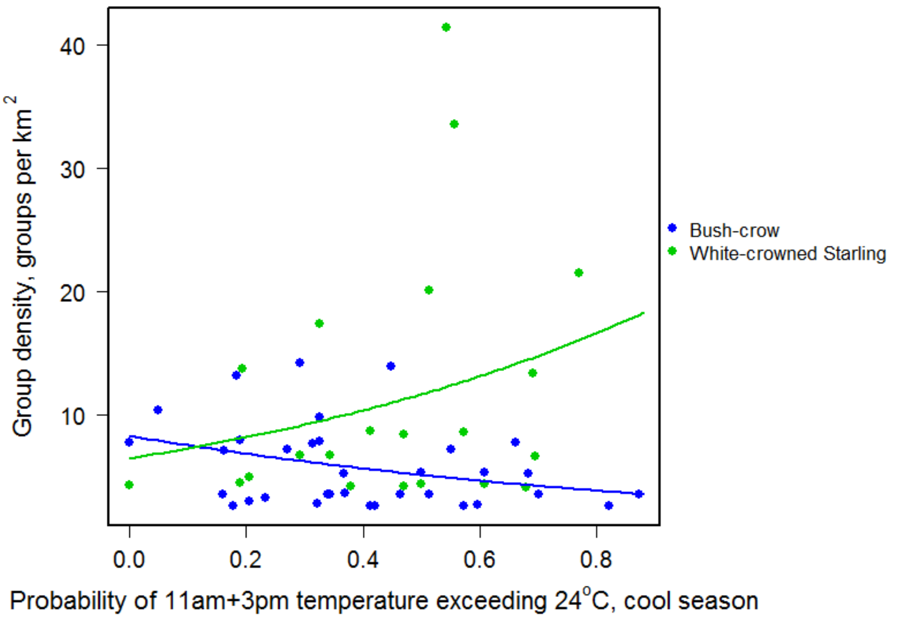
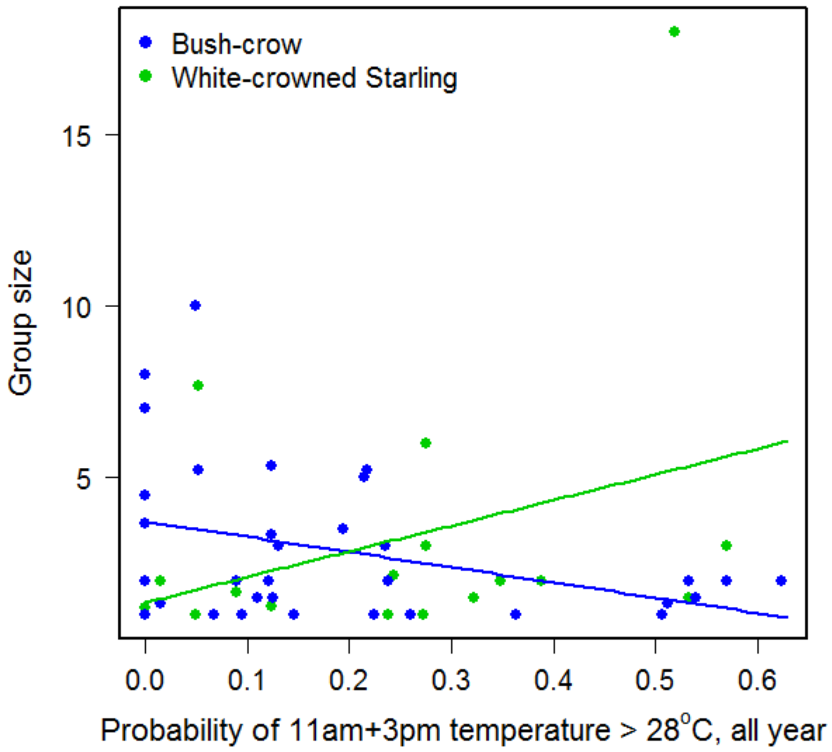


Figure 4.10: The response of Bush-crow (blue) and White-crowned Starling (green) group size to the probability of 11am or 3pm temperature exceeding 28°C across the whole year. Points show data from individual transects. The lines show the predicted group sizes from the model with a temperature by species interaction.



Lapse rate and nest height

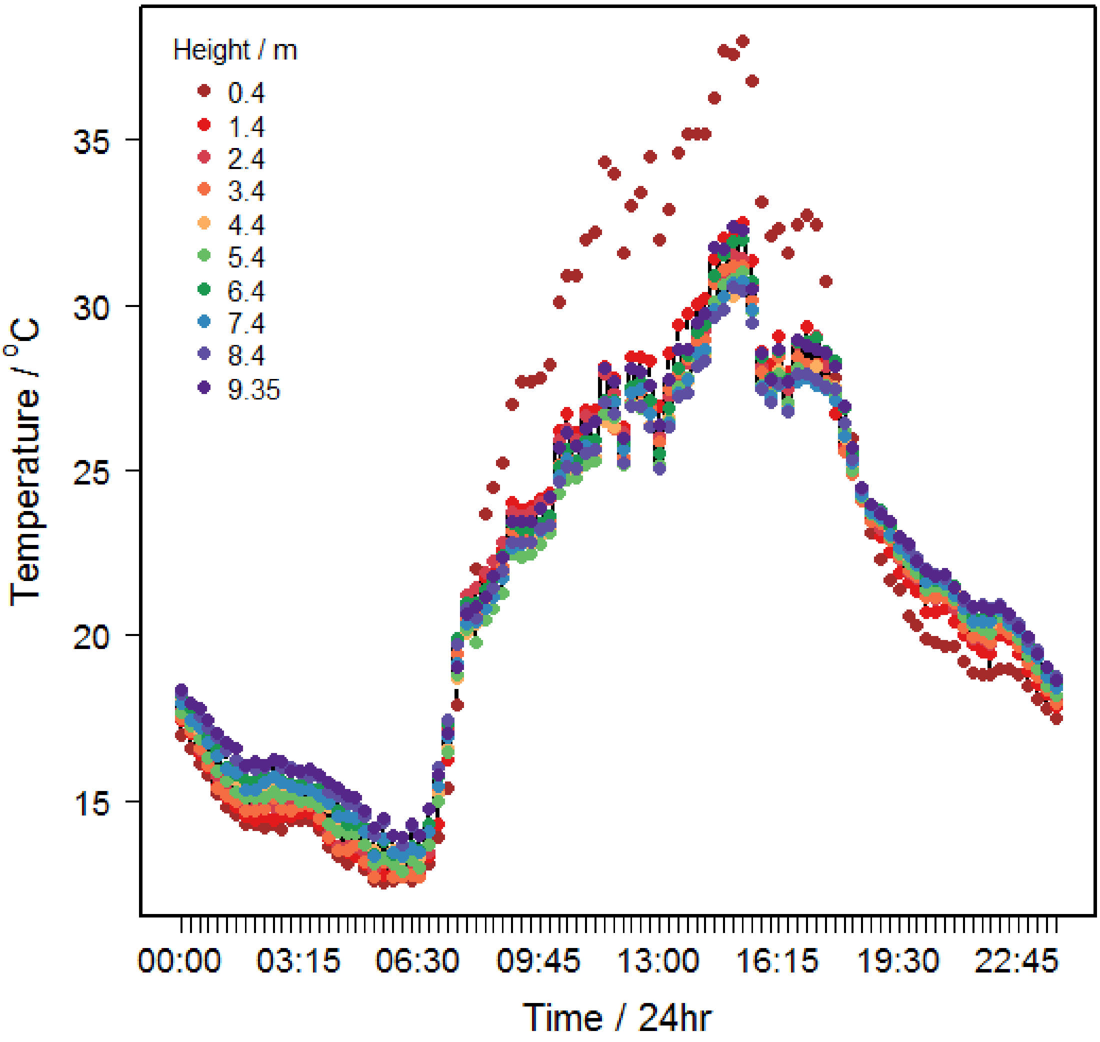
The data showed the expected diurnal temperature variation (warmer during the day and cooler at night), with the greatest variation in temperature occurring in the afternoon. As found previously, the highest temperatures tended to occur around 3pm. The highest daytime temperatures occurred closest to the ground (Figure 4.11).

Models fitted to untransformed temperatures with Gaussian and Gamma error structures and a selection of link functions all suffered from unequal variance and non-normal errors. The Box-Cox model produced a maximum lambda value of -1.85, which was used as a power transformation of the response variable. This model did not suffer from unequal variance or non-normal errors, and so was chosen as the preferred model structure. There was a significant interaction between time of day and height, with the highest temperatures being recorded close to the ground during the day, but the lowest temperatures found there at night (F = 21.52, d.f. = 95, P < 0.001). This means that further above the ground temperatures remain more stable over a 24-hour period.

There was no effect of temperature on the mean percentile of local tree height at which nests were built by either species, but Bush-crows build their nests much higher than White-crowned Starlings (mean percentile of tree height = 0.76 and 0.35 respectively, F = 61.7, d.f. = 1, P < 0.001).

The random effects model on individual nests showed the same pattern, with no effects of temperature or location within the range. The difference in height percentile between Bush-crow and White-crowned Starling nests was again significant (χ^2 = 62.5, d.f. = 1, P < 0.001).

Figure 4.11: The effect of time of day and height above the ground on the temperature recorded across a five day period. Points show mean values for each height and time across five days.



4.3.3 Effects of habitat on local occurrence and density

The models of the effect of habitat variables on Bush-crow occurrence and density all simplified to a minimum adequate model, from which neither further deletion of terms nor re-addition of removed terms was supported by a likelihood-ratio test. One model, of nest density, initially reached a minimal model, to which soil bulk density had to be returned, but this then produced a minimum adequate model. None of the Poisson models were over-dispersed. The results from each model are presented in Table 4.4–Table 4.8 and Figure 4.12–Figure 4.16. In each case, the effect estimate and standard error for each retained term in the minimal model are presented, along with the results from the likelihood-ratio test between the minimum model and the model with each variable removed. Since the effect of temperature is of particular interest *a priori* (Donald et al., 2012), the estimate, standard error and likelihood-ratio tests for the relevant temperature term when re-added to the minimal model are also shown.

The models fitted to fewer sites, but including the two soil variables, all retained at least one soil term, except for the model of bird density. For this dependent variable, given that both soil variables were removed, the results from the first model, fitted to more sites, were preferred. For all other response variables, results from models with and without soil data are presented.

Table 4.4: Minimum adequate models from logistic regressions of habitat features against Bush-crow nest presence. *A*) Model fitted to data from all sites, without soil variables. *B*) Model fitted to data from triangular transects, with soil variables.

A) Presence of Bush-crow nests, all sites (no soil data). Marginal $R^2 = 0.447$					
Term	Estimate	Standard error	χ^2	DF	P
Intercept	-0.208	0.457	-	-	-
Cool season exceedence of 28°C at 11am or 3pm	0.963	0.443	5.66	1	0.017
Bush density	-1.861	0.550	20.38	1	< 0.001
% grass cover	1.850	0.497	22.75	1	< 0.001

B) Presence of Bush-crow nests, triangular transects (with soil data). Marginal $R^2 = 0.276$					
Term	Estimate	Standard error	χ^2	DF	P
Intercept	-0.799	0.562	-	-	-
Soil wetness	-1.314	0.653	4.90	1	0.027
Soil bulk density	-1.807	0.688	8.69	1	0.003
Bush density	-2.534	0.839	17.99	1	< 0.001
% bare ground	-1.548	0.700	6.34	1	0.012
% grass cover	1.102	0.622	4.23	1	0.040
Cool season exceedence of 28°C at 11am or 3pm	0.838	0.511	3.09	1	0.079

Figure 4.12: The effects of temperature, bush density and grass cover on the probability of Bush-crow nest occurrence across all sites, and of soil bulk density and wetness and bare ground on triangular transects (Table 4.4). Points show data from individual transect legs. Curves show predicted responses (from logistic models) to each independent variable, with all others held at their mean.

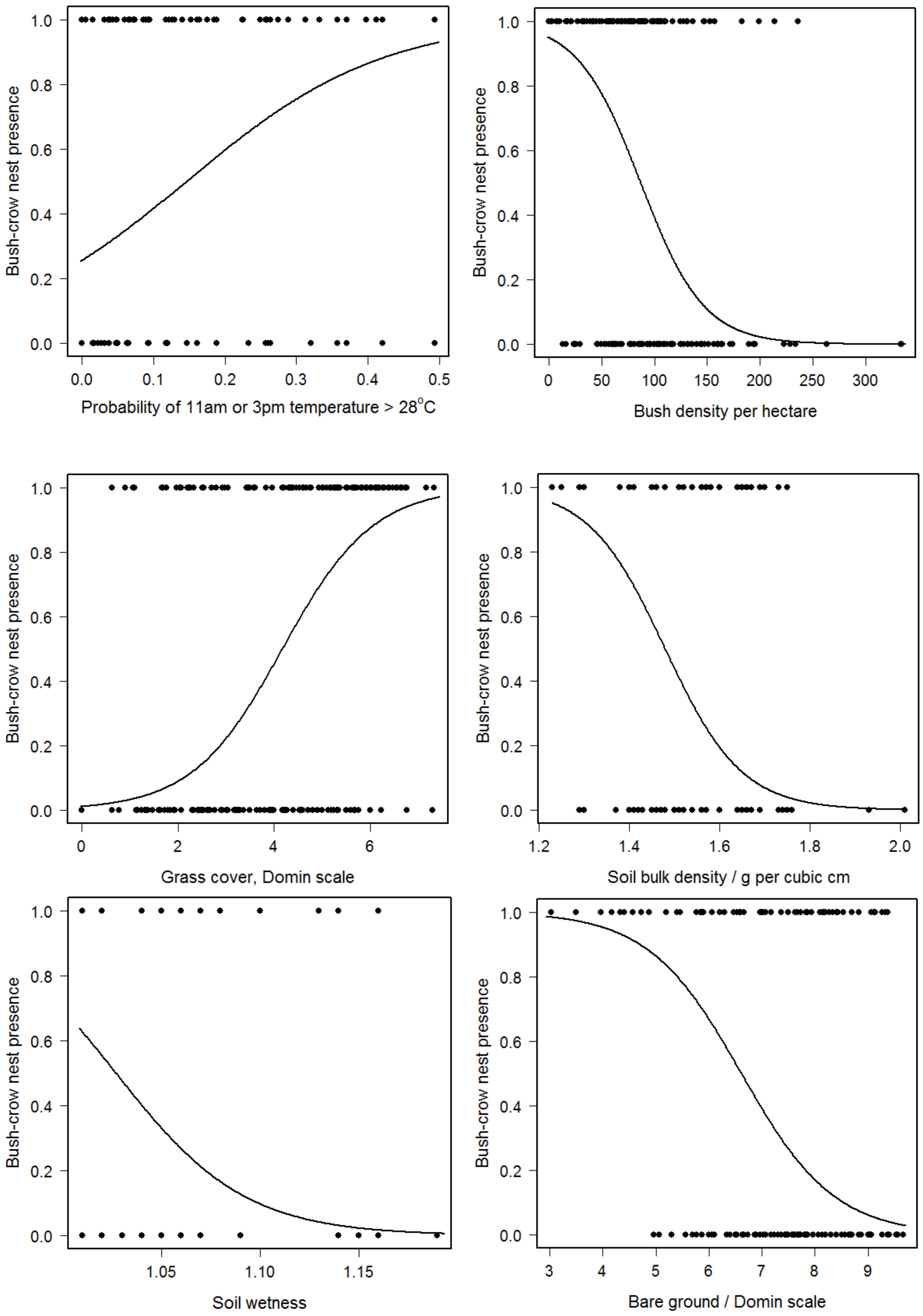


Table 4.5: Minimum adequate models from logistic regressions of habitat features against Bush-crow presence. *A*) Model fitted to data from all sites, without soil variables. *B*) Model fitted to data from triangular transects, with soil variables.

A) Presence of Bush-crows, all sites (no soil data). Marginal $R^2 = 0.150$

Term	Estimate	Standard error	χ^2	DF	P
Intercept	-1.679	0.378	-	-	-
Bush density	-0.645	0.312	5.45	1	0.020
% grass cover	0.638	0.264	6.79	1	0.009
Cool season exceedence of 24^{o}C at 3pm	-0.142	0.262	0.30	1	0.587

B) Presence of Bush-crows, triangular transects (with soil data). Marginal $R^2 = 0.392$

Term	Estimate	Standard error	χ^2	DF	P
Intercept	-3.212	1.082	-	-	-
Soil bulk density	-1.272	0.669	5.78	1	0.016
Bush density	-2.045	0.966	11.34	1	< 0.001
% grass cover	1.081	0.470	6.94	1	0.008
Cool season exceedence of 24^{o}C at 3pm	0.177	0.488	0.13	1	0.714

Figure 4.13: The effects of bush density and grass cover on the probability of Bush-crow bird occurrence across all sites, and of soil bulk density on triangular transects (Table 4.5). Points show data from individual transect legs. Curves show predicted responses (from logistic models) to each independent variable, with all others held at their mean.

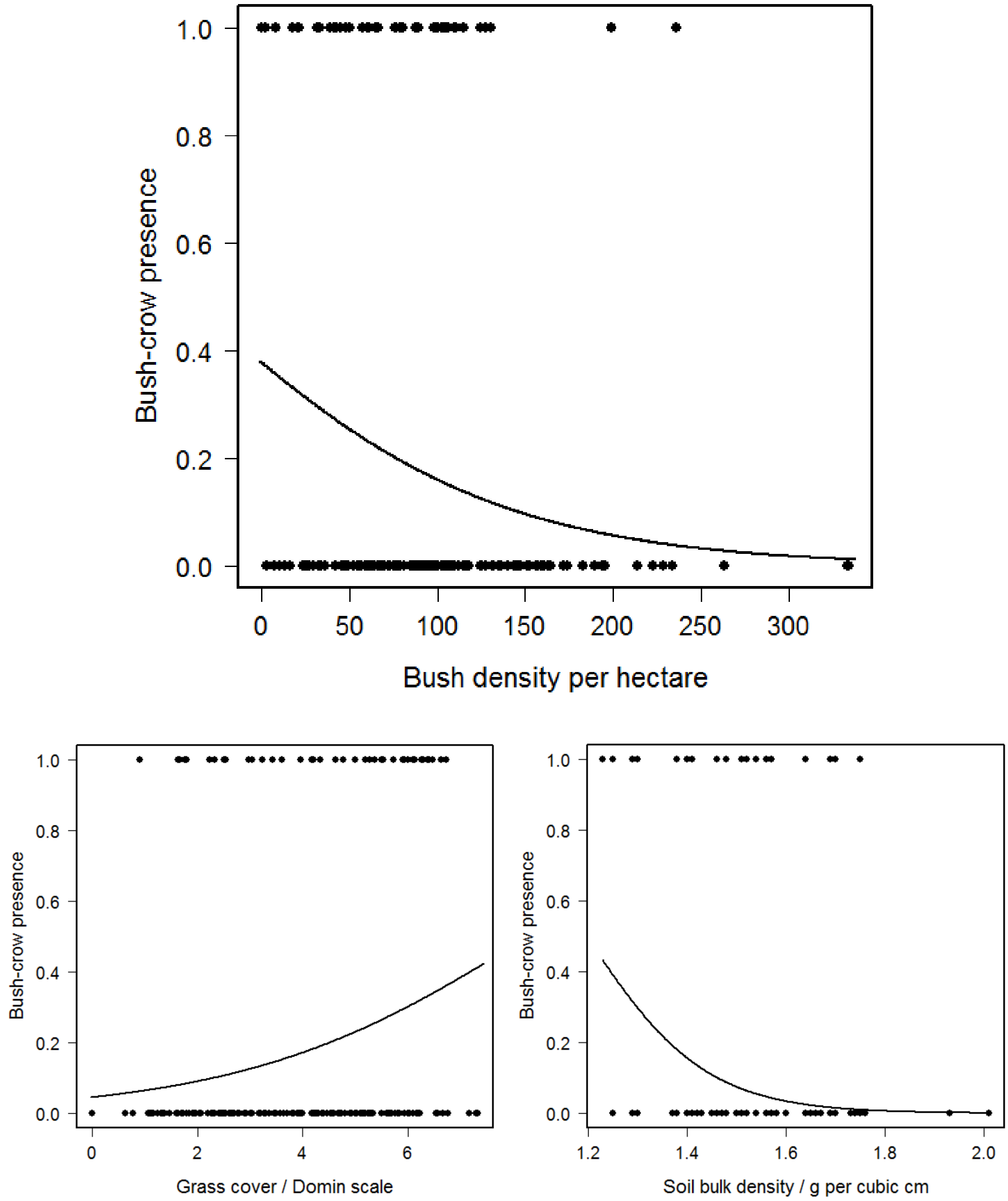


Table 4.6: Minimum adequate models from Poisson regressions of habitat features against Bush-crow nest density. *A*) Model fitted to data from all sites, without soil variables. *B*) Model fitted to data from triangular transects, with soil variables.

A) Density of Bush-crow nests, all sites (no soil data). Marginal $R^2 = 0.162$

Term	Estimate	Standard error	χ^2	DF	P
Intercept	-3.441	0.222	-	-	-
Average tree height	0.158	0.075	4.62	1	0.032
Bush density	-0.766	0.131	38.05	1	< 0.001
Grass	0.424	0.096	19.74	1	< 0.001
Cool season exceedence of 26°C at 3pm	-0.002	0.129	0.0001	1	0.991

B) Density of Bush-crow nests, triangular transects (with soil data). Marginal $R^2 = 0.248$

Term	Estimate	Standard error	χ^2	DF	P
Intercept	-3.652	0.263	-	-	-
Tree density	-0.456	0.180	6.73	1	0.010
Average tree height	0.193	0.096	4.27	1	0.039
Soil wetness	-0.577	0.243	5.74	1	0.017
Bush density	-0.777	0.205	15.5	1	< 0.001
% bare ground	-0.541	0.153	8.79	1	0.003
(% bare ground)^2	-0.166	0.077	13.68	2	0.001
Soil bulk density	-0.547	0.244	5.12	1	0.024
Cool season exceedence of 26°C at 3pm	0.349	0.196	3.26	1	0.071

Figure 4.14: The effects of tree height, bush density and grass cover on Bush-crow nest density across all sites, and of tree density and soil bulk density and wetness on triangular transects (Table 4.6). Points show data from individual transect legs. Curves show predicted responses (from Poisson models) to each independent variable, with all others held at their mean.

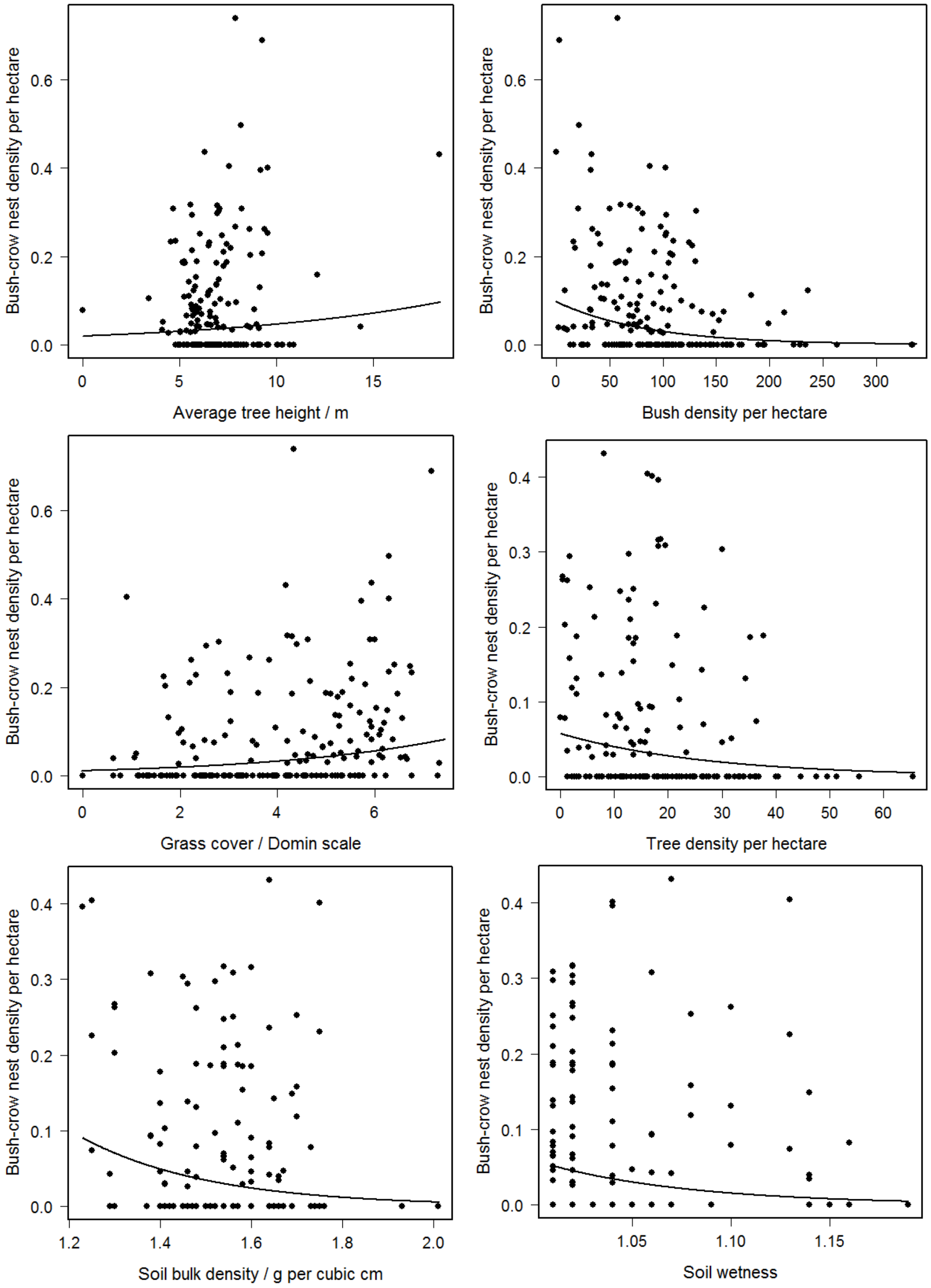


Table 4.7: Minimum adequate models from Poisson regressions of habitat features against Bush-crow bird density.

Density of Bush-crow birds, all sites (no soil data). Marginal $R^2 = 0.084$					
Term	Estimate	Standard error	χ^2	DF	P
Intercept	-5.495	0.581	-	-	-
Average tree height	0.286	0.148	3.99	1	0.046
Presence of a village within 1km	1.065	0.346	10.84	1	0.001
Dung density (Goat)	-0.727	0.230	4.51	1	0.034
(Dung density (Goat))^2	0.113	0.045	10.18	2	0.006
Bush density	-1.046	0.257	18.99	1	< 0.001
Cool season exceedence of 26^{o}C at 11am or 3pm	-0.277	0.300	0.83	1	0.361

Figure 4.15: The effects of tree height, goat dung density, bush density and proximity of a village on Bush-crow bird density across all sites (Table 4.7). Points show data from individual transect legs. Curves show predicted responses (from Poisson models) to each independent variable, for sites less than (red) and further than (blue) 1km from a village, with all other variables held at their mean.

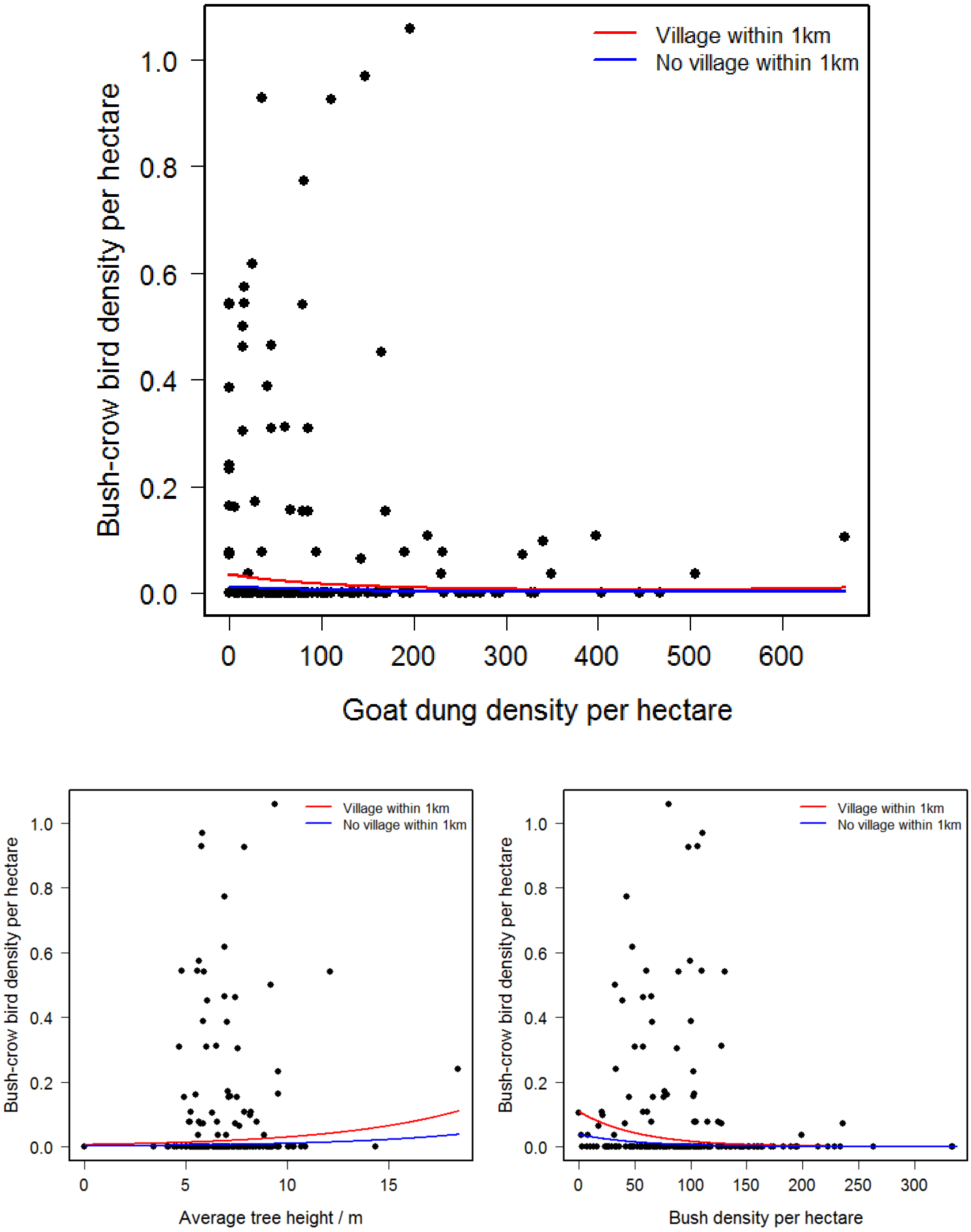


Table 4.8: Minimum adequate models from Poisson regressions of habitat features against Bush-crow group density. *A*) Model fitted to data from all sites, without soil variables. *B*) Model fitted to data from triangular transects, with soil variables.

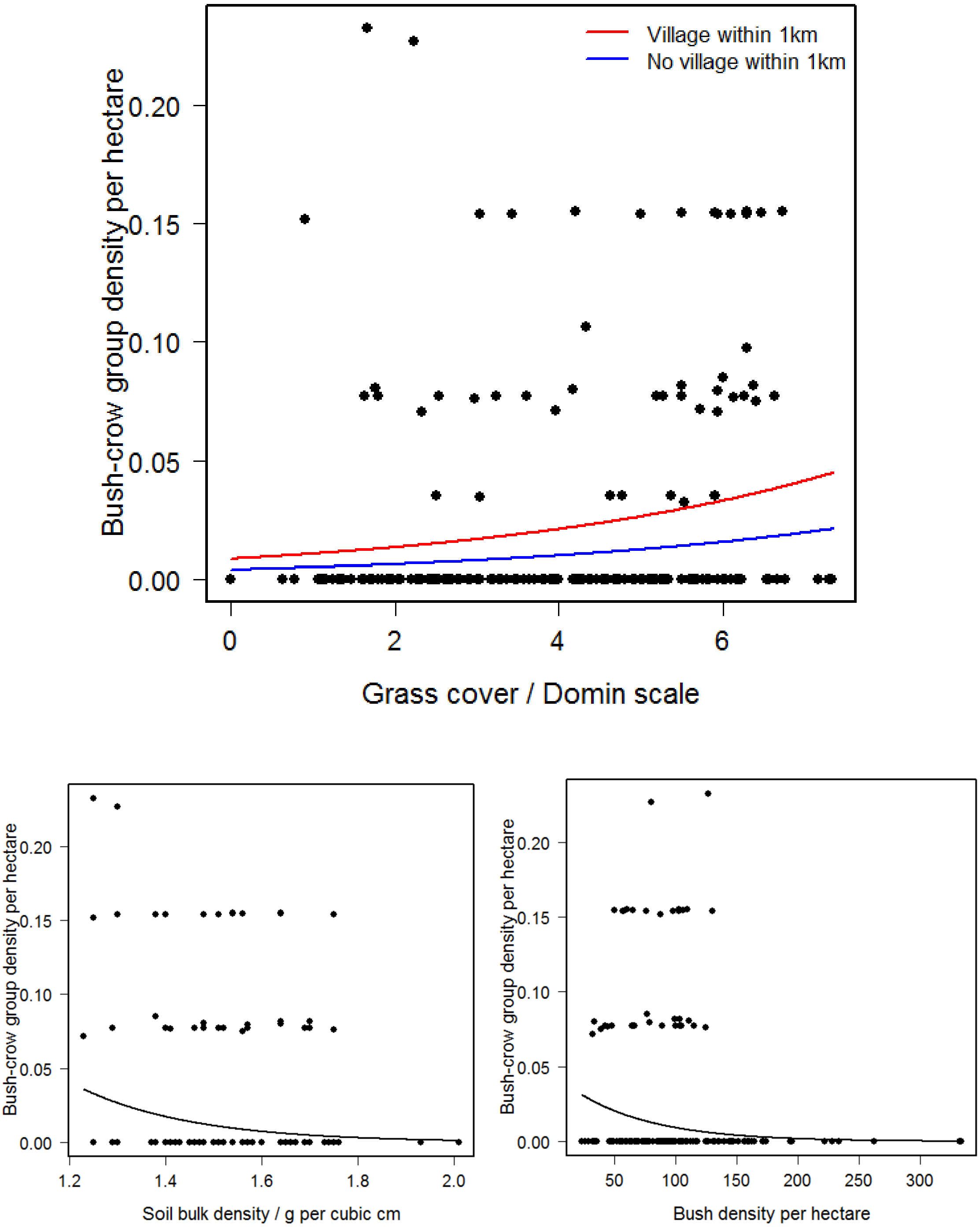
A) Density of Bush-crow groups, all sites (no soil data). Marginal $R^2 = 0.049$

Term	Estimate	Standard error	χ^2	DF	P
Intercept	-4.736	0.363	-	-	-
Presence of a village within 1km	0.749	0.346	5.02	1	0.025
% grass cover	0.391	0.173	5.38	1	0.020
Cool season exceedence of 24°C at 11am or 3pm	-0.106	0.181	0.35	1	0.557

B) Density of Bush-crow groups, triangular transects (with soil data). Marginal $R^2 = 0.165$

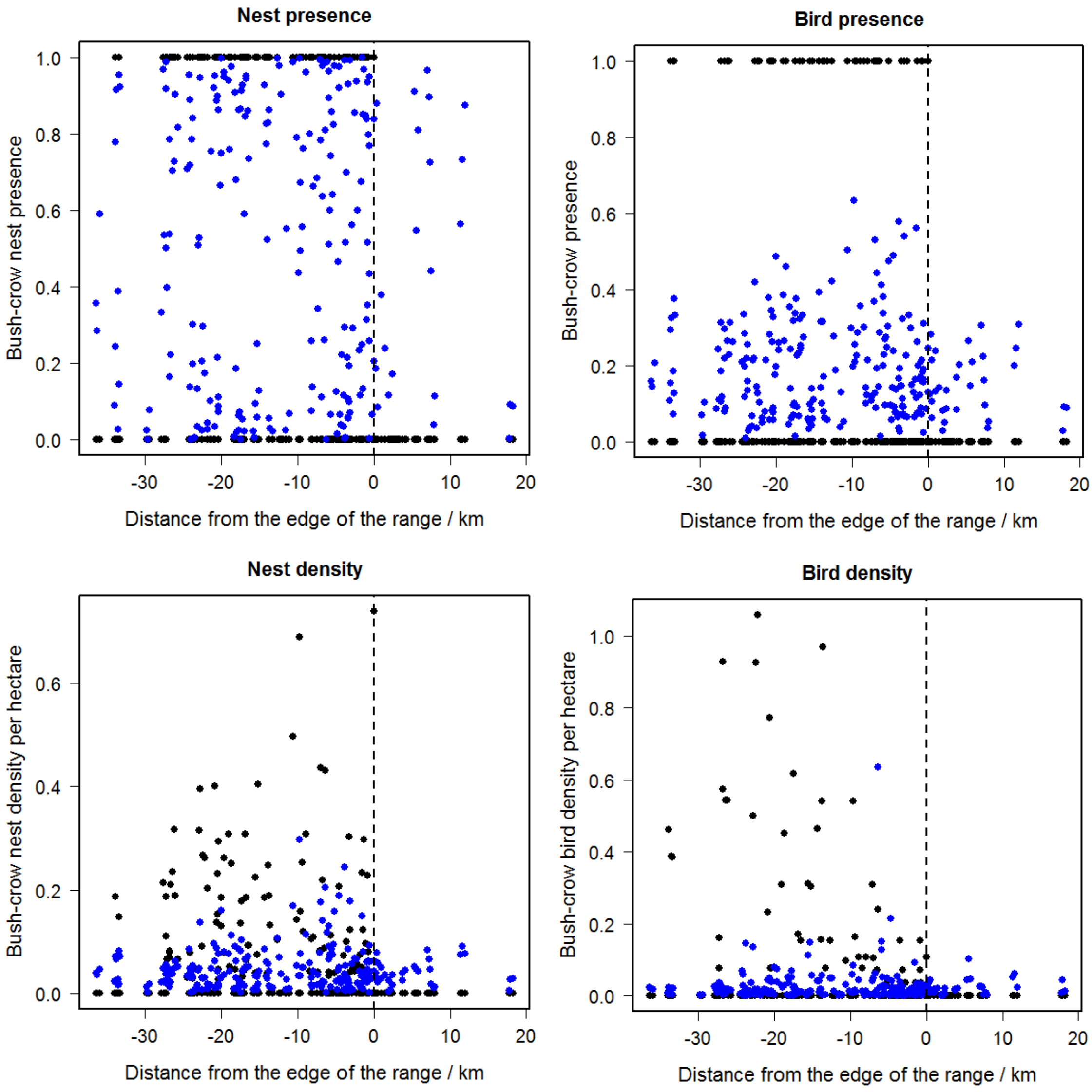
Term	Estimate	Standard error	χ^2	DF	P
Intercept	-4.816	0.423	-	-	-
Soil bulk density	-0.652	0.294	5.30	1	0.021
Bush density	-0.802	0.333	7.94	1	0.005
% grass cover	0.552	0.229	6.24	1	0.013
Cool season exceedence of 24°C at 11am or 3pm	-0.080	0.254	0.10	1	0.755

Figure 4.16: The effects of grass cover and village presence on Bush-crow group density across all sites, and of soil bulk density and bush density on triangular transects (Table 4.8). Points show data from individual transect legs. Curves show predicted responses (from Poisson models) to each independent variable, for sites less than (red) and further than (blue) 1km from a village, with all other variables held at their mean.



Predictions of each model across all sites showed no difference in the predicted probability of occurrence or predicted density inside and outside of the Bush-crow's range, showing that habitat has little effect in determining the Bush-crow's distribution (Figure 4.17).

Figure 4.17: Observed and predicted Bush-crow bird and nest occurrence and density inside (negative) and outside (positive) of the species' range. Black points show data from individual transect legs, blue points show the predicted occurrence or density on each leg according to the minimum adequate habitat models fitted to sites within the Bush-crow's range (see text, and Table 4.4–Table 4.7).



4.3.4 Effects of temperature and habitat on global distribution

I used the methods described in Section 3.7 to produce *k*-fold cross-validation AUC scores for each of seven model algorithms fitted to each set of species data. As expected, AUC scores were substantially higher when all available data were used to fit a single model than when data were partitioned *k*-fold (Table 4.9).

Table 4.9: Bush-crow SDM AUC scores for each model algorithm for all variables, climate-only and habitat-only variables. For each variable set, results are compared for predictions based upon models fitted to all the data and *k*-fold validation in which the prediction for each location is based only upon data from other locations. Letters correspond to model groups whose 95% C.I.s overlapped.

Model	All predictors k-fold	All predictors All data	Climate only k-fold	Climate only All data	Habitat only k-fold	Habitat only All data
RF	0.825 a	0.9998 a	0.796 b	0.999 a	0.709 a	0.9998 a
GLM	0.790 b	0.885 c	0.747 c	0.811 e	0.692 a	0.811 d
BRT	0.822 a	0.940 b	0.824 a	0.930 b	0.718 a	0.873 b
GAM	0.785 b	0.933 b	0.790 b	0.910 c	0.709 a	0.843 c
FDA	0.755 c	0.890 c	0.779 b	0.858 d	0.711 a	0.819 d
MARS	0.765 c	0.886 c	0.791 b	0.870 d	0.717 a	0.835 c
MAXENT	0.756 c	0.849 d	0.754 c	0.896 c	0.685 a	0.837 c

For the Bush-crow, model AUC scores always dropped when habitat variables alone were modelled, but for some algorithms remained similar between the full and climate-only models. This serves to highlight the ability of climatic factors alone to predict the Bush-crow's range. The Random Forests (RF) and Boosted Regression Trees (BRT) algorithms produced the highest AUC scores for all three sets of predictor variables (all predictors, climate-only and habitat-only) when fitted to all Bush-crow data, and for the *k*-fold models with all environmental predictors. However, for the *k*-fold Bush-crow models with climate variables alone, BRT performed the best, whilst with habitat variables alone all seven model algorithms were indistinguishable.

The *k*-fold cross-validation found that the Generalised Linear Models (GLM) performed best for White-crowned Starlings (AUC = 0.920), followed by Flexible Discriminant

Analysis (FDA) and Generalised Additive Models (GAM) (AUC = 0.904 and 0.896, respectively). For the Superb Starling, Multiple Adaptive Regression Splines (MARS) was the best performing model (AUC = 0.971), followed by BRT, GAM and GLM (AUC = 0.965, 0.955 and 0.952 respectively).

To assess variable importance, the algorithms with *k*-fold AUC scores greater than 0.8 for each species were re-fitted with each variable left out in turn for another *k*-fold run. The importance of each variable was calculated by subtracting the *k*-fold AUC for the model with the variable missing from the *k*-fold AUC for the maximal model, with that variable included. I call this difference delta AUC. For the Bush-crow, the RF and BRT models showed the greatest reduction in AUC when all five climate variables were removed, which highlights the importance of climate to the models. Much smaller reductions were observed when any single variable was removed. Maximum temperature of the warmest month and precipitation of the driest quarter were the most important explanatory variables for the Bush-crow's distribution, judging by delta AUC in both the RF and BRT models (Figure 4.18; *A*). For both the White-crowned (Figure 4.18; *B*) and Superb Starlings (Figure 4.18; *C*) the most important climatic variable was precipitation of the wettest quarter, with delta AUCs much higher than for any other variable.

Delta AUC scores for each variable for the best Bush-crow (BRT), White-crowned Starling (GLM) and Superb Starling (MARS) climate-only models were standardised by dividing each score by the sum of the scores for all five variables in the models. The standardised maximum temperature and precipitation of the driest quarter scores were much higher for the Bush-crow than the starlings, for which the precipitation of the wettest quarter score was higher (Figure 4.19).

Figure 4.18: Delta AUC scores for each variable from the two best fitting model algorithms, assessed by *k*-fold cross-validation, for *A*) Bush-crow (RF and BRT), *B*) White-crowned Starling (GLM and FDA) and *C*) Superb Starling (MARS and BRT). Points represent the bioclimatic variables used to build the models.

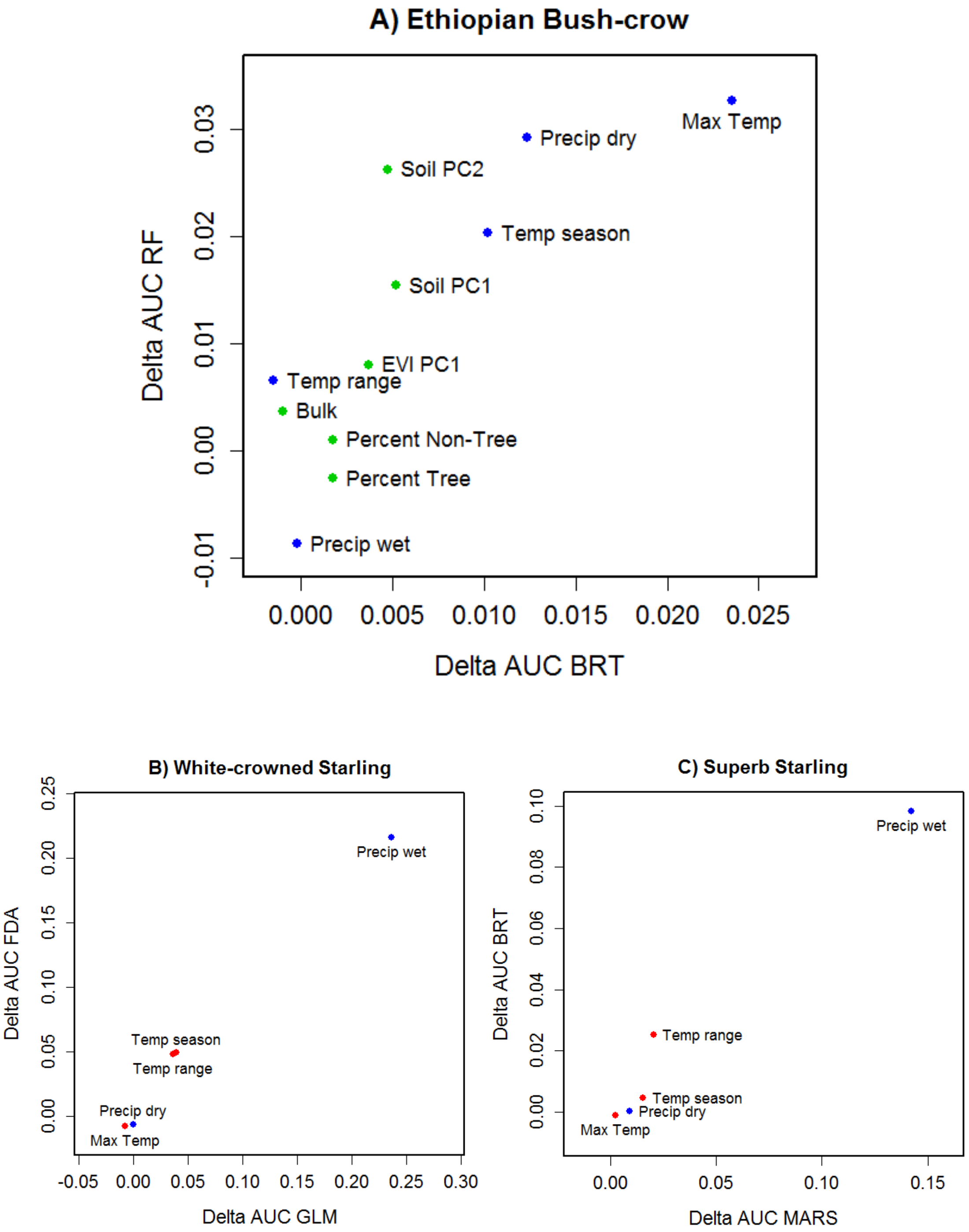
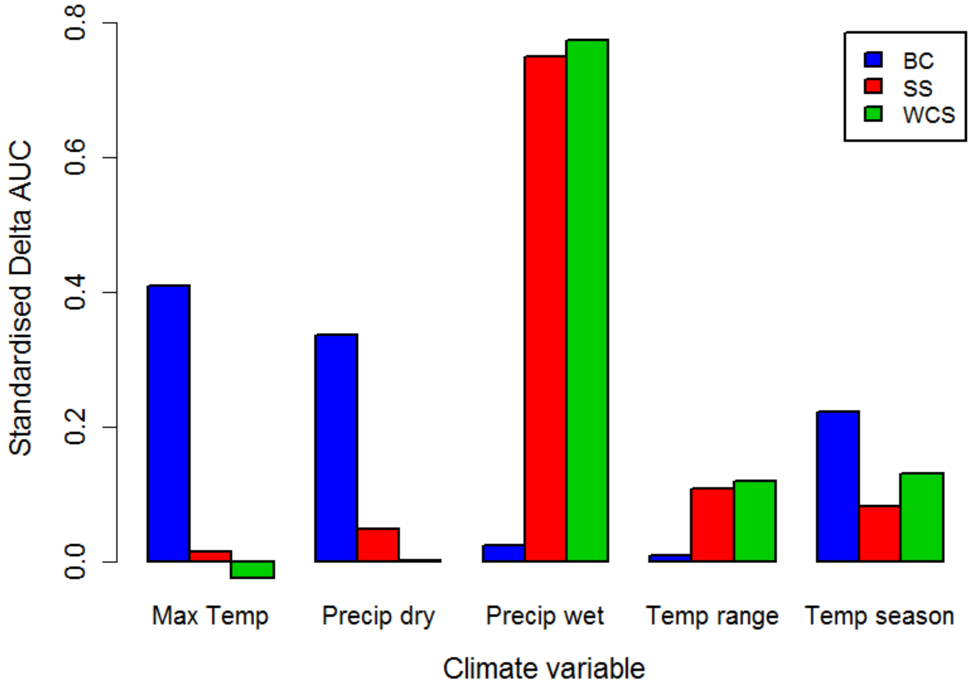


Figure 4.19: Standardised delta AUC scores from the climate-only distribution models fitted for Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Delta AUC scores were obtained by subtracting the *k*-fold AUC score for the model without the variable of interest from the *k*-fold score for the model with all five climate variables. Scores were standardised by dividing each one by the sum of all five scores for the species.



Plots of modelled Bush-crow probability of occurrence against each covariate for the best models (*k*-fold AUC scores greater than 0.8) indicated a strong temperature threshold of 30°C, above which Bush-crows did not occur (Figure 4.20). The second most important variable, precipitation of the driest quarter, also showed a narrow peak in predicted Bush-crow occurrence around 30mm. Although Bush-crows were only predicted to occur at low tree densities, this term was not as important in the models (Figure 4.18).

By contrast, the two starling species both showed the strongest response to precipitation of the wettest quarter, with a sharp decline in probability of occurrence when it exceeded 400mm (White-crowned Starling, Figure 4.21; *A*) and 500mm (Superb Starling, Figure 4.21; *B*). In contrast with the Bush-crow, slight declines in White-crowned Starling probability of occurrence only occurred around a maximum temperature of 38–40°C, whilst the Superb Starling showed no response at all to maximum temperature.

Figure 4.20: The response of probability of Bush-crow occurrence to each bioclimatic variable. Lines show the predicted response to each variable according to the Random Forests (red) and Boosted Regression Trees (blue) algorithms, with all other variables held at their mean.

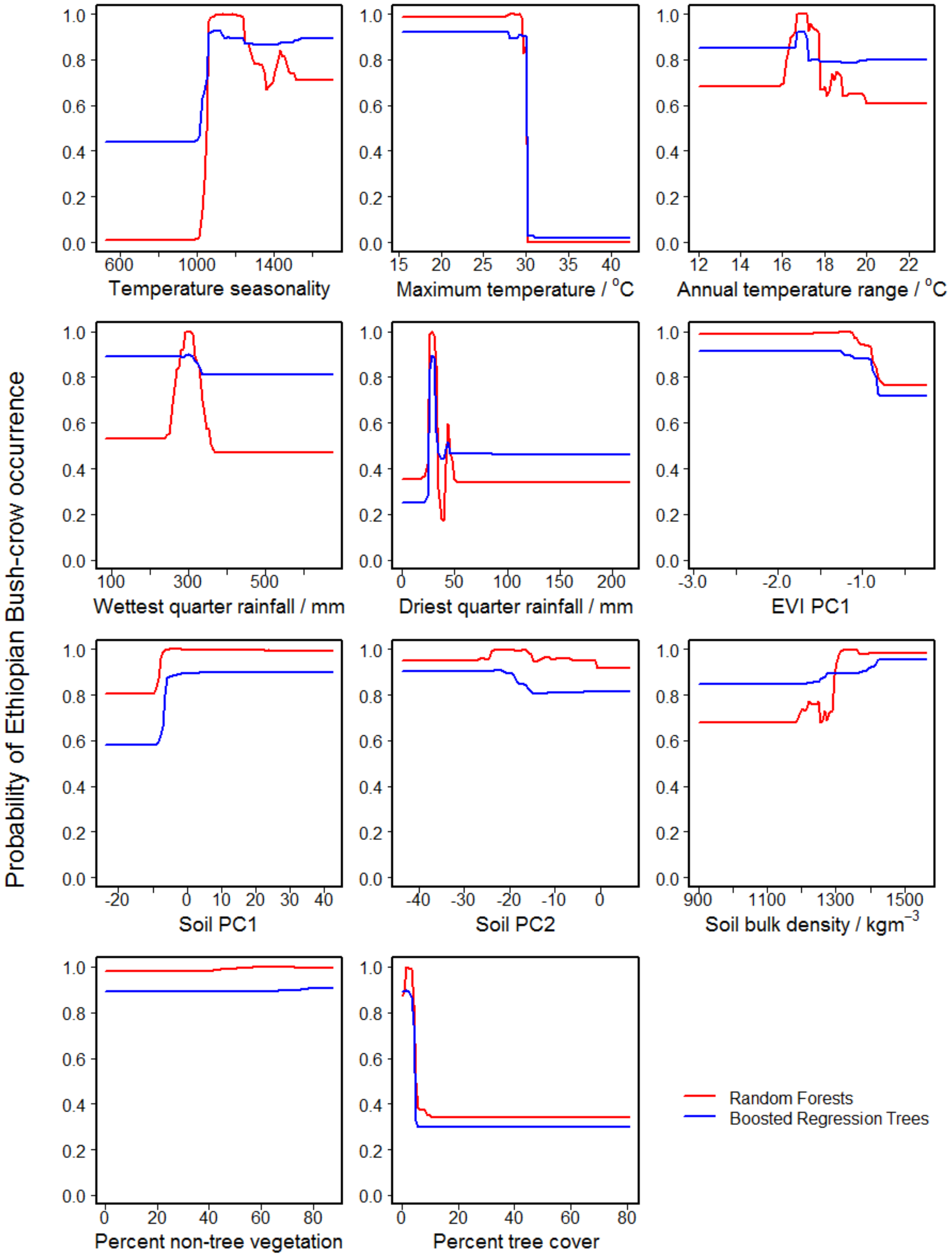
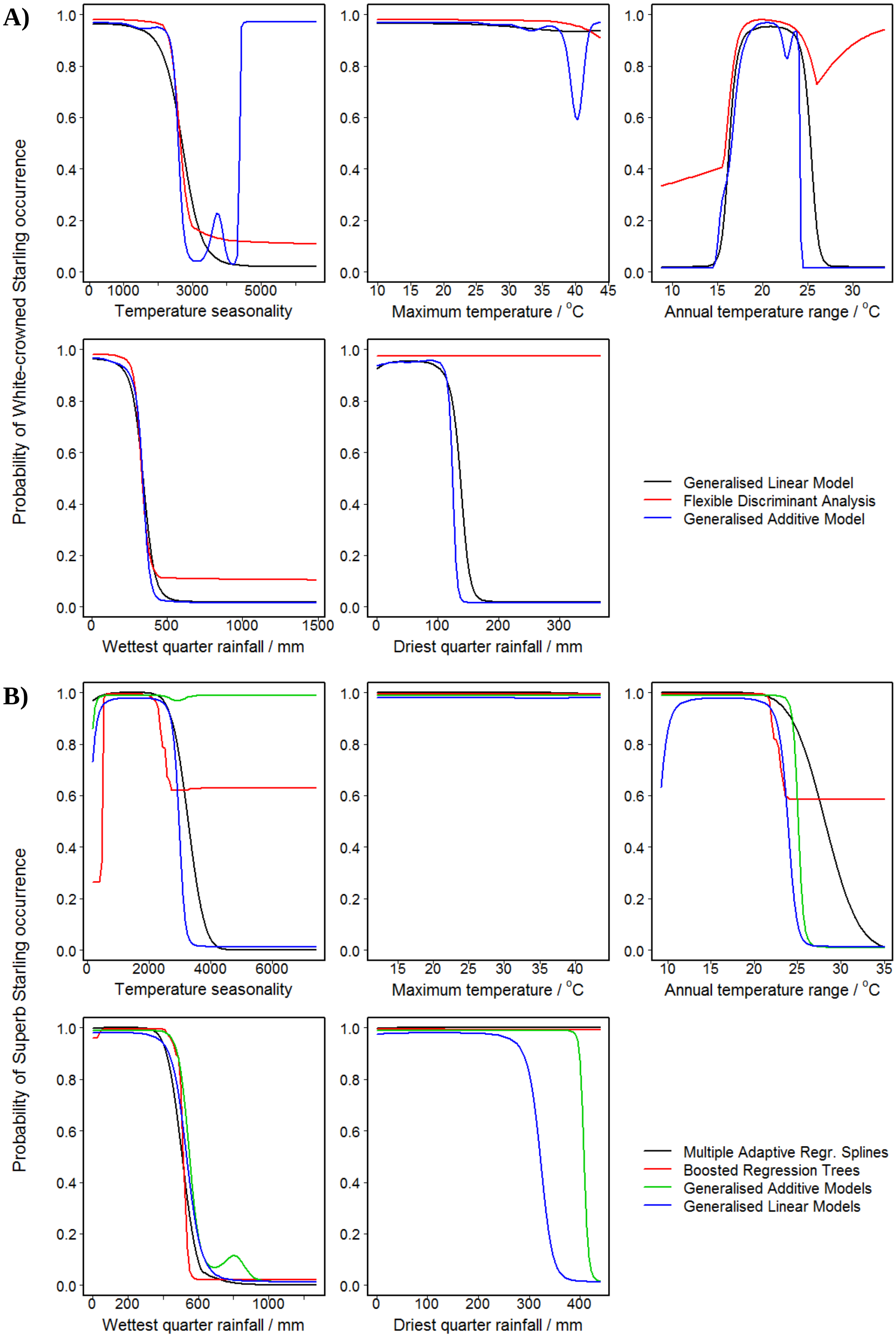
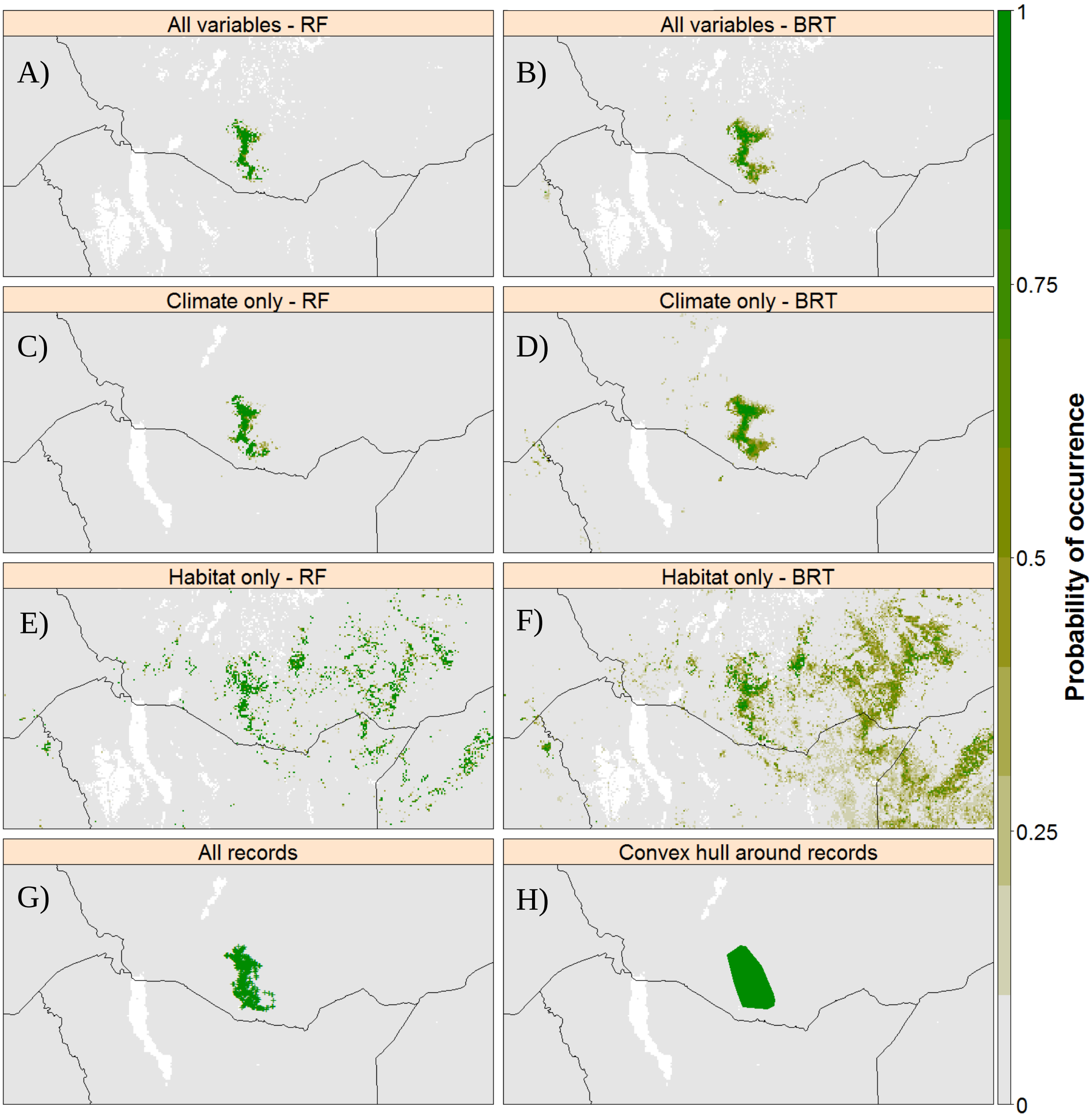


Figure 4.21: The predicted response of probability of occurrence to each climatic variable for the best models for *A*) White-crowned Starling and *B*) Superb Starling, according to *k*-fold cross-validation.



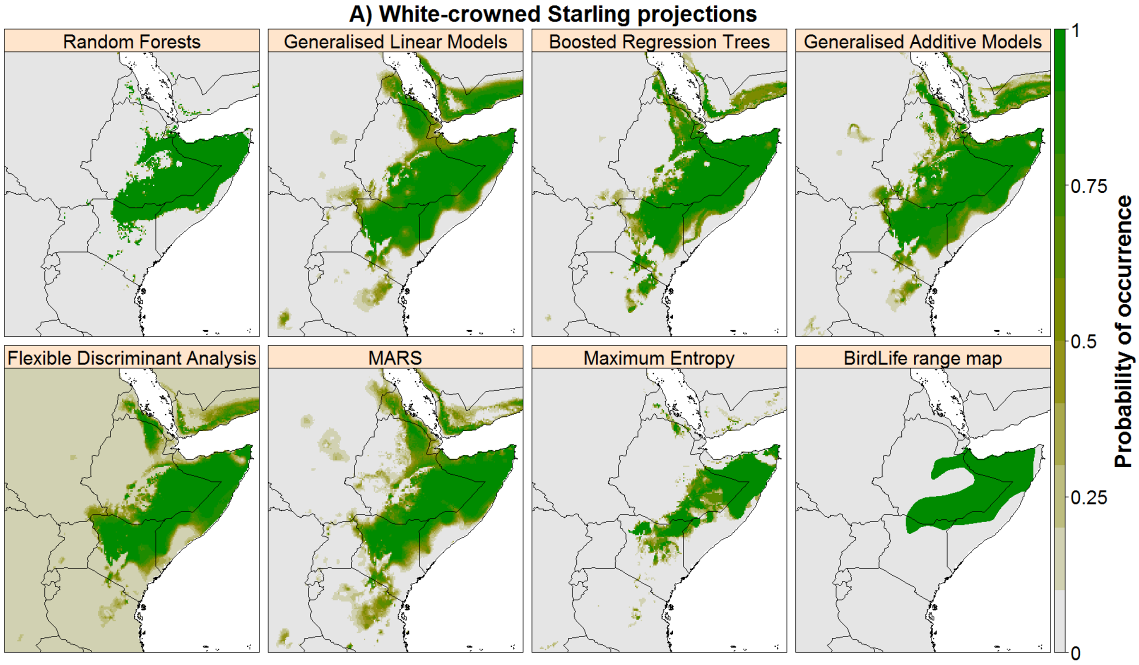
I used the RF and BRT models fitted to all Bush-crow data to produce six simulations of the Bush-crow's current range. The models fitted to all 11 variables (Figure 4.22; *A*, *B*) produced the best predictions of the Bush-crow's true range (Figure 4.22; *G*, *H*), with the climate-only models performing reasonably (Figure 4.22; *C*, *D*) and the habitat-only models poorly (Figure 4.22; *E*, *F*).

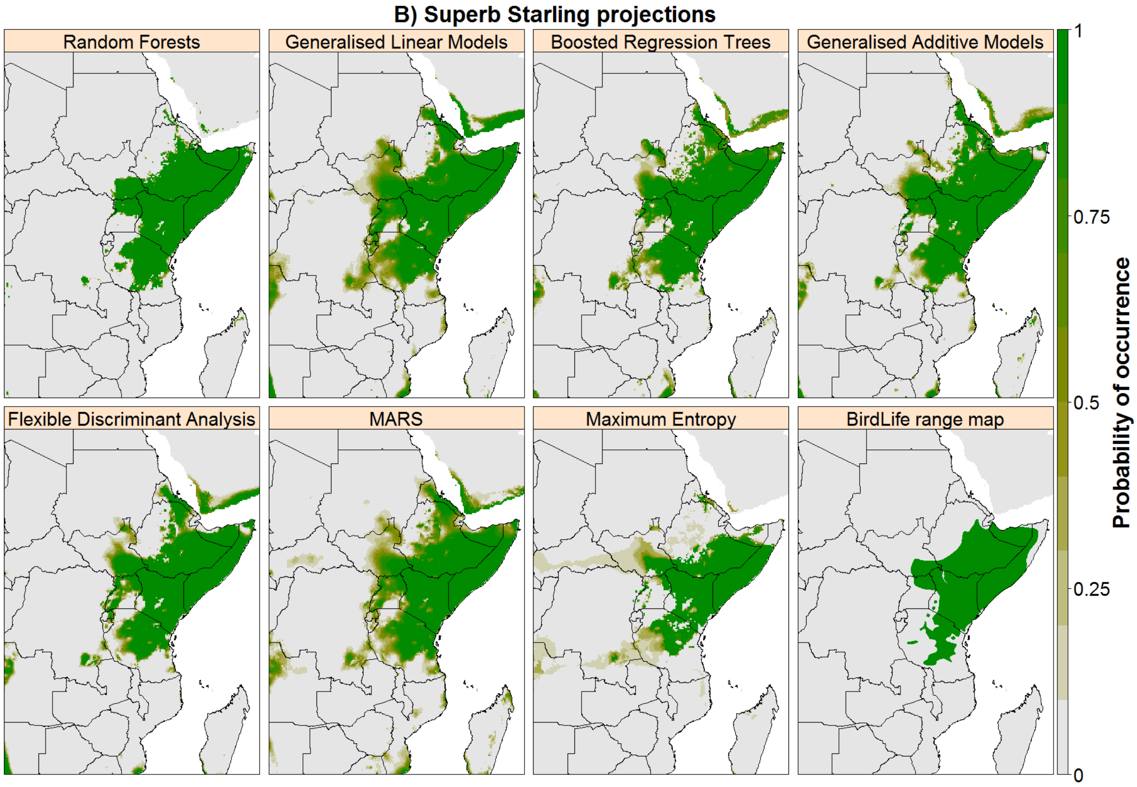
Figure 4.22: Simulations of the Bush-crow's current range using models fitted to all Bush-crow records with the Random Forests (RF: panels *A*, *C*, *E*) and Boosted Regression Trees (BRT: panels *B*, *D*, *F*) algorithms, with climate and habitat predictor variables (*A*, *B*), climate variables alone (*C*, *D*), and habitat variables alone (*E*, *F*). The simulations are compared with all species records (*G*), and the convex hull fitted around the outermost species records (*H*) (Donald et al., 2012).



Simulated distributions for the two starlings under each algorithm were compared with their range maps (BirdLife International and NatureServe, 2015) (Figure 4.23).

Figure 4.23: Probability of occurrence of *A*) White-crowned Starling and *B*) Superb Starling according to each model algorithm. Green represents a high probability of occurrence, grey represents a low probability. The BirdLife range map is shown in the bottom right of each plot.





4.4 Discussion

4.4.1 Preliminary investigation of temperature patterns

Preliminary investigation suggested that the most important determinant of Bush-crow presence was the temperature in the hot season rather than the cool season. This goes against the hypothesis that the chicks and/or juveniles are negatively affected by high temperatures (Jones, 2013; Töpfer and Gedeon, 2012), although if high temperatures adversely affect juvenile birds throughout their first year, then this could still be important in determining the species' response to hot season temperatures.

4.4.2 Effects of temperature on local occurrence and density

Logistic regressions of species' occurrence against temperature showed that, on a local scale, temperature does not affect Bush-crow or White-crowned Starling presence at a site. However, high probability of exceedance of temperature thresholds of 24–26^{o}C in the cool season or across the whole year had a negative effect on Bush-crow bird and group densities, whilst White-crowned Starling densities increased at these warmer sites. Both species were less numerous at sites where temperatures often exceeded 24^{o}C in the hot season. Overall, White-crowned Starling groups occurred at higher densities than Bush-crow groups at sites where they were present.

As the frequency with which temperature thresholds between 26–30^{o}C were exceeded increased, Bush-crow group size decreased but White-crowned Starling group size increased. Bush-crows are thought to be obligate co-operative breeders (Bladon et al., 2016; Gedeon, 2006) and a decline in group size, however caused, might negatively affect breeding success (Mumme, 1992). If nest helpers are the previous season's offspring, as is commonly the case in co-operative breeders (Mumme, 1992), then small group size might reflect lower past breeding success. Unfortunately, I was unable to measure breeding success directly to test the hypothesis that temperature negatively affects Bush-crow breeding success.

The Bush-crow's nest provides a thermally-stable nesting environment (Töpfer and Gedeon, 2012), which may act to buffer the nest against high temperatures. Over a 24-hour period, temperatures are more stable higher above the ground, which could provide an explanation for why Bush-crows often chose to nest right at the top of trees (Benson, 1942; Bladon et al., 2016). However, there was no effect of temperature or proximity to the edge of the range on the height at which nests were built, which suggests that choice of nest location is not a behavioural response to high temperatures.

4.4.3 Effects of habitat on local occurrence and density

When the response of Bush-crow presence and density to temperature and habitat variables within the species' range was modelled, only one model retained the temperature variable, with a surprising positive effect of the probability of 11am or 3pm temperatures exceeding 28^{o}C in the cool season on Bush-crow nest presence. This result contradicts those found in the models of temperature only, where temperature had no effect on bird or nest presence, but negatively affected density and group size. The lack of temperature effects elsewhere, however, suggests that within the Bush-crow's range temperature is unimportant in determining the species' occurrence.

The most important variable across models was bush density, having a negative effect on presence and density of nests and birds. Bush-crows are most commonly found in open *Acacia* woodland (Gedeon, 2006; Mellanby et al., 2008), and are not present in areas with more bush cover. Goat dung density was included in the models as a measure of stocking density, and had a negative effect on bird density. High stocking density leads to over-grazing and eventually scrub encroachment (Tefera et al., 2007a), which is further exacerbated by the cessation of burning in parts of the Bush-crow's range (Solomon et al., 2007). Encroachment has been previously suggested to have a negative impact on Bush-crow populations (Borghesio and Giannetti, 2005), and my results support this conclusion. The extent of the problem across the Bush-crow's range has not been quantified, although my personal observations suggest that scrub encroachment may be common.

Habitat management within the Borana National Park should focus on scrub clearing, to open up areas where bushes have encroached. This work is currently undertaken by human development charities (pers. obs.) but could be extended owing to the benefits available to both local people (Dalle et al., 2006; Tefera et al., 2007a) and Bush-crows. Additionally, grazing management, such as that enforced by the traditional '*gaadaa*' pastoral system, should be strengthened, to tackle the problem of over-grazing and subsequent scrub encroachment in new areas. The ban on burning within the National Park could also be lifted, as this would provide local people with a quicker and more effective way to control scrub in areas where it has become a problem (Solomon et al., 2007; Tefera et al., 2007a).

High soil bulk density had a negative effect on bird and nest presence, and nest and bird group density. Gedeon (2006) suggested that Bush-crows prefer to forage in areas of loosely-packed soil, and this result provides some quantification of this. Bush-crows utilise a range of foraging strategies (Jones et al., in review; Chapter 5), but amongst the most common is digging for subterranean prey. Loosely-packed soil presumably makes this easier, and therefore increases foraging efficiency, leading to a preference for nesting in areas of low soil density.

Conversely, increasing grass cover had a positive effect on bird and nest presence, and nest and bird group density. Grass cover is likely to provide Bush-crows with foraging opportunities, as they frequently peck insects from vegetation (Jones et al., in review; Chapter 5). Greater grass cover is also likely to be indicative of open areas within *Acacia* woodland, with fewer herbs and bushes. Similarly, Bush-crow nest presence and density decreased with increasing bare ground. Despite their strong effects on nests and groups, the three variables likely to affect foraging opportunities – soil bulk density, percent grass cover and percent bare ground – had no effect on bird density, suggesting, perhaps, that they are most important for determining suitable breeding areas.

Soil wetness, included in the models as a potential measure of invertebrate abundance (Sutherland and Green, 2004), had no effect on birds, but was negatively correlated with both nest occurrence and density. Rather than affecting food supply, this variable could instead indicate the birds’ preference for drier areas, as was found previously (Donald et al., 2012), although the reason for this preference is not clear.

There was no effect of tree density or height on Bush-crow occurrence, but density of both nests and birds was positively affected by mean tree height, and nest density was negatively affected by tree density. This emphasises the species’ preference for areas of tall, open *Acacia* woodland (Gedeon, 2006; Mellanby et al., 2008).

Bird and group density were both higher at sites within a kilometre of a village, which supports previous observations that the species associates positively with people (Gedeon, 2006; Hundessa, 1991). One reason for this may be the presence of cattle herds, amongst whose dung Bush-crows often forage (pers. obs.). However, cattle and equid dung density was retained by only one model, albeit with a positive effect on bird density.

Contrary to expectations, the proximity of roads, which have been previously suggested to negatively affect Bush-crows via habitat disturbance (Borghesio and Giannetti, 2005), had no effect on either density or probability of occurrence.

There was no effect of distance to the edge of the range in any of the models, which is unexpected given that it may be expected that the centre of a species range generally provides better habitat than the edges (Brown, 1984). However, when the models were used to predict the probability of occurrence and density inside and outside of the Bush-crow's range, there was no difference between the predictions on either side of the range edge. This suggests that habitat does not play an important role in determining the Bush-crow's distribution, as previously suggested by remotely-sensed NDVI data which was used as a proxy for habitat suitability (Donald et al., 2012).

4.4.4 Effects of temperature and habitat on global distribution

The lack of importance of habitat in determining the Bush-crow's distribution is further confirmed by my own species distribution models, which included a wider range of habitat variables than previous models (Donald et al., 2012). Habitat-only models achieved much lower AUC scores, and failed to successfully describe the Bush-crow's distribution, predicting occurrence across a much wider area.

Bush-crows showed the strongest response to maximum temperature of the warmest month, and to a lesser extent dry season precipitation. This is similar to previous results (Donald et al., 2012), albeit that the range of model algorithms used and variables tested makes my results more robust. Under these models, the Bush-crow's current range is simulated to be significantly smaller than previously thought (Donald et al., 2012), placing it at a higher risk of extinction.

The result for the Ethiopian Bush-crow contrasted with those for the White-crowned and Superb Starlings, two ecologically similar, sympatric, but wider ranging species. The two starlings showed little or no response to temperature, with their ranges instead being most strongly described by areas of low wet season precipitation. This provides further evidence that the Bush-crow's small global range is determined primarily by temperature.

4.5 Conclusion

The restricted range of the Ethiopian Bush-crow is described by a climate envelope based predominantly on maximum temperature of the warmest month, with a secondary effect of dry season precipitation. The sympatric White-crowned Starling's and Superb Starling's ranges are better described by the amount of wet season precipitation.

At a local scale, high temperatures have a negative effect on Bush-crow density and mean group size at a site. This effect is not seen in the White-crowned Starling, which increases in local density and group size at higher temperatures, at least in the cool season. Surprisingly, there is no effect of temperature on Bush-crow probability of occurrence.

Within the Bush-crow's range, a number of habitat variables correlated with Bush-crow occurrence and density, most importantly bush density, soil bulk density and wetness, and tree density (which had negative effects) and grass cover, tree height and village presence (which had positive effects). However, habitat models failed to predict Bush-crow absence outside of the range, just as habitat-only distribution models failed to do.

There is compelling evidence that the Bush-crow's global distribution is driven by its response to temperature at a broad scale, and by habitat availability at a local scale, but the mechanism by which the temperature limitation occurs is unknown. Possible mechanisms are investigated in the next chapter.

5 THE EFFECTS OF TEMPERATURE ON ETHIOPIAN BUSH-CROW, WHITE-CROWNED STARLING AND SUPERB STARLING BEHAVIOUR

"This village is like White Horse Hill. There are no toilets."

5.1 Introduction

The degree to which the boundaries of the small global range of the Ethiopian Bush-crow correlate with climatic and remotely-sensed habitat data has been described previously (Donald et al., 2012) and in Chapter 4 of this thesis. These studies found an association between the Bush-crow's geographical range and an area of lower temperature than the neighbouring areas outside the range, an association not seen in the ecologically similar White-crowned Starling *Lamprotornis albicapillus* and Superb Starling *Lamprotornis superbus* (Chapter 4). Although this suggests that temperature might play a direct or indirect role in limiting the Bush-crow's distribution it does not provide information on the mechanism of the limitation, which could involve effects of temperature on breeding success, juvenile survival or adult survival caused by physiological tolerances, or an influence of temperature on foraging ability or prey availability. Three possible mechanisms are investigated in this chapter: the impacts of temperature on thermoregulatory behaviour, foraging ecology and juvenile behaviour.

Extreme weather events, such as heat waves and droughts, can have adverse effects on many aspects of avian biology, including foraging (Cunningham et al., 2013a). These effects are mediated through a bird's ability, or otherwise, to respond, either physiologically or behaviourally, to stressors such as high temperatures or limited water availability (Whitfield et al., 2015; Wolf, 2000). In Southern Pied Babblers *Turdoides bicolor* foraging efficiency, the rate of food intake per unit effort, is reduced by the need for thermoregulatory behaviour in hot weather (du Plessis et al., 2012). This is despite the fact that there is no change in foraging effort. When daytime temperatures exceed 35.5^{o}C, Babblers are no longer able to obtain enough food to counter typical overnight weight loss. Over an extended period, this can lead to a loss of condition, and therefore ultimately limit the species' ability to survive in warmer areas at the edge of their range (du Plessis et al., 2012).

High temperatures can force behavioural changes which trade-off thermal requirements against foraging behaviour (Martin et al., 2015; Oswald et al., 2008). Magpies *Pica pica* in northern Cyprus actively select their thermal environment when air temperatures rise above 31^{o}C, spending more time perched in the shade and less time foraging (Kelly et al., 2004). Southern Fiscals *Lanius collaris* prefer to hunt from sunny perches, but switch to shaded perches when temperatures exceed 35^{o}C, which reduces foraging success by 50% (Cunningham et al., 2015).

Many bird species are known to exhibit behavioural and physiological responses to high temperature (Wolf, 2000). However, if temperature is important in driving the global distribution of the Ethiopian Bush-crow, then it would be expected that individual birds would exhibit behavioural responses to temperature at lower environmental temperatures than sympatric species with similar foraging ecology but less restricted ranges, such as the White-crowned and Superb Starlings. In this Chapter I investigate the thermoregulatory and foraging responses of the three species to changes in local temperatures at foraging sites, to see whether they provide a mechanism by which the Bush-crow's thermal range-restriction operates.

At high ambient temperatures birds are forced to change their behaviour to maintain a stable body temperature (Ricklefs and Hainsworth, 1968). As temperatures increase, birds which become heat stressed are expected to become less active and spend more time in the shade, as a mechanism to reduce body temperature and save water (Cunningham et al., 2015; Martin et al., 2015; Wolf and Walsberg, 1996). If the Bush-crow's range-restriction is driven by a physiological inability to cope with high temperatures not seen in the starlings, then it would be expected that Bush-crows would reduce their activity, move to the shade, and begin panting at lower ambient temperatures than the two starling species.

The unusual structure of the Bush-crow's nest produces a thermally stable environment (Töpfer and Gedeon, 2012), and, coupled with the high level of juvenile care invested by adult birds (Bladon et al., 2016), this suggests that young Bush-crows may suffer the most at high temperatures. If juvenile Bush-crows are more severely affected by heat than adult birds, it would be expected that juveniles will change their behaviour at even lower temperatures, a result which was obtained in a preliminary study (Jones, 2013). However, as juveniles develop into adults, their tolerance of high temperatures would have to change, and this should be reflected in an age-related increase in activity levels and occupation of sun-lit areas at high temperatures.

As birds become heat-stressed, their foraging behaviour may be affected in a number of ways. First, the number of foraging attempts which they are able to make per unit time may decrease. However, birds tending juveniles may still be required to put more effort into foraging than those in adult only groups, in order to provide enough food for their young. Second, independent of foraging effort, a bird's ability to forage successfully may also be impacted by temperature (du Plessis et al., 2012), with a lower proportion of foraging attempts successfully obtaining food. Either of these responses may result in a third change, a reduction in the absolute rate of food intake (prey items per unit time) with increasing temperature. Morever, the need to thermoregulate whilst foraging at high temperatures may further impact a bird's ability to gather food, and therefore its foraging efficiency. Ultimately, such an effect may drive range limitations, because if prey intake rates are insufficient to meet energetic demands, then individuals will lose condition over time, and may not be able to persist in an area in the long term (du Plessis et al., 2012).

If foraging efficiency varies with temperature, it might be expected that prey selection would also need to change in order to acquire enough food when efficiency is low, with a preference for larger or more energy-rich prey at high temperatures. Prey selection may also vary with the presence of dependent juveniles in the group. Bush-crows utilise a range of foraging techniques to acquire food (Gedeon, 2006). If the energetic cost or likely success rate of these techniques varies, then birds may adjust their foraging technique according to their physiological state, as determined by temperature.

Finally, if juvenile Bush-crows are more heavily impacted by high temperatures than adults, one might expect adults to invest more in care (in terms of allofeeding) as temperatures rise, to compensate for the juveniles' reduced ability to forage for themselves. As the number of juveniles in the group increases, adult birds should have to feed a higher proportion of the food they catch to juveniles. Conversely, as the number of adult birds in the group rises, each bird may feed fewer items to the juveniles. When investment is high, it is perhaps more worthwhile to feed larger prey items to juveniles to sate their appetite quickly, and to keep smaller items for oneself. Unlike Bush-crows, White-crowned Starlings are only observed feeding juveniles occasionally, and Superb Starlings appear not to feed juveniles at all (pers. obs.).

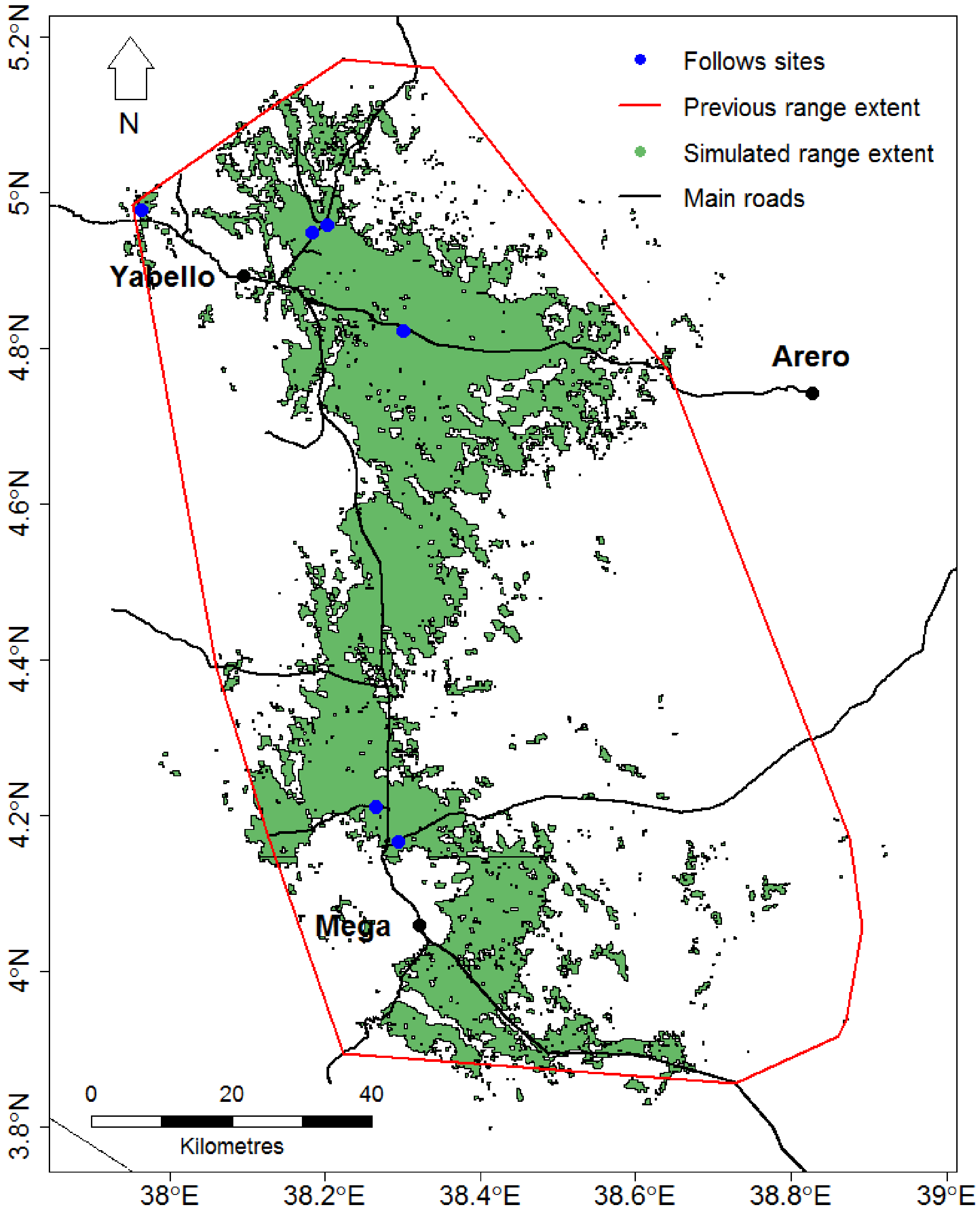
This chapter aims to investigate the mechanisms underlying the Bush-crow's climatically-driven range restriction, by investigating how temperature affects daily activity patterns, and thermoregulatory and foraging behaviour. By comparing the results with the White-crowned and Superb Starlings, whose ranges are not determined by temperature (Chapter 4), I am able to control for additional influences on behaviour, such as time of day and prey availability, which may otherwise confound the results.

5.2 Methods

5.2.1 Site selection

Six study locations where Bush-crows occurred were chosen, selected both to represent areas in the centre and close to the edge of the Bush-crow's range, and to include sites which were at the hotter and cooler extremes of temperatures recorded within the species' range (Section 3.5; Figure 5.1). Each site was visited on two pairs of days in 2014, with a gap of at least a week between the two. Within each pair, one day was spent following Bush-crow groups, and the other following starling groups. White-crowned Starlings were followed preferentially, but Superb Starlings were followed at three sites where White-crowned Starlings were difficult to find.

Figure 5.1: A map of the sites used for Bush-crow and Starling behavioural studies (blue), overlaid on the Bush-crow's simulated suitable range based on the Random Forests algorithm (in green, see Chapter 4) and the previously reported range extent in red (Bladon et al., 2016; Donald et al., 2012).



5.2.2 Data collection

In April and May 2013, 57 Bush-crows were caught and colour-ringed at five sites. These birds provided the focus for a preliminary study of the impacts of temperature on behaviour (Jones, 2013). Using these results for guidance, I further developed the methods and collected additional data on these and other birds in 2014.

Two studies were conducted, alternately, throughout the day on the focal species. Group ID was always recorded, either using the presence of colour-marked birds or by carefully noting where the same or different groups were chosen for consecutive observations, with multiple observations being conducted on most groups. Where group size fluctuated between observations (groups sometimes split into smaller foraging units and come together again later), the largest number of adults and juveniles observed for that group was used for analysis.

Behavioural follows

Two datasets, collected by myself in 2014 and by Sam Jones in 2013, were used for analysis. In 2013, only data on Bush-crows were collected, with 48 follows on adult birds and 41 on juveniles. In 2014 Bush-crows, White-crowned and Superb Starlings were all followed, with adult and juvenile samples sizes of 44 and 50, 11 and 25, and 14 and 28 respectively.

Groups with post-fledging juveniles were identified, and time was taken to approach without disturbing behaviour (generally to 10-15m). A timer was used to measure 1-minute intervals for focal animal sampling (Altmann, 1974). At the end of each interval, the activity of a focal adult, watched continuously, was recorded, along with its position (in the sun, in the shade or under cloud cover), and a count of the behaviour and position of all visible juveniles was made. If the focal adult was lost from view, a new bird was chosen (and recorded as such) for the next interval. If the group was lost from view for two consecutive budgets the follow was stopped, and a new one started when the group was refound.

The recorded activities were categorised as active (foraging, allofeeding, on the ground or at the nest) or inactive (perched at rest, preening or allopreening). Records of birds in flight or alert were excluded from the analysis because these behaviours were likely to have been elicited by stimuli such as predators or alarm calls and not been affected by temperature. Data on juvenile activity were converted to a modal activity and location for each minute.

Foraging watches

Foraging adults were approached to a distance of 5-10m, and watched continuously with binoculars. Data were recorded orally onto a Dictaphone (Sony ICDPX333.CE7 MP3 Digital Voice Recorder) and later transcribed. The success of all foraging attempts was recorded, with technique identified as pecking, digging, turning an object (usually dung), chasing flying prey, stealing from another bird, or being allofed. The size of captured prey was divided into four classes relative to the length of the bill ("tiny", indiscernible compared to the length of the beak; "small", less than half the length of the beak; "medium", from a half to the full length of the beak; "large", longer than the length of the beak), as used previously (Donald et al., 2012; Jones, 2013). I also recorded whether or not each item was fed to a juvenile. Panting is a commonly used strategy for behavioural thermoregulation, and its occurrence and duration on each watch was recorded. This was converted to a proportion of each watch spent panting, and all foraging behaviour was recorded as being "whilst panting" or "whilst not panting". Recordings were paused if the bird was not visible (for example if it walked behind a bush), and note was taken of any periods where the bird ceased foraging. Watches were ended when the bird ceased foraging and flew off. One hundred watches of Ethiopian Bush-crows were completed, along with 30 watches of White-crowned Starlings and 50 watches of Superb Starlings, on both adult only and adult plus juvenile groups.

Temperature data

Temperature data were collected slightly differently in the two years. At the start of each day two iButton Thermochrons® (Maxim Integrated, DS1921G-F5) were put out at the site, one in constant sun and the other in constant shade. These recorded temperature data every minute at locations nearby and comparable to those being used by the birds for foraging. In 2013, the units were left directly on the ground, whereas in 2014 they were glued to golf tees pressed into the soil to lift them off the ground. Golf tees were used in 2014 to try to better measure air temperature at the ground, but comparison of the temperature data from the two years showed that the two datasets were not directly comparable, with the 2013 temperatures being 4–6^{o}C higher. When conducting the behavioural follows analyses, I therefore fitted separate models to 2013 and 2014 data.

The mean temperatures recorded on each iButton across the duration of each behavioural follow and foraging watch provided a single ‘shade’ and ‘sun’ temperature for each observation.

5.2.3 Statistical analysis

Behavioural follows

I used the behavioural data to investigate the following questions. How does temperature affect the activity levels and choice of location (in the sun or in the shade) of adult birds of each species, and does this response vary with the presence of dependent juveniles in the group? Do adult and juvenile birds of each species differ in their response to temperature, in terms of activity levels and choice of location? How does temperature affect the activity levels and choice of location of juvenile birds of each species, and does this response vary with age?

1) Activity models

To investigate whether each species’ activity levels varied with temperature, I fitted logistic regressions to my activity budgeting data. The number of active records as a proportion of active and inactive behavioural records from each behavioural follow was the response variable, and I assumed binomial errors and a logit link. Temperature, temperature squared (to obtain a quadratic model), species and a species by temperature interaction (2014 data only) were fitted as independent variables. Behavioural changes such as thermoregulation are likely to be determined by the temperature which the bird is experiencing in its current location (sun or shade). For analyses of activity, I therefore used a weighted temperature term, in which the temperatures recorded in the sun and shade were weighted by the number of observations which the bird spent in the sun or not in the sun (i.e. in the shade or under cloud cover) respectively. This is termed “weighted temperature”.

2) Location models

To investigate whether Bush-crows and Starlings differ in the amount of time they spend in the shade at a given temperature, I fitted logistic regressions with the proportion of behavioural records where the bird was in the shade or sun as the response variable (records which occurred under cloud cover were excluded). Again, temperature, temperature squared (to obtain a quadratic model), species and a species by temperature interaction (2014 data only) were fitted as independent variables. The location in which a bird chooses to be, either in the sun or in the shade, is likely to be determined solely by the temperature experienced in the sun, i.e. if it is too hot in the sun, it will move to the shade. For analyses of location, I therefore used the temperature in the sun (termed “sun temperature”) as the independent temperature variable.

To assess the thermoregulatory benefit of moving to the shade, I tested the difference in mean temperatures in the sun and shade during behavioural follows on both adult and juvenile birds using one-tailed paired t-tests.

3) Model structures

To investigate the effect of temperature on adult behaviour, and to see whether this changed depending on whether or not they had dependent young, I fitted models to the focal adult data, with group type (with or without juveniles) and a group type by temperature interaction as additional independent variables. I expected that birds caring for juveniles would be forced to remain more active at higher temperatures than birds from adult-only groups. Group type could only be included in the 2014 models, because only a single adult-only group with associated temperature data was observed in 2013.

I combined the adult and juvenile data on activity and location, and fitted models to investigate whether their responses to temperature differed. I included bird type (adult or juvenile) and a bird type by temperature interaction as independent variables, with the expectation that juvenile birds would respond more rapidly to rising temperatures than adults.

I used date as a simple proxy for age, and fitted models to the juvenile data with date and an interaction between date and temperature as additional independent variables. I expected that juvenile birds’ response to temperature would become less severe as they developed.

Model selection was carried out by backwards stepwise selection, with the deletion of each term tested using a likelihood-ratio test. Once a minimum model, in which all remaining terms were significant, was obtained, the significance of those terms was tested by deletion, and the re-addition of deleted terms checked, again using a likelihood-ratio test (Crawley, 2005).

To control for the effect of having multiple follows on the same group, group ID was included as a random effect. When models were over-dispersed, a random effect of observation was nested within group ID. I also fitted these models without random effects, and tested significance using a Wald *F*-test in place of the likelihood ratio test.

Foraging watches

I used the data from my foraging watches to answer the following questions. How does temperature affect the proportion of time spent panting by each species? How does temperature affect the foraging effort, foraging success and food intake rate of the three species? Do the three species alter their choice of foraging technique in response to temperature? Does temperature affect the size of prey consumed by each species? Does temperature affect the care that adult birds provide to juveniles, in terms of the number of prey items offered to them?

I fitted a series of Poisson and logistic regressions to answer these questions. Temperature in the sun, species and the temperature by species interaction, as well as a quadratic temperature term, were included as independent variables, with additional effects of group type (with or without juveniles), and foraging type (panting or not) included where appropriate (specified below). All two-way interactions except those with the quadratic temperature term were included in each maximal model.

Most models were fitted with each foraging watch on a single bird as a single observation, in which case a random effect of group ID was included. When further analyses split the data into foraging bouts within watches (to investigate the impact of panting), a random effect of watch ID was nested within group ID. Where Poisson or binomial response variables were over-dispersed, a random effect of observation was nested within group ID or watch ID (du Plessis et al., 2012).

Model selection was carried out via backwards stepwise selection, with the removal of each term assessed using a likelihood-ratio test between the model with and without the term (Crawley, 2005). Once a minimal model was obtained, the significance of the remaining terms was assessed in the same way.

Dealing with over-dispersion in random effects models is not straightforward so, to investigate the effects of this on the parameter estimates, I refitted each over-dispersed model without random effects, and accounted for the over-dispersion by using a quasi-Poisson or quasi-binomial error structure. The removal of terms during model selection was then assessed using Wald *F*-tests.

1) Proportion of time spent panting

Inspection of scatter plots indicated that the data were not straightforward to analyse using ordinary least squares regression with the proportion of the watch spent panting (P_{pant}) as the dependent variable and temperature as the independent variable. This is because (a) many values of P_{pant} were zero or one, (b) values of P_{pant} between zero and one were widely scattered for a given value of temperature, and (c) residual variation in P_{pant} was non-normal and appeared to vary with temperature in a way that could not easily be dealt with by standard transformations of P_{pant}, such as logit, Box-Cox or arcsine square root. It was noted that these problems resemble those addressed by the statistical model of avian primary moult developed by Underhill and Zucchini (1988). Therefore, I fitted an equivalent model to that used by Underhill and Zucchini for their Type 2 data. This model requires moult scores for individual birds in pre-moult, moult and post-moult to be sampled with equal probability (Underhill and Zucchini, 1988). In my models, P_{pant} was taken to be equivalent to primary moult score and temperature was taken to be equivalent to calendar date. Therefore, a bird which did not pant at all during a foraging watch was equivalent to a bird in pre-moult, a bird which panted continuously throughout the watch was equivalent to a bird post-moult, and birds which panted for part of the foraging watch were equivalent to birds in-moult. Hence, my model had three parameters: (1) the mean of the temperatures at which individual birds begin to show some panting behaviour ($P_{pant} > 0$), (2) the difference between the temperature at which a typical individual begins to show panting behaviour and that at which it pants throughout the watch (this difference is taken to be the same for all individuals), and (3) the standard deviation of the temperatures at which individual birds begin to show some panting behaviour. I fitted Underhill-Zucchini models using the '*moult*' package (Erni et al., 2013) in R (R Core Team, 2016). I fitted eight models, representing all possible combinations of each of the three parameters being the same or different among the three species. I used the sample size, the residual deviances and numbers of fitted parameters of these models to calculate the information criterion AIC_c

and AIC_c weights for each model following the method of Burnham and Anderson (2002). I used expected mean P_{pant} values for each of a range of temperatures for each species from the model with the lowest AIC_c value and model-averaged mean P_{pant} values obtained by averaging across all eight models in the set using AIC_c weights. I compared selected pairs of models using likelihood-ratio tests.

2) Foraging effort

To investigate the effect of temperature on Bush-crow and Starling foraging effort, I fitted a Poisson regression to the count of foraging attempts in each watch, with group type included as an independent variable, and the natural logarithm of watch duration as an offset. The data were over-dispersed.

Within individual foraging watches, birds exhibited bouts of panting whilst foraging, and bouts of foraging without panting. To investigate whether panting affects the birds' foraging effort, I split the data for each watch into bouts of foraging with and without panting. I fitted a Poisson regression with the count of foraging attempts within each watch period as the dependent variable, with group type and foraging type as additional independent variables, and the natural logarithm of watch period duration as an offset. The data were over-dispersed.

3) Foraging technique

Bush-crows utilise a range of foraging techniques to acquire food (Gedeon, 2006), most commonly pecking from vegetation, digging and turning over objects (normally dung). Three rarer methods were also observed during watches; chasing aerial prey, stealing food from conspecifics, and being allofed by conspecifics. All techniques were also observed for White-crowned Starlings, and all but stealing and allofeeding for Superb Starlings.

To investigate whether each species' choice of foraging technique varies with temperature, I fitted a series of Poisson models to the count of attempts using each capture technique in turn, with the natural logarithm of the time spent foraging (in minutes) as an offset. The data for pecking and digging were over-dispersed, but the dung turning data were not.

4) Proportion of foraging attempts successful

I investigated the impact of temperature on foraging success by fitting a logistic regression to the proportion of foraging attempts which were successful in obtaining food. The data were over-dispersed.

To investigate the impact of panting on foraging success, I fitted the same models to bouts of foraging within each watch, with foraging type included as an independent variable. These data were not over-dispersed.

To test for an impact of foraging technique on success, I used the data for individual foraging attempts with success as a binary variable, and fitted models with technique used (peck, dig, chase or turn dung) included as a predictor variable. The model with all four techniques failed to converge, owing to the small number of occasions where the two starling species chased items or turned dung. I removed these points, and fitted a model to just the pecking and digging data for all species, and then fitted the model to Bush-crow data alone, which allowed the turn dung technique to be included.

5) Food intake rate

To investigate whether temperature affected the species' rate of food intake, I fitted a Poisson regression to the count of items caught in each watch, with the natural logarithm of the amount of time spent foraging (in minutes) as an offset. The data were over-dispersed.

To test for an effect of panting whilst foraging on intake rate, I then fitted a Poisson regression to periods within each watch, with foraging type (panting or not) as an additional independent variable.

6) Prey size

To investigate whether prey size caught changed with temperature, I fitted Poisson models similar to those used for efficiency, with the count of prey of each size as the dependent variable, the natural logarithm of the amount of time spent foraging (in minutes) as an offset, and group type included as an independent variable.

To investigate the change in the Bush-crow’s dietary composition further, I then fitted a series of logistic regressions, scoring each prey size in turn as a “success”. There were too few non-zero observations of large items to model them. Data for medium and small items were not overdispersed, but those for tiny items were.

7) Juvenile care

To see whether Bush-crows’ investment in juvenile care varied with temperature, I modelled the per capita intake rate of juveniles from the focal adult per unit time. I fitted a Poisson regression to the count of food items on each watch which were fed to juveniles, with the natural logarithm of the product of the number of juveniles in the group and the watch duration in minutes as an offset. The ratio of adults to juveniles in the group and the food intake rate of the focal adult were fitted as additional explanatory variables.

I tested whether Bush-crows prefer to feed larger prey items to juveniles using a chi-squared test. I summed the number of prey items of each size caught by focal Bush-crows from groups with juveniles, and used this as the expected probability distribution for prey items of each size which were fed to juveniles.

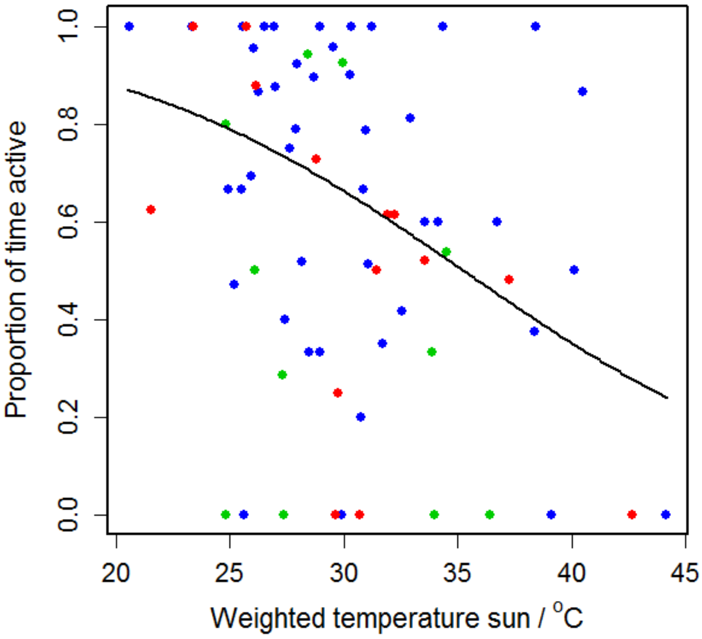
5.3 Results

Behavioural follows

1) Adult behaviour

Both the 2013 and 2014 minimum adequate models with a random effect of group ID included only the temperature term. As weighted temperature increased, all species spent less time engaged in active behaviours (2014: $\chi^2 = 8.70$, d.f. = 1, P = 0.003; 2013: $\chi^2 = 10.53$, d.f. = 1, P = 0.001) (Figure 5.2). There was no difference between species in the 2014 model ($\chi^2 = 5.04$, d.f. = 2, P = 0.080). The fixed effects models produced similar results for 2014, but in 2013 found no effect of temperature.

Figure 5.2: Relationship of the proportion of time spent active to weighted temperature for adult Bush-crows (blue), White-crowned Starlings (green) and Superb Starlings (red). Points show data from individual follows in 2014. The curve shows the predicted values for all three species from the model fitted with random effects.



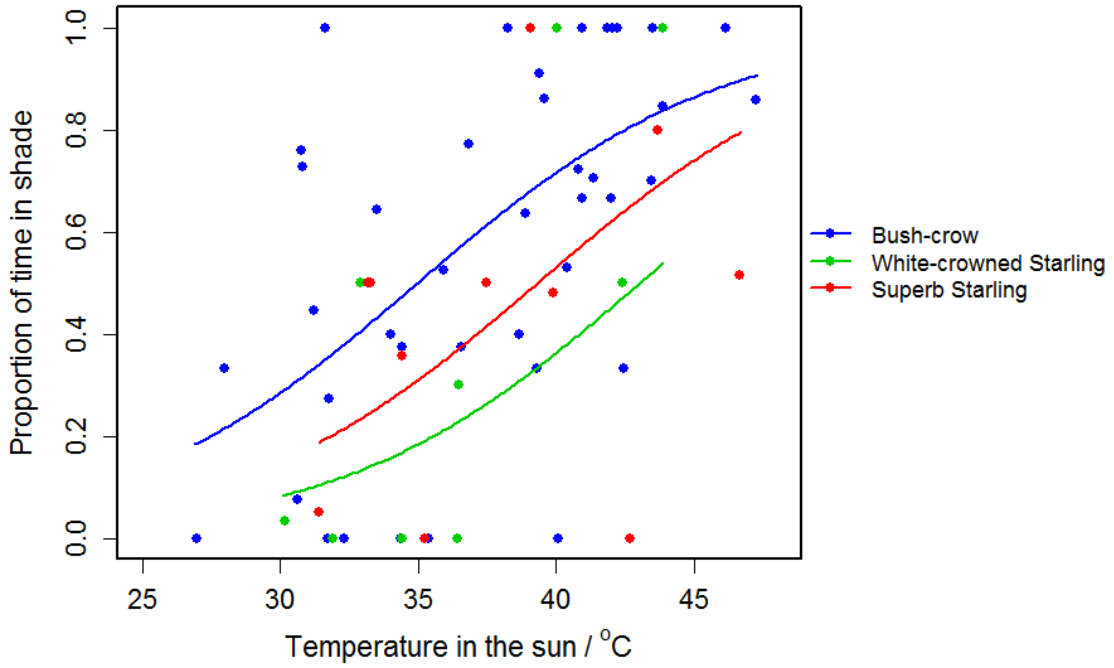
2) Adult location

The random effects model fitted to 2014 data found that all species increased the amount of time spent in the shade as temperature in the sun rose (χ^2 = 22.50, d.f. = 1, P < 0.001), and Bush-crows spent more time in the shade than either starling species at any given temperature (χ^2 = 7.78, d.f. = 2, P = 0.020). There was no effect of group type, and no interaction between species and temperature (Figure 5.3). The 2013 models found the same effect of temperature in the sun on Bush-crows.

The 2014 fixed effects model was not over-dispersed, and additionally retained the species by temperature interaction (deviance = 15.71, d.f. = 2, P < 0.001), with White-crowned Starlings initially moving to the shade at higher temperatures than either Bush-crows or Superb Starlings, but then spending more time there with smaller increases in temperature.

In 2014, the mean temperature in the sun was 11.2°C warmer than in the shade during follows on adult birds (t = 18.00, d.f. = 99, P < 0.001).

Figure 5.3: Relationship of the proportion of time spent in the shade to temperature in the sun for adult Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual follows in 2014. Curves show predicted values from the random effects model.

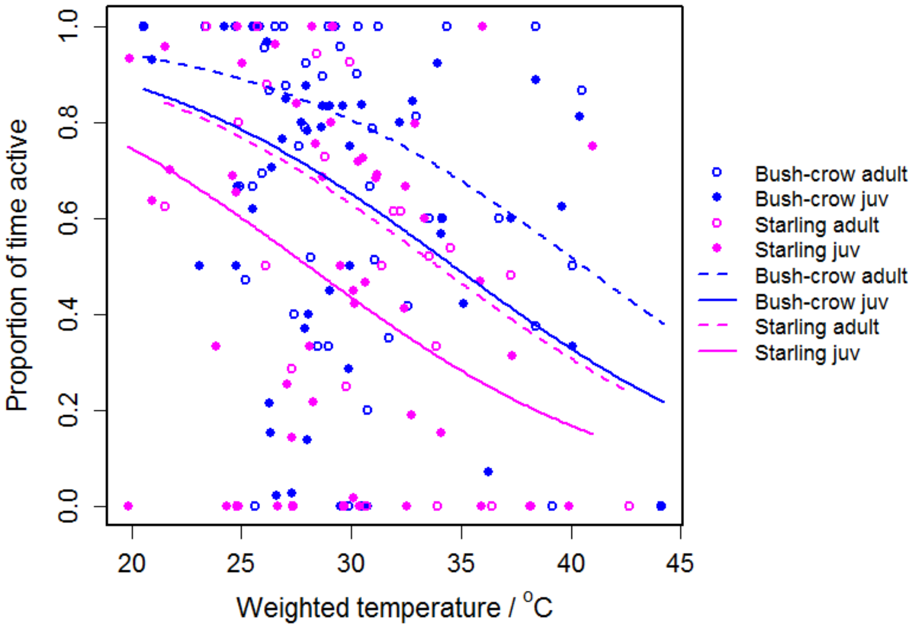


3) Adult and juvenile behaviour

In the 2014 random effects models, the two starling species showed very similar responses, so species was reduced to a two level factor, Bush-crow and Starling. All species showed a reduction in activity as weighted temperature increased (χ^2 = 14.70, d.f. = 1, P < 0.001), with adult birds of all species being more active at any given temperature than juveniles (χ^2 = 6.33, d.f. = 1, P = 0.012). The starlings reduced their activity levels at lower weighted temperatures than Bush-crows (χ^2 = 4.00, d.f. = 1, P = 0.046) (Figure 5.4). In the fixed effects model the species term was not retained, even when it was reduced to two levels, but the effects of temperature and bird type were the same.

There was no effect of weighted temperature in the 2013 random effects model, and only the bird type term was retained. Adult birds were more active than juveniles (χ^2 = 34.29, d.f. = 1, P < 0.001). The same result was found in the 2013 fixed effects model.

Figure 5.4: Relationship of the proportion of time spent active to weighted temperature for Bush-crows (blue) and Starlings (pink). Points show data from individual follows in 2014. Curves show predicted values for adult (open circles, dashed lines) and juvenile birds (filled circles, solid lines) from the model fitted with random effects.

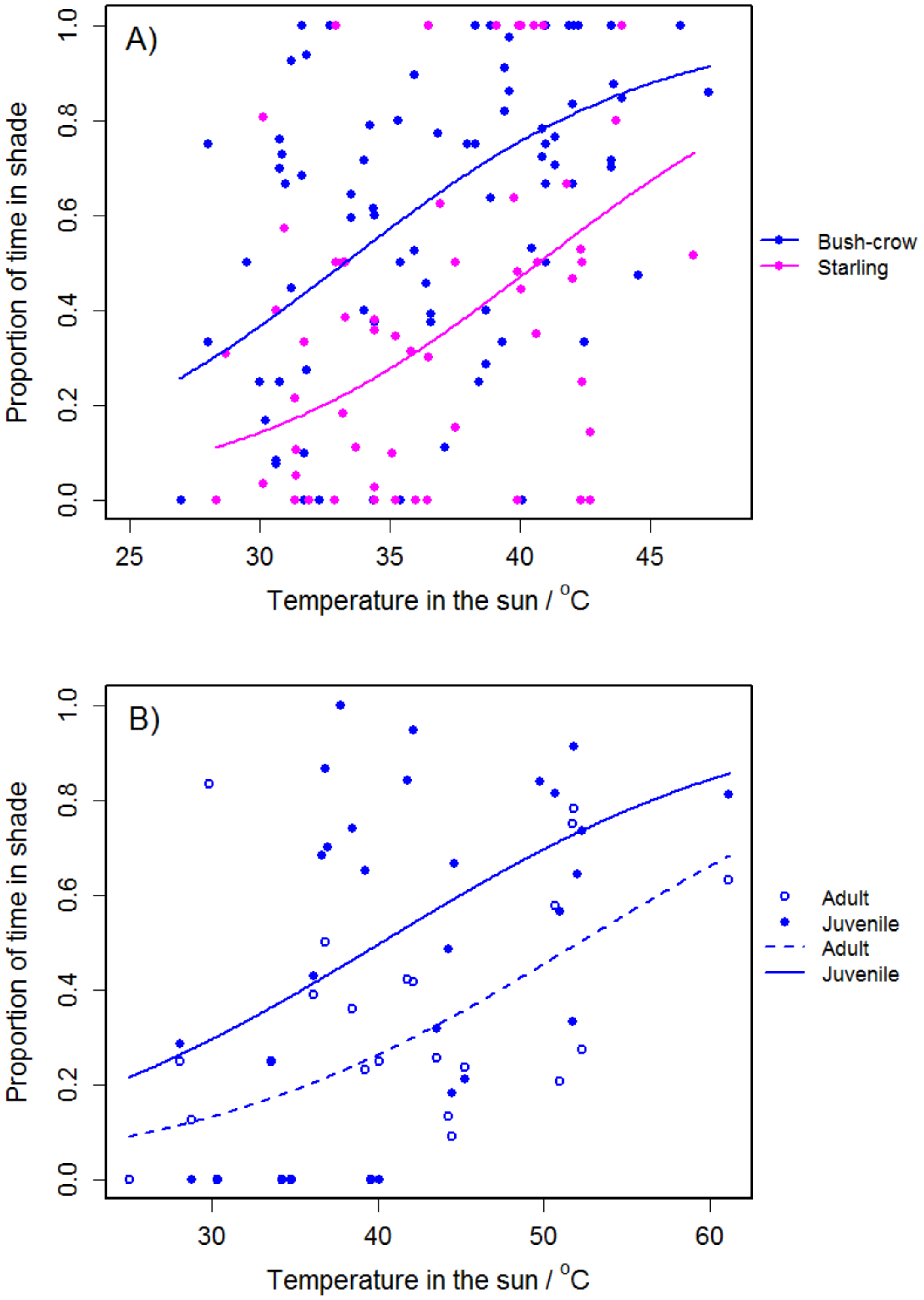


4) Adult and juvenile location

The 2014 random effects model found that the two starling species were similar, and the species term was reduced to two factor levels, Bush-crow and Starling. As temperature in the sun increased all birds spent more time in the shade (χ^2 = 26.17, d.f. = 1, P < 0.001), but Bush-crows moved to the shade at lower temperatures than Starlings (χ^2 = 11.23, d.f. = 1, P = 0.001). There was no difference between adult and juvenile birds (χ^2 = 1.85, d.f. = 1, P = 0.174) (Figure 5.5; *A*). In addition to these terms, the fixed effects model also retained bird type and the bird type by temperature interactions. Adults spent less time in the shade than juveniles at lower temperatures, but increased their time in the shade more rapidly as temperature in the sun rose (F = 3.99, d.f. = 1, P = 0.048).

The 2013 random effects model showed Bush-crows spent more time in the shade at higher temperatures (χ^2 = 12.55, d.f. = 1, P = 0.0004), and juvenile Bush-crows spent more time in the shade at a given temperature than adult birds (χ^2 = 6.74, d.f. = 1, P = 0.009) (Figure 5.5; *B*). The fixed effects model was similar.

Figure 5.5: The effect of temperature in the sun on the proportion of time spent in the shade by *A*) Bush-crows (blue) and White-crowned or Superb Starlings (pink) in 2014, and *B*) Bush-crow adults (open circles, dashed line) and juveniles (filled circles, solid line) in 2013. Points show data from individual follows. Curves show predicted values from the random effects models. The temperature range differs between the two years due to differences in data collection (see text).

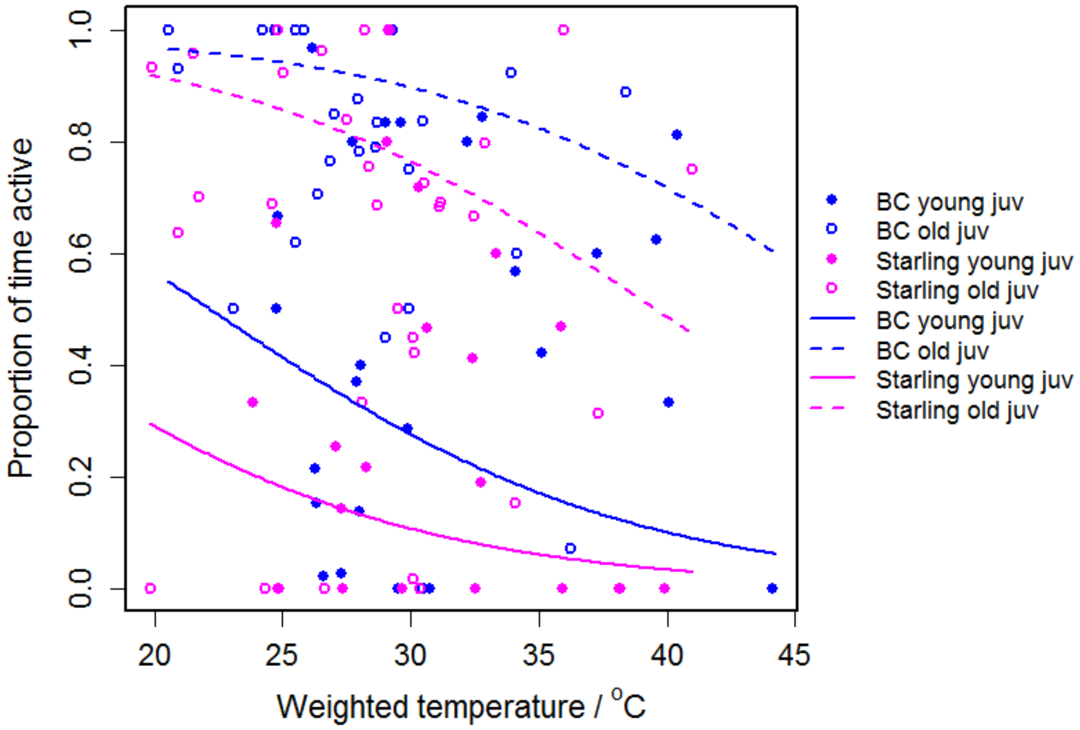


5) Juvenile behaviour

The 2014 random effects model found that juvenile birds were less active at higher weighted temperatures than at lower ones ($\chi^2 = 8.64$, d.f. = 1, P = 0.003), but that older birds were more active at a given weighted temperature than younger birds ($\chi^2 = 15.94$, d.f. = 1, P < 0.001). Starling juveniles were less active than Bush-crow juveniles ($\chi^2 = 5.23$, d.f. = 1, P = 0.022) (Figure 5.6). The fixed effects model was similar, except that the species term was not retained, even with the two starling species combined (F = 3.37, d.f. = 1, P = 0.070). The decrease in activity with weighted temperature was still significant (F = 9.64, d.f. = 1, P = 0.002), as was the increase in activity with age (F = 36.65, d.f. = 1, P < 0.001).

There were no significant terms in the 2013 model with random effects. In the fixed effects model, the proportion of time spent active increased with Bush-crow juvenile age (F = 7.17, d.f. = 1, P = 0.011).

Figure 5.6: Relationship of the proportion of time spent active to weighted temperature for juvenile Bush-crows (blue) and Starlings (pink) of different ages. Points show data from individual follows in 2014. Curves show predicted values from the random effects model for the earliest (filled circles, solid lines) and latest (open circles, dashed lines) dates on which juvenile birds were observed.



6) Juvenile location

The 2014 model with random effects found that there was no effect of age on the proportion of time spent in the shade, but Bush-crow juveniles spent more time in the shade than Starling juveniles (χ^2 = 9.18, d.f. = 1, P = 0.002), and all birds spent more time in the shade when temperatures in the sun were higher (χ^2 = 9.59, d.f. = 1, P = 0.002) (Figure 5.7). The 2013 random effects model found the same effect of temperature on time spent in the shade (χ^2 = 7.67, d.f. = 1, P = 0.006), and no effect of juvenile age.

The 2014 fixed effects model did not retain the temperature term (F = 3.64, d.f. = 1, P = 0.060), and instead found that juveniles of both species spent less time in the shade as they got older (F = 6.05, d.f. = 1, P = 0.016) (Figure 5.8). Once again, Bush-crow juveniles spent more time in the shade at a given age than Starling juveniles (F = 12.06, d.f. = 1, P = 0.001). The 2013 fixed effects model found the same effect of age.

In 2014, the mean temperature in the sun was 9.5°C warmer than in the shade during follows of juvenile birds (t = 18.32, d.f. = 132, P < 0.001).

Figure 5.7: Relationship of the proportion of time spent in the shade to temperature in the sun for juvenile Bush-crows (blue) and Starlings (pink). Points show data from individual follows in 2014. Curves show the predicted values from the random effects model.

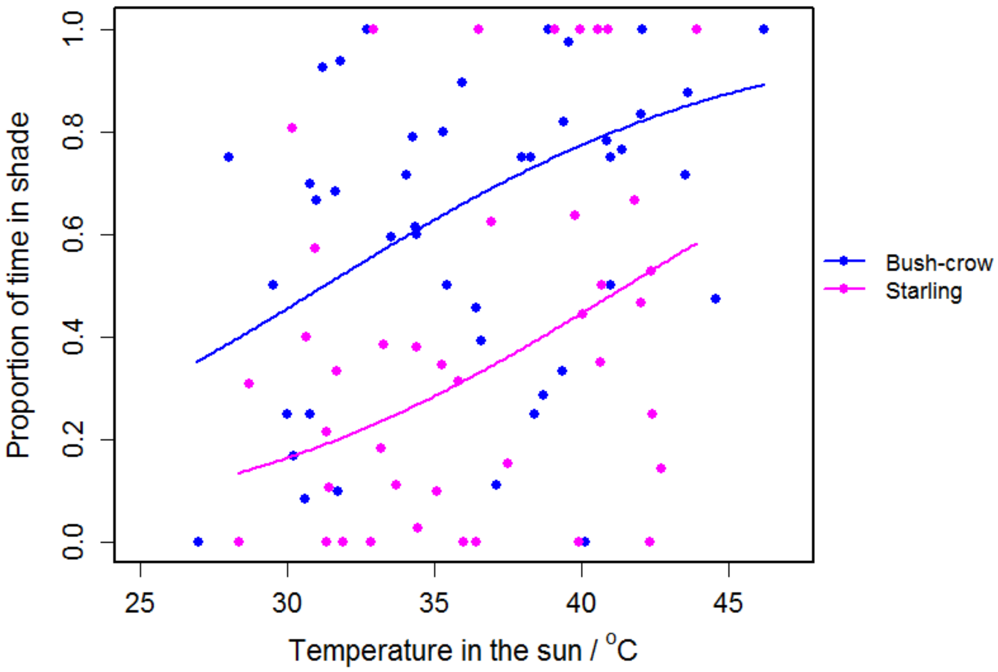
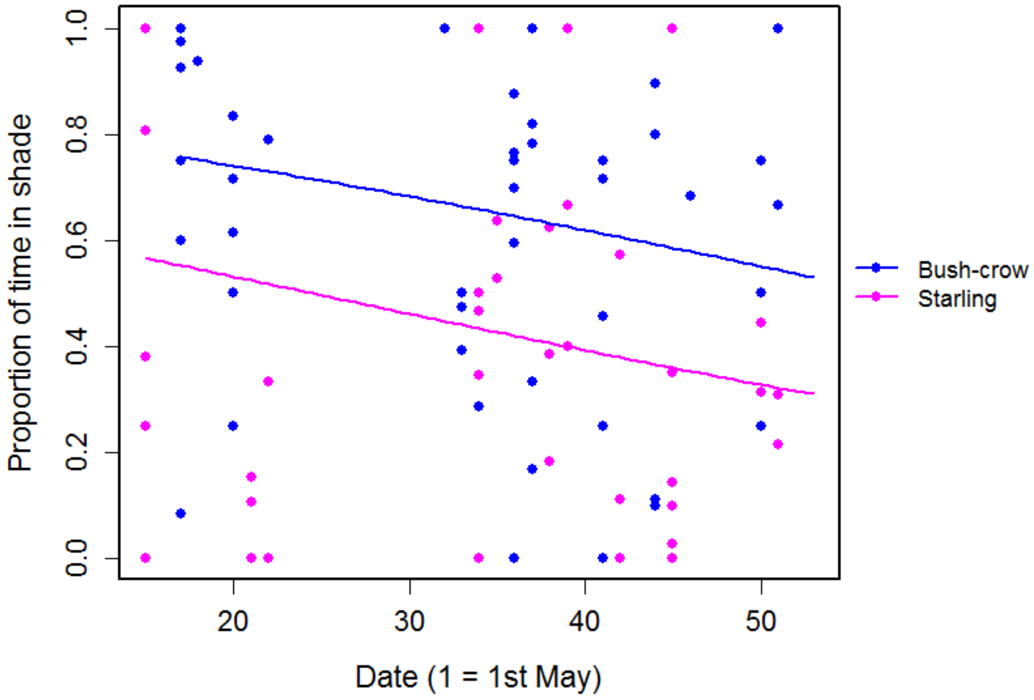


Figure 5.8: Relationship of the proportion of time spent in the shade to date (as a proxy for juvenile age) by Bush-crows (blue) and Starlings (pink). Points show data from individual follows in 2014. Curves show predicted values from the model fitted without random effects.



Foraging watches

1) Proportion of time spent panting

There was significant variation among the three species in the proportion of time spent panting. A likelihood-ratio test found a large difference in residual deviance between the model with the three parameters assumed to be the same for all species (Model 1) and that in which each species had a different value for all parameters (Model 8) (χ^2 = 16.26, d.f. = 6, P = 0.012). The model with the lowest AIC_c value was that with the mean and standard deviation of the temperature at the start of panting different among species, but the difference in mean temperatures at the start of panting and when panting became continuous constant across species (Model 6; Table 5.1; Table 5.2). Curves showing expected mean values of the proportion of time spent panting in relation to temperature were similar for Model 6 and the results from model averaging across all eight models (Figure 5.9). Ethiopian Bush-crows showed a more rapid rise in the proportion of time spent panting with increasing temperature than either of the two starling species (Figure 5.10).

Table 5.1: Comparison of Underhill-Zucchini models of the panting behaviour of Ethiopian Bush-crows, White-crowned Starlings and Superb Starlings. Each row represents a model formulation. The model specification identifies which of the three parameters of the model (Mean = mean temperature of panting start; Difference = difference between the mean temperatures of panting start and panting continuously; SD = standard deviation of panting start distribution) were assumed to be common (same value) for all three species (C) or species-specific (S).

	Model specification						
Model code	**Mean**	**Difference**	**SD**	**No. fitted parameters**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weight**
1	C	C	C	3	501.69	6.85	0.014
2	S	C	C	5	495.30	0.46	0.348
3	C	S	C	5	504.31	9.47	0.004
4	C	C	S	5	502.92	8.08	0.008
5	C	S	S	7	505.58	10.74	0.002
6	S	C	S	7	494.84	0.00	0.439
7	S	S	C	7	497.62	2.78	0.109
8	S	S	S	9	498.35	3.51	0.076

Table 5.2: Maximum-likelihood estimates of parameters of the Underhill-Zucchini model of panting behaviour with asymptotic standard errors. Results are for the model with the lowest AIC$_c$ value (Model 6 in Table 5.1).

	Mean temperature of panting start (°C)		Standard deviation of panting start distribution (°C)		Difference in mean temperatures: panting continuously minus start panting (°C)	
Species	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Ethiopian Bush-crow	38.6	1.2	8.5	4.0	13.2	3.1
White-crowned Starling	56.3	14.0	20.7	14.8	As above	
Superb Starling	47.8	4.2	10.2	5.8	As above	

Figure 5.9: Proportion of time spent panting by *A*) Ethiopian Bush-crows, *B*) White-crowned Starlings and *C*) Superb Starlings in relation to temperature near the ground surface in sunlit areas. Points show data from individual watches. Curves show expected mean proportions from Model 6 (blue; Table 5.1 and Table 5.2) and model-averaging across a set of eight alternative models (red).

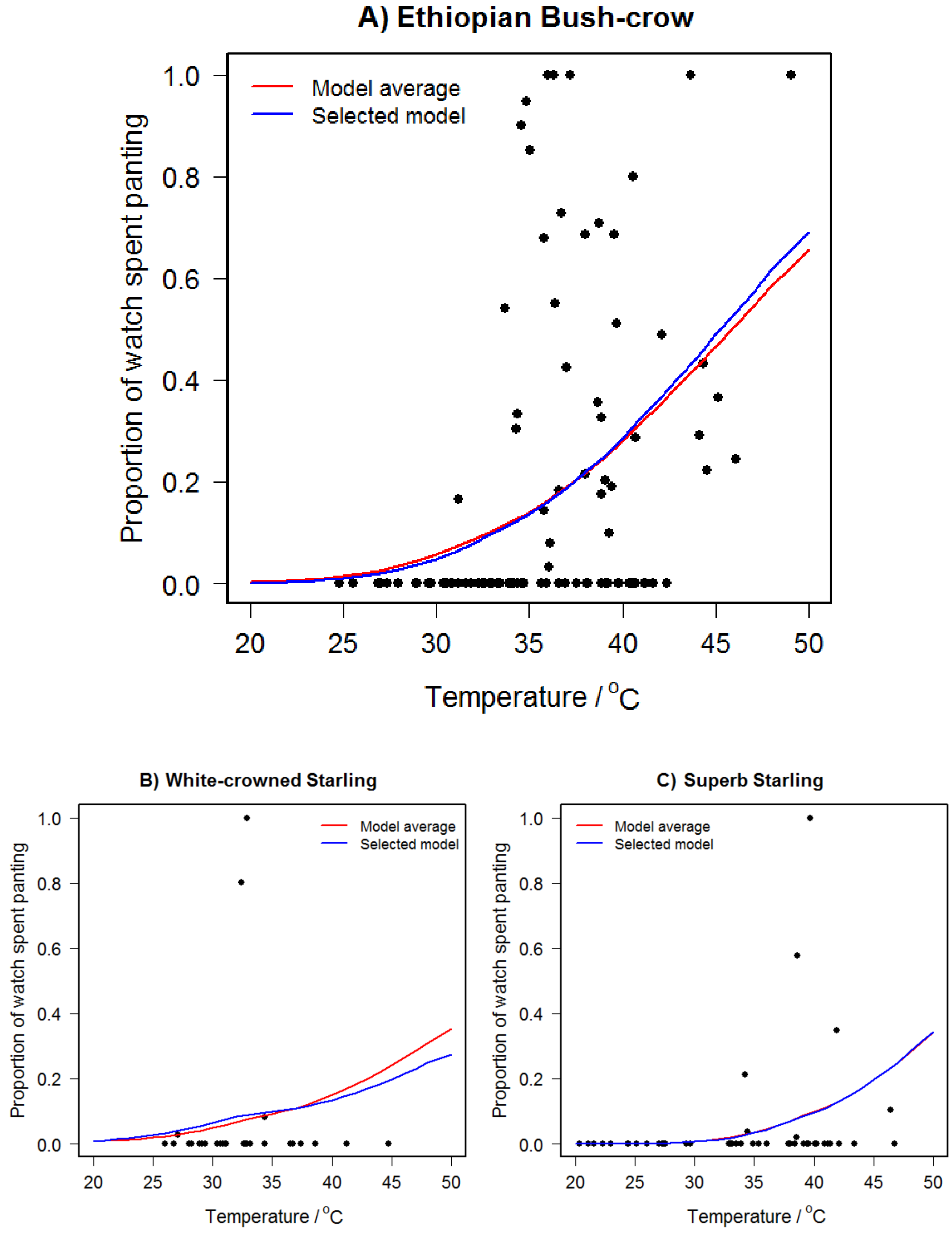
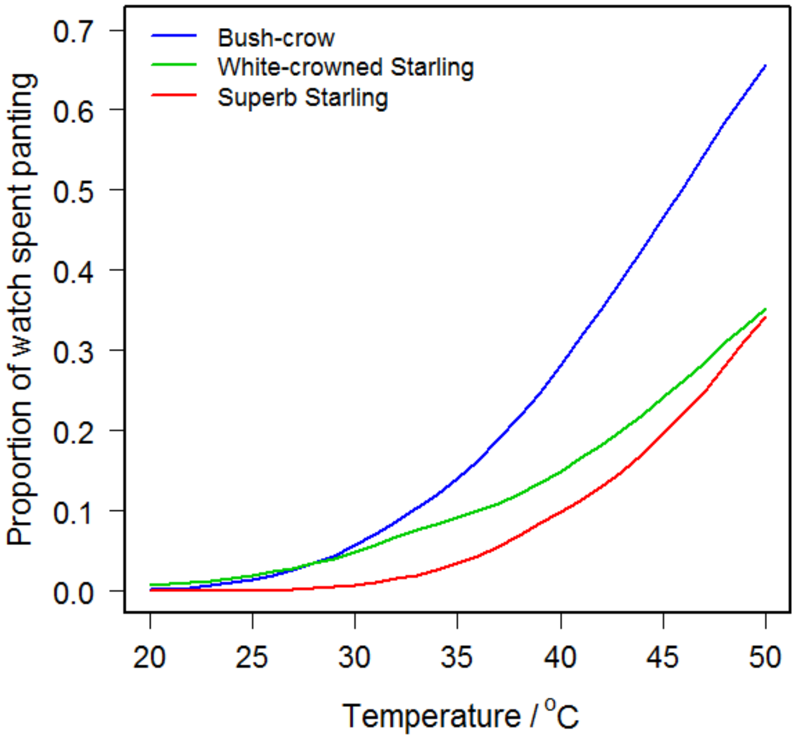


Figure 5.10: Proportion of time spent panting by Ethiopian Bush-crows (blue), White-crowned Starlings (green) and Superb Starlings (red) in relation to temperature near the ground surface in sunlit areas. Curves show expected mean proportions from model-averaging across a set of eight alternative models.



2) Foraging effort

Bush-crows and Superb Starlings reduced their foraging effort as temperature increased, while White-crowned Starlings increased effort, giving a significant species by temperature interaction (χ^2 = 9.88, d.f. = 2, P = 0.007) (Figure 5.11). The results from the fixed effects model were similar.

All species made fewer foraging attempts per minute whilst panting than when they were not panting (χ^2 = 5.11, d.f. = 1, P = 0.024) and the same species by temperature interaction was observed (χ^2 = 8.79, d.f. = 2, P = 0.012) (Figure 5.12). The model without random effects was similar, except that foraging type was removed from the model, and group type retained instead. All species increased foraging effort when juveniles were present in the group (F = 5.63, d.f. = 1, P = 0.018) (Figure 5.13).

Figure 5.11: The response of foraging effort (attempts per minute) to temperature during the foraging watch for Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual watches. Lines show predicted values from the model fitted with random effects. The response is presented on a log-scale in order to display the variation in the data better.

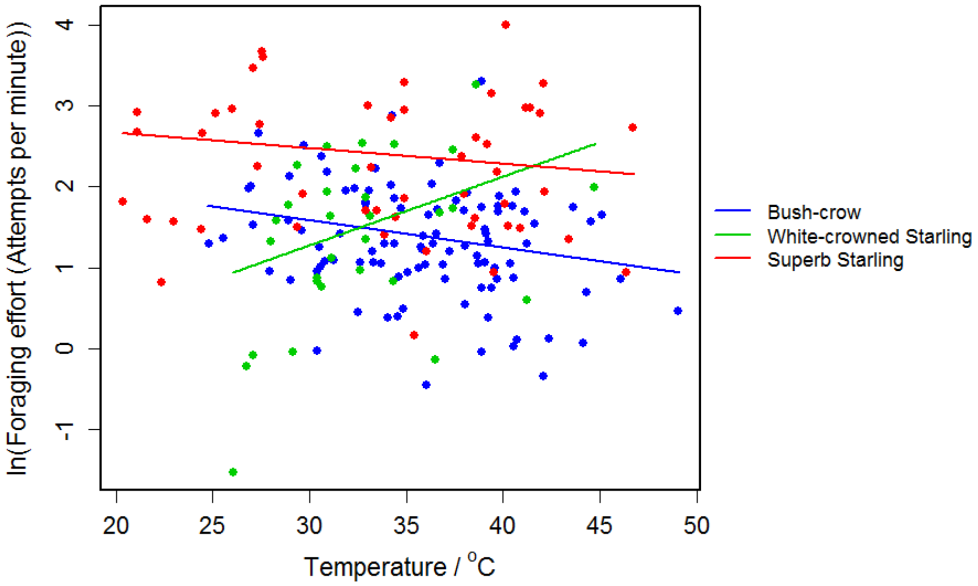


Figure 5.12: The effect of temperature and thermoregulation on foraging effort by Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from foraging bouts within watches. Lines show predicted values from the model fitted with random effects. Birds which were panting (closed circles, solid lines) foraged less than birds which were not (open circles, dashed lines).

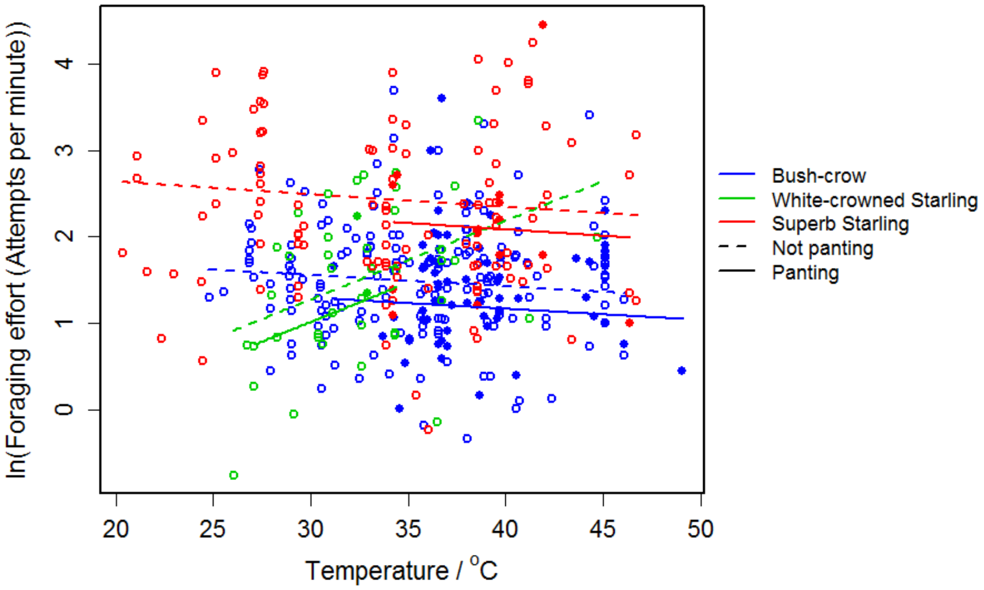
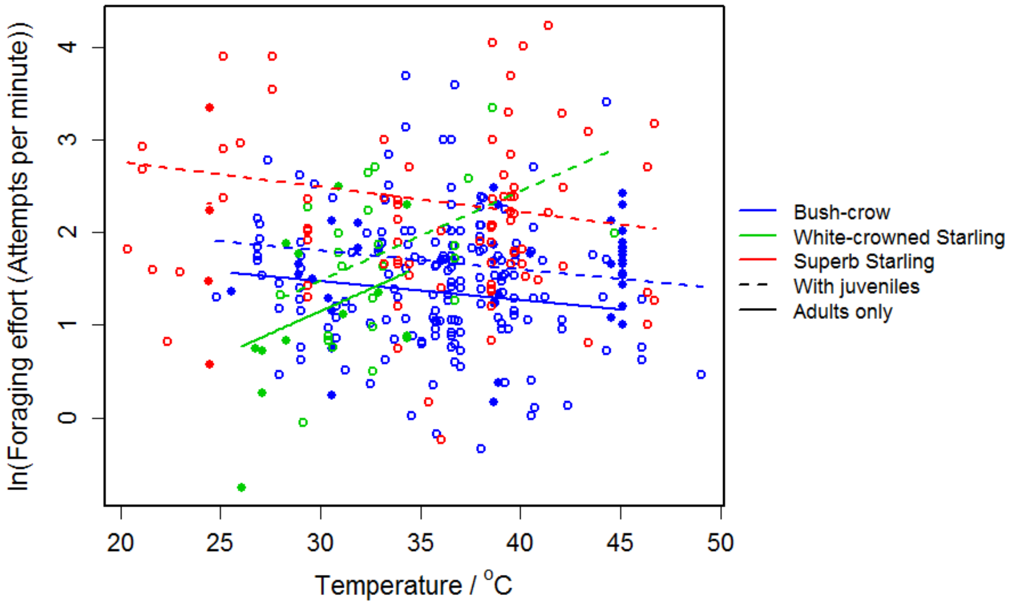


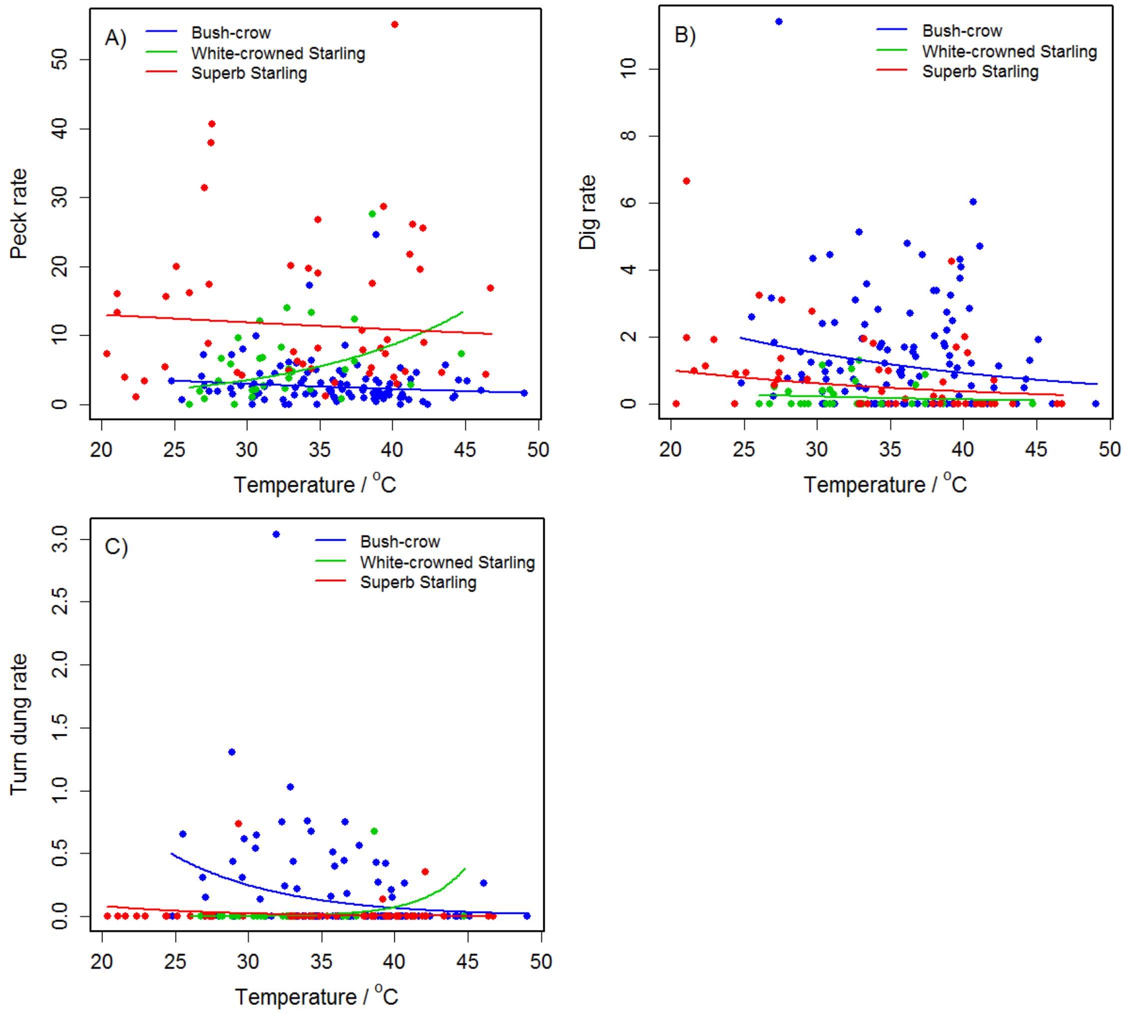
Figure 5.13: The effect of temperature and group type on foraging effort by Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual watches. Lines show predicted values from the model fitted without random effects. Birds in adult only groups (closed circles, solid lines) foraged less than birds in groups with juveniles (open circles, dashed lines).



3) Foraging technique

Bush-crows and Superb Starlings showed a slight reduction in the number of pecks per unit time made at higher temperatures, whilst White-crowned Starlings increased their pecking rate (χ^2 = 8.00, d.f. = 2, P = 0.018). Bush-crows showed a more marked reduction in dung turning rates at high temperatures, whilst White-crowned Starlings increased their use of this technique (χ^2 = 6.53, d.f. = 2, P = 0.038). All three species showed a reduction in digging rate as temperatures rose (χ^2 = 8.41, d.f. = 1, P = 0.004), and both White-crowned and Superb Starlings dug less than Bush-crows (χ^2 = 31.11, d.f. = 2, P < 0.001) (Figure 5.14).

Figure 5.14: The effect of temperature on the number of times *A*) pecking, *B*) digging and *C*) turning dung were used as foraging techniques by Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual watches. Curves show the predicted response from Poisson models fitted with the count of each technique in turn as the response variable.

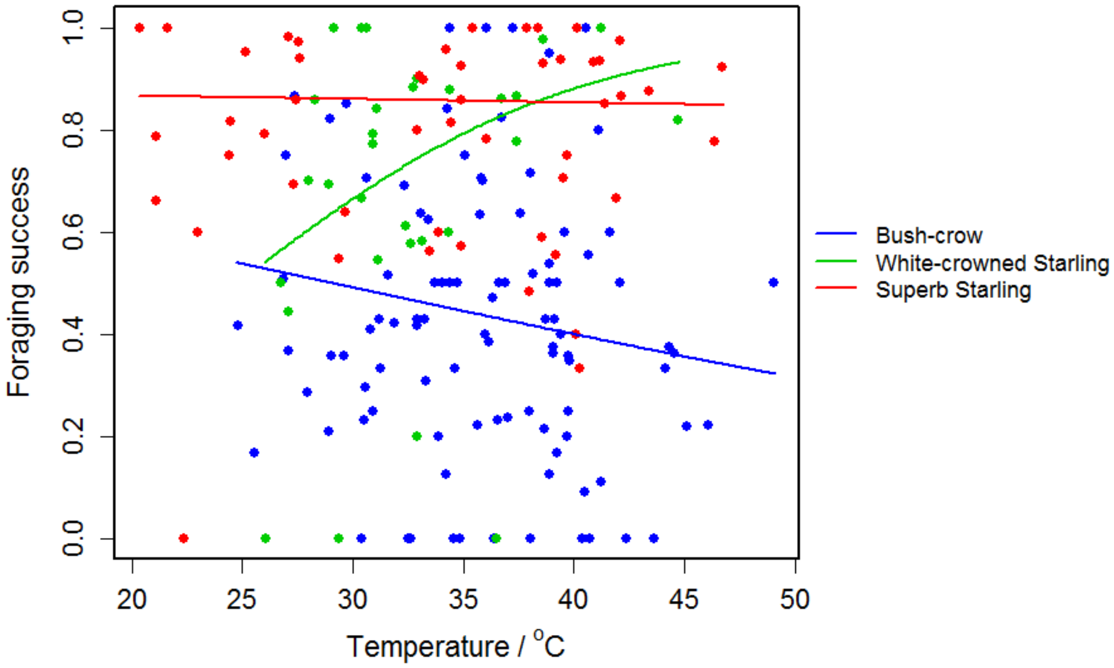


4) Proportion of foraging attempts successful

As temperatures increased, Bush-crows showed a reduction in foraging success, whilst White-crowned Starlings increased their success and Superb Starlings did not respond (χ^2 = 6.38, d.f. = 2, P = 0.041) (Figure 5.15). The model without random effects was similar, except that the single effect of temperature was also significant (t = -2.34, P = 0.020).

There was no effect of panting on foraging success in models fitted within watches, but again the temperature by species interaction was significant.

Figure 5.15: The effect of temperature on the proportion of foraging attempts which were successful for Bush-crows (blue), White-crowned (green) and Superb Starlings (red), across all foraging techniques. Points show data from individual watches. Curves show predicted values for models fitted with random effects.



Pecking was more successful than digging for all species (χ^2 = 85.51, d.f. = 1, P < 0.001). The temperature by species interaction was significant (χ^2 = 6.17, d.f. = 2, P = 0.046; Figure 5.16), as Bush-crow success declined with increasing temperatures, while White-crowned Starling success increased and Superb Starling success was not affected. In the Bush-crow only model, both the interaction between temperature and technique (χ^2 = 4.77, d.f. = 2, P = 0.092) and temperature alone (χ^2 = 3.26, d.f. = 1, P = 0.071) were close to significance, but only the technique term was retained in the model (χ^2 = 71.98, d.f. = 2, P < 0.001). Pecking was more successful than digging, which was more successful than dung turning.

5) Food intake rate

Bush-crow food intake rate declined with increasing temperature, whilst White-crowned Starling intake rate increased, and Superb Starlings were unaffected, giving a significant temperature by species interaction (χ^2 = 10.64, d.f. = 2, P = 0.005) (Figure 5.17). The model without random effects was similar.

Figure 5.16: The effects of temperature and foraging technique on the proportion of attempts successful for Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual foraging attempts within watches. Curves show predicted probability of obtaining an item from digs (dashed lines) and pecks (solid lines).

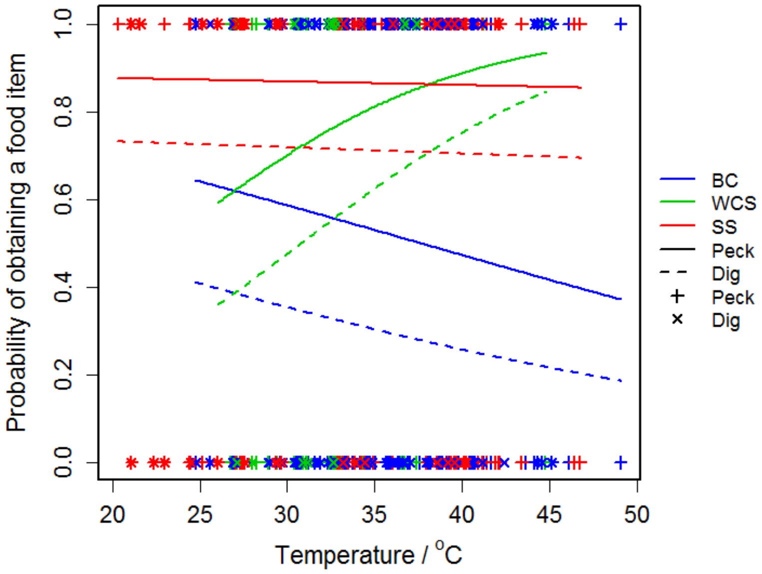
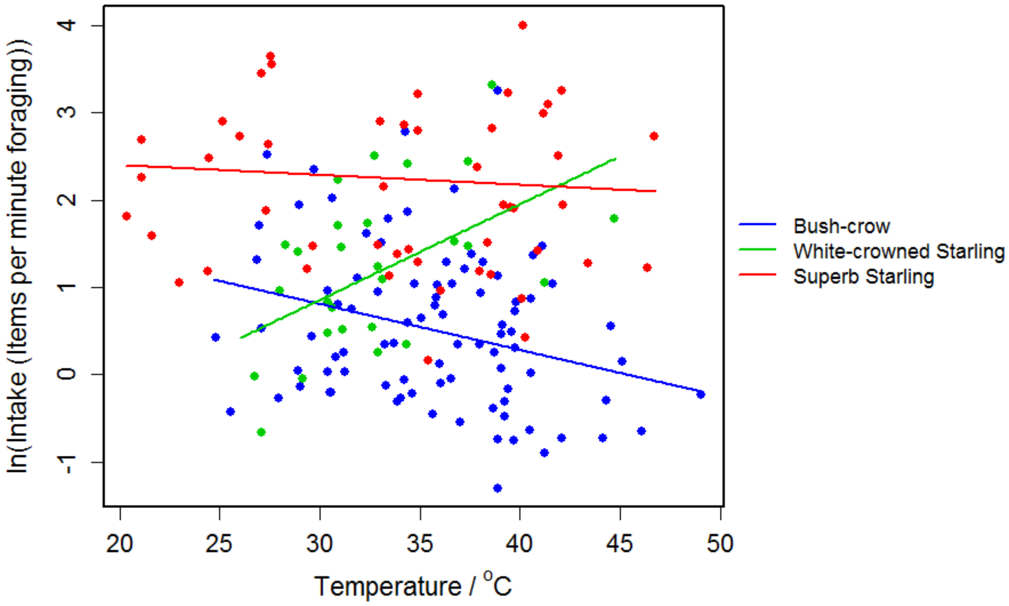
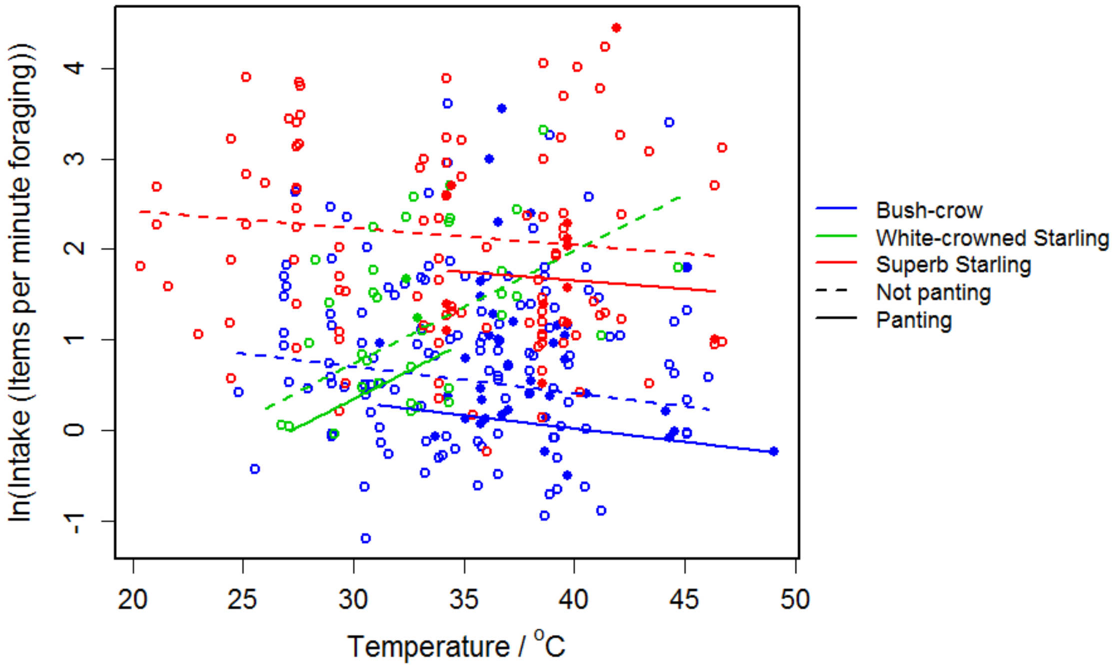


Figure 5.17: The response of food intake rate (items consumed per minute foraging) of Bush-crows (blue), White-crowned (green) and Superb Starlings (red) to temperature during the watch. Points show data from individual watches. Lines show predicted values for models fitted with random effects. The response is presented on a log-scale in order to display the variation in the data better.



All species showed a reduction in food intake rate when panting at the same time as foraging, compared to when foraging alone (χ^2 = 4.86, d.f. = 1, P = 0.028), and the same difference between species occurred as before (χ^2 = 9.62, d.f. = 2, P = 0.008) (Figure 5.18). The model without random effects showed no effect of panting on foraging efficiency, but the temperature by species interaction remained (F = 7.02, d.f. = 2, P = 0.001). The difference between models is likely due to the correlation between temperature and panting causing different models to select slightly different structures.

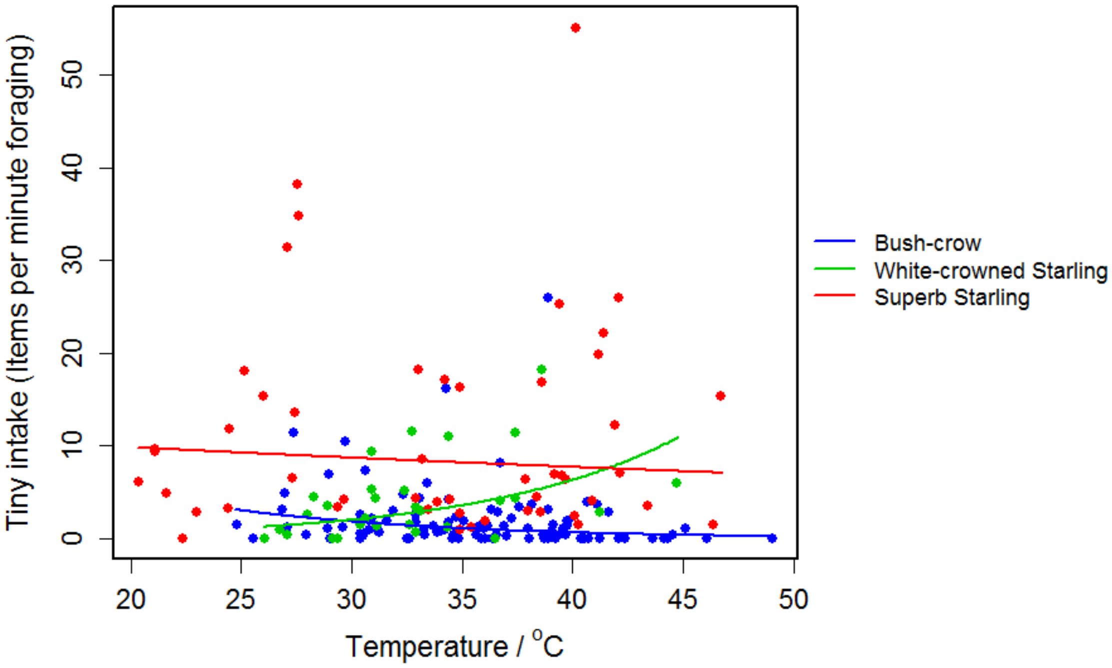
Figure 5.18: The effects of temperature during the watch and panting whilst foraging on food intake rate by Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from bouts of foraging with and without panting from within watches. Panting whilst foraging (filled circles, solid lines) resulted in fewer items being consumed per minute than when birds foraged without panting (open circles, dashed lines). The response is presented on a log-scale in order to display the variation in the data better.



6) Prey size

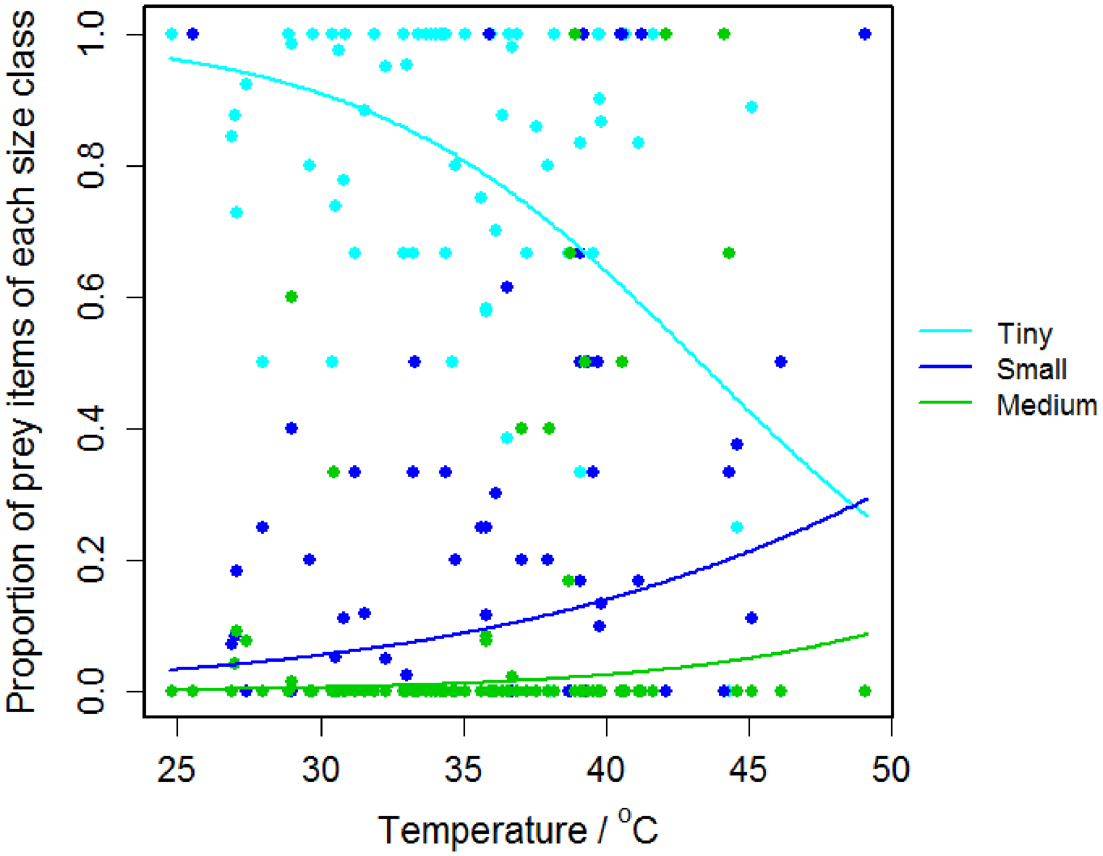
Bush-crows and Superb Starlings showed a reduction in their intake rate of tiny items as temperature increased, but White-crowned Starlings increased their intake rate, leading to a significant temperature by species interaction (χ^2 = 14.10, d.f. = 2, P = 0.001) (Figure 5.19). The model without random effects was similar. There were no effects on the number of small prey items caught. All species increased their rate of medium prey intake as temperatures increased (χ^2 = 4.30, d.f. = 1, P = 0.038), and there was no difference between species (χ^2 = 2.72, d.f. = 2, P = 0.26). The fixed effects model produced a similar result.

Figure 5.19: The effect of temperature on the intake rate of tiny prey items by Bush-crows (blue), White-crowned (green) and Superb Starlings (red). Points show data from individual watches. Curves show predicted intake rates from the model fitted with random effects.



There was no effect of group type on Bush-crow prey item size, but Bush-crows caught a higher proportion of medium (χ^2 = 9.03, d.f. = 1, P = 0.003) and small (χ^2 = 8.08, d.f. = 1, P = 0.005) items, and a lower proportion of tiny items (χ^2 = 10.89, d.f. = 1, P = 0.001) at higher temperatures (Figure 5.20).

Figure 5.20: The effect of temperature on the proportion of prey items caught by Bush-crows which were tiny (pale blue), small (dark blue) and medium (green) in size. Points show data from individual watches. Curves show predicted proportions from three logistic regressions fitted to each size class in turn. There were too few non-zero observations to fit a model for large prey items, which results in the three predicted proportions presented not always summing to one.



7) Juvenile care

The random effects model did not converge, so the results from the fixed effects model were used. As the ratio of adults to juveniles within a Bush-crow group increased, each focal adult fed juveniles fewer food items per juvenile per unit time (χ^2 = 7.89, d.f. = 1, P = 0.005). Temperature had a quadratic effect, with birds feeding more items to juveniles at mid-range temperatures than at high or low temperatures (χ^2 = 8.64, d.f. = 2, P = 0.013) (Figure 5.21). The observed size distribution of prey items fed to juveniles differed significantly from the distribution of sizes caught (χ^2 = 237.6, d.f. = 3, P < $2.2\text{x}10^{-16}$). Larger items were more likely to be fed to juveniles (Table 5.3).

Figure 5.21: The effects of Bush-crow group composition (adult to juvenile ratio) and temperature on the rate at which food was fed to juveniles by the focal adult. Curves show variation in the predicted feeding rates at *A*) three different temperatures as the ratio of adults to juveniles in the group increases, and *B*) two different group compositions as temperature increases. Points show data from individual foraging watches, split in *B*) to groups with more than twice as many adults as juveniles (green), groups with more than twice as many juveniles as adults (blue) and groups with equal numbers of adults and juveniles (black).

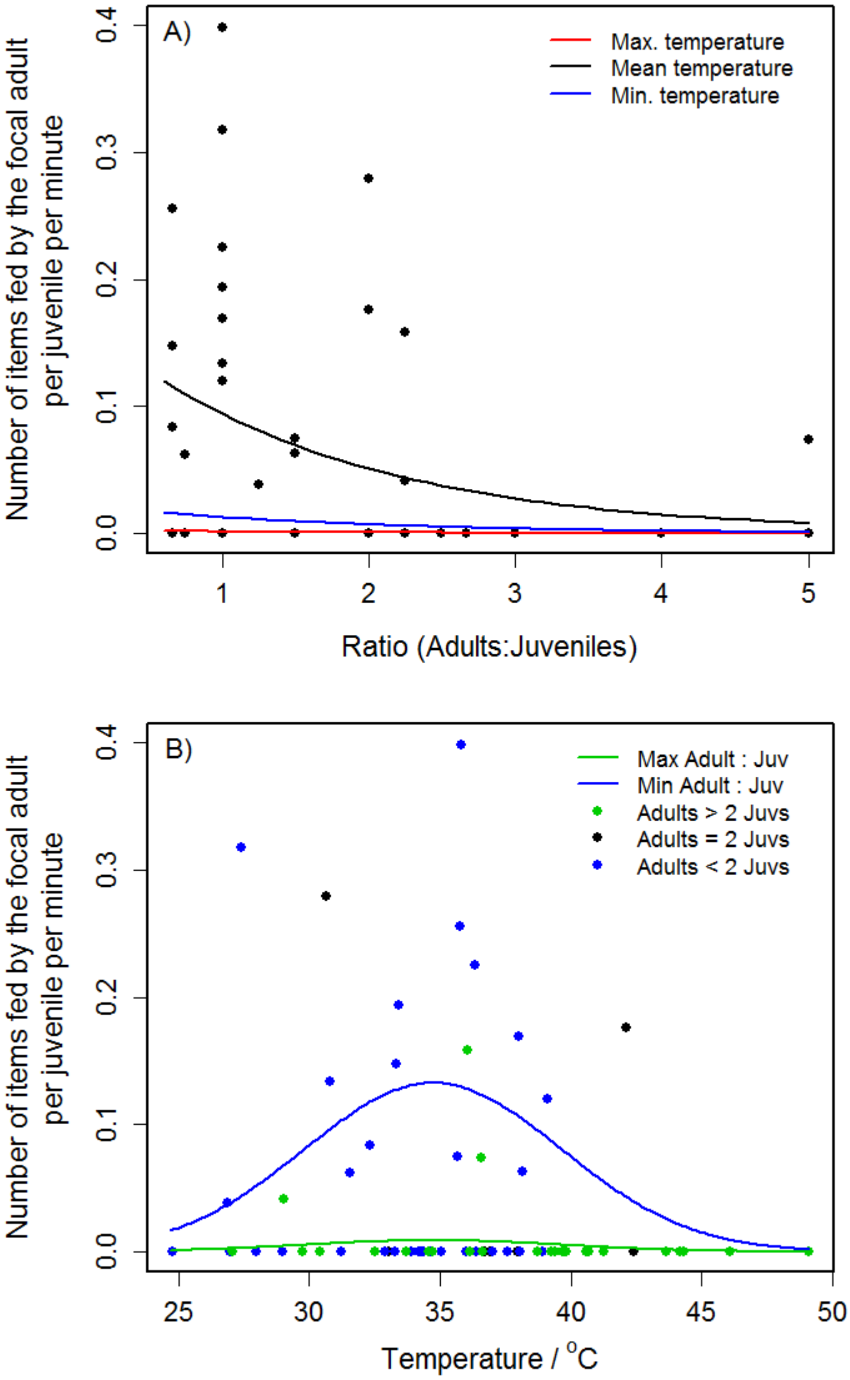


Table 5.3: The number of prey items in each size class which were caught by foraging Bush-crows, and the number of those caught which were fed to juveniles.

Item size	Number caught	Number fed to juveniles	Proportion
Tiny	735	8	0.01
Small	73	21	0.29
Medium	24	6	0.25
Large	6	6	1.00

5.4 Discussion

Contrary to expectations, Bush-crow adults and juveniles showed higher activity levels than either White-crowned or Superb Starlings at any given temperature. However, Bush-crows also spent more time in the shade than either starling species, which offered them a reduction in environmental temperatures of 9.5–11.2^{o}C, and is likely to provide further benefits in terms of a reduction of evaporative water loss (Wolf and Walsberg, 1996). Given that their foraging ability declined more severely with temperature, moving to the shade may allow Bush-crows to remain more active despite increases in environmental temperature.

Adult Bush-crows remained more active and spent less time in the shade at any given temperature than juvenile Bush-crows, and older juveniles were more active and spent less time in the shade than younger birds, suggesting that it is the juveniles which are more heavily impacted by temperature. Physiological thermoregulatory ability takes time to develop in young birds (Mishaga and Whitford, 1983), and if this period is extended in Bush-crows then it may explain the juvenile birds' additional requirement to engage in behavioural thermoregulation. This is supported by the fact that the Bush-crow's nest provides a thermally-stable environment throughout the day (Töpfer and Gedeon, 2012), and may be a further part of the driving mechanism behind the species' climatic range-restrictions (Donald et al., 2012; Chapter 4).

As temperature increased, Bush-crows, White-crowned and Superb Starlings all increased the proportion of time spent panting. However, Bush-crows responded at much lower temperatures than either starling species, suggesting that they are more severely physiologically affected by temperature. This reflects the finding in Chapter 4 that the Bush-crow's range is strongly temperature determined, whilst the ranges of the two starling species are not. This provides strong evidence that the Bush-crow's climatic range-restriction is driven by a direct inability to cope with high temperatures.

Temperature had a negative effect on Bush-crow foraging effort, proportion of attempts successful and intake rate, but a positive effect on the same responses in White-crowned Starlings. When panting was included in the effort and intake rate models, it had a significant negative effect, whilst the temperature effect was removed. Panting is correlated with temperature, and it seems that the negative effects of temperature on Bush-crow foraging ability are mediated through their increased panting at higher temperatures, an effect which has been detected elsewhere (du Plessis et al., 2012). A reduction in foraging ability with temperature, especially when combined with increased physiological costs of thermoregulation (Tieleman and Williams, 1999), would be expected to lead to an inability to survive in areas which consistently exceed a species' thermal tolerance (Wolf, 2000).

Digging and turning over objects to search for prey are techniques which were more commonly used by Bush-crows than by either starling species, which both showed a preference for pecking. However as temperatures rose, Bush-crows decreased their frequency of digging and turning over objects, with little change in pecking rates. There are three possible reasons for this: (1) pecking may require less effort, making it more energetically favourable at higher temperatures; (2) pecking may be more successful, offering a better return on investment at higher temperatures when overall foraging effort, success and intake rate are declining; (3) the prey species captured by pecking could be different, and perhaps larger, than those captured by digging and turning, and the difference in technique used may be driven by a preference for different prey at different temperatures. Pecking was found to be more successful than digging or turning objects, and its relative efficacy did not vary with temperature, which supports the second of these hypotheses. Pecking may be more successful because it targets prey that have already been seen, whereas digging and turning objects are opportunistic behaviours where the bird is still searching for food.

The variation in Bush-crow prey size with temperature, with a decrease in tiny items and an increase in medium-sized items, further supports the finding that Bush-crows are forced to forage selectively at high temperatures. This may be because decreased foraging success necessitates targeting bigger items in order to meet energy requirements. As temperatures rise in South Africa, Southern Pied Babblers *Turdoides bicolor* struggle to gain enough weight during the day to counter overnight weight loss (du Plessis et al., 2012). A similar problem in Bush-crows could lead birds to favour both the most effective capture techniques and most energy-rich (larger) prey items when exposed to higher temperatures.

The amount of food fed to juveniles by adult Bush-crows varied with group composition; a higher proportion was fed when the ratio of adults to juveniles was low. This is intuitive, when there are fewer adults to provide food, each must invest more in provisioning. The response to temperature was quadratic, with birds increasing provisioning at low temperatures, but decreasing it at higher temperatures. This may first reflect the increasing need of the juveniles as temperatures rise, as they are less active and therefore less able to forage themselves, but subsequently, at the highest temperatures, adults might be forced to protect their own condition by keeping food to themselves (du Plessis et al., 2012), even if this is at a cost to the young.

Bush-crows selectively offered food to juveniles based on prey size. Larger items were more commonly fed, whilst smaller items were kept for themselves. Selection for larger and against smaller prey items has been recorded in other species feeding offspring (McCarty and Winkler, 1999a), and is likely to be a mechanism to maximise young birds’ growth and development.

The models presented in this chapter did not include an effect of time of day. Time of day may be expected to affect, for example, foraging effort, with higher feeding rates observed in the morning and evening than during the middle of the day (Robbins, 1981), a pattern which also correlates with diurnal changes in temperature. However, I found that Bush-crows show a stronger response to any given high temperature than two sympatric starling species. Given that all three species were observed throughout the day, this result is likely to be robust to any effect of time of day on an individual species’ behaviour.

5.5 Conclusion

The effects of temperature on Bush-crow behaviour appear to be extensive and severe. Rising temperatures resulted in more time spent panting and in the shade, a reduction in foraging effort, proportion of attempts successful and intake rate, and a change in both the preferred method of prey capture, and of the size of target prey. Juveniles showed a stronger response to temperature than adult birds, becoming less active and seeking shade at lower temperatures, and this effect was further pronounced in the youngest birds. Adult birds tending young were forced to compensate for this by remaining more active and feeding more food items to juveniles at high temperatures than birds not caring for young. Such compensation may come at a further cost to the adults' own condition.

These effects are contrasted directly with those of two ecologically similar, sympatric, but wider ranging species, the White-crowned and Superb Starlings, whose ranges are not limited by high temperatures (Chapter 4). The foraging behaviour of these two species showed a less severely negative or even a positive response to temperature compared with the Bush-crow, which emphasises the impacts of temperature on the Bush-crow.

Combined with the findings in Chapter 4, this suggests that the Bush-crow's limited range is indeed determined by a direct, physiological inability to cope with high temperatures.

6 FACTORS AFFECTING THE DISTRIBUTION OF THE WHITE-TAILED SWALLOW

“Tollobre, tollobre! Maybe rain is coming, maybe big problem!”

6.1 Introduction

First described in 1942, the White-tailed Swallow *Hirundo megaensis* is an enigmatic species confined to a small geographical range in southern Ethiopia (Benson, 1942; BirdLife International, 2016b). Several authors have noted its peculiar distribution (Benson, 1946, 1942; Syvertsen and Dellelegn, 1991), being common though patchily distributed within its range, but never, until 2006, having been seen outside a small area of around 5,500km^2 surrounding Yabello and Mega in southern Ethiopia (Gabremichael et al., 2009). Collar and Stuart (1985) suggested that its range boundaries might be linked to the 1,500m altitudinal contour. Since 2006, there have been records from outside the previously known breeding range. A small number of sightings have been reported from the Liben Plain, 100km east of its core range (Gabremichael et al., 2009), but there are still no nest records from this region, and it is unclear whether individuals move between the two areas (Bladon et al., 2015). Donald et al (2012) found that the distribution of the Ethiopian Bush-crow *Zavattariornis stresemanni*, which is sympatric with the White-tailed Swallow, save for the absence of Bush-crows from the Liben Plain, is well described by a climate envelope model. The Bush-crow’s range has a cooler, drier climate than the surrounding areas (Chapter 4). This leads to the intriguing possibility that the ranges of both the Bush-crow and the Swallow might be restricted by similar attributes of the local climate, albeit probably by a different mechanism (see Chapters 5 and 7).

The Ethiopian Bush-crow is phylogenetically distinctive, with its moderately close relatives being the Asian Ground Jays *Podoces* and the monogeneric Piapiac *Ptilostomus afer* (Ericson et al., 2005). By contrast the White-tailed Swallow is very closely related to the Pearl-breasted Swallow *H. dimidiata* of southern Africa (Dor et al., 2010), and many other species in this genus are found in Africa and on every other continent except Antarctica. The White-tailed Swallow and Pearl-breasted Swallow differ genetically less (0.7%) than do any other pair of species in the genus (range: 2.0-11.6%). Even different populations of the Barn Swallow *H. rustica* can differ more from each other (range: 0.25-1.6%; Dor et al. (2010)). Other species or closely-related species pairs native to dry, open habitats have similarly disjunct distributions in eastern and southern Africa. They include Spike-heeled Lark *Chersomanes albofasciata* and Liben/Rudd's Larks *Heteromirafra archeri/ruddi* (Spottiswoode et al., 2013). This pattern may be the result of vicariance following the loss of a dry corridor that formerly linked the arid zones of eastern and southern Africa (Moreau, 1966). Although widely distributed across southern Africa, the occurrence of the Pearl-breasted Swallow is patchy, with no obvious determinant of its range boundaries (Harrison et al., 1997; SABAP2, 2016). This raises the question of whether the Pearl-breasted Swallow's range might be described by similar environmental variables to that of the White-tailed Swallow. If so, the White-tailed Swallow might have a much smaller range than the Pearl-breasted Swallow principally because suitable climatic conditions occur across a much smaller area of eastern than of southern Africa.

Here, I present the first study investigating the factors affecting the distribution and abundance of the White-tailed Swallow, using similar methods to those described in Chapters 3 and 4. I then compare the factors affecting the White-tailed Swallow's range with those describing that of the Pearl-breasted Swallow. I aim to determine whether the White-tailed Swallow's restricted range is described by local climate patterns and, if so, whether comparison with the distribution of the Pearl-breasted Swallow indicates an evolutionary history which has determined this climatic limitation.

6.2 Methods

6.2.1 Temperature patterns within the White-tailed Swallow's range

The methods used to collect transect data on Swallow occurrence and abundance are described in Section 3.2, and the methods used to generate site-specific temperature data are given in Section 3.4.2. Using these temperature variables, I plotted a series of exploratory graphs to investigate possible differences in temperature between sites where White-tailed Swallows were and were not detected. I split all locations with temperature data into sites where White-tailed Swallows had been recorded, and sites where they had not. For most sites, this information came from bird transects, but additional sites with comparable temperature data were treated as follows. White-tailed Swallow nesting sites were treated as presences. Bush-crow behavioural follows sites (Chapter 5) where I saw Swallows were treated as presences, and those where I did not see Swallows were not used, as I could not be sure that these represented true absences. I did not use habitat-only transects as absences because I could not say for certain that Swallows were not present there.

6.2.2 White-tailed Swallow response to local temperatures

I fitted the same series of logistic and Poisson regressions described in Section 4.2.2 to the White-tailed Swallow data (see Sections 3.3 and 3.5.3) to analyse the relationship of White-tailed Swallow presence and density to temperature.

6.2.3 Effects of temperature and habitat on the global distribution of the White-tailed and Pearl-breasted Swallows

For the Pearl-breasted and White-tailed Swallows to be able to inhabit climatically and ecologically similar ranges, the available bioclimatic environments in Ethiopia and southern Africa should be similar. To investigate this, I plotted histograms of the range of environmental variables (listed in Section 3.6.4) found in Pearl-breasted and White-tailed Swallow presence locations. Pearl-breasted Swallows are migratory (Maclean, 1993), and so the range of environmental variables experienced in a location across the entire year does not reflect the range experienced by the birds in areas where they are not present year-round. I compared the histograms for the White-tailed Swallow with those for the Pearl-breasted Swallow north and south of 26^{o}S, as an approximation of areas where the species is resident (to the north) and migratory (to the south) (Turner, 2004).

I used the species distribution modelling (SDM) methods described in Section 3.7 to fit models for the White-tailed Swallow and Pearl-breasted Swallow.

For the White-tailed Swallow, I collated presence data using all GPS bird and nest records from 2005–2015, including previous records collected by Kai Gedeon, Claire Spottiswoode, Paul Donald, Steve Rooke, Merid Gabremichael, Yilma Dellelegn and Richard Mellanby and colleagues (Mellanby et al., 2008), my casual records of White-tailed Swallows, all georeferenced locations of Swallows recorded on my transects, and all White-tailed Swallow nesting locations from my 2014 study (Chapter 7). For absence data, I then took the mid-point of all 1-km transect legs on which White-tailed Swallows had not been recorded, and used these as true absence locations. This resulted in 574 presence and 236 true absence points. To increase the range of environmental variables on which the models were built, I then took a random sample of 4,764 pseudo-absences (5,000 – 236 true absences) from a tile stretching from 33.17^{o}–43.67^{o}E and 1.86^{o}–6.87^{o}N. I restricted these points to be at least 10km from any presence location.

For the Pearl-breasted Swallow, I used species occurrence data downloaded on 22nd April 2016 from the Southern Africa Bird Atlas Project 2 (SABAP2, 2016; Figure 6.1). SABAP2 records a species' presence in pentads (5' latitude by 5' longitude), with squares which have been surveyed but lack records constituting true absences. The same environmental variables as used for the White-tailed Swallow in Ethiopia (from WorldClim (Hijmans et al., 2005), MODIS (Didan et al., 2015; Townshend et al., 2011) and the Africa Soil Information Service (Hengl et al., 2015); Section 3.7.2) were downloaded for southern Africa.

The Pearl-breasted Swallow has a patchy distribution across southern Africa, so rather than using spokes radiating from the centre of the species' range (c.f. Figure 3.17) for cross-validation, I divided the range into 12 equally sized panels (Huntley et al., 2007; Figure 6.1). The large number of true absences covering a wide area meant that pseudo-absence selection was not necessary. I assessed model performance by *k*-fold cross-validation AUC scores, and projected the best models for each species across their own range, and the range of the other species. For projections of the Pearl-breasted Swallow models in Ethiopia, I used the White-tailed Swallow data to calculate AUC scores to assess how well the Pearl-breasted Swallow model predicted the White-tailed Swallow data.

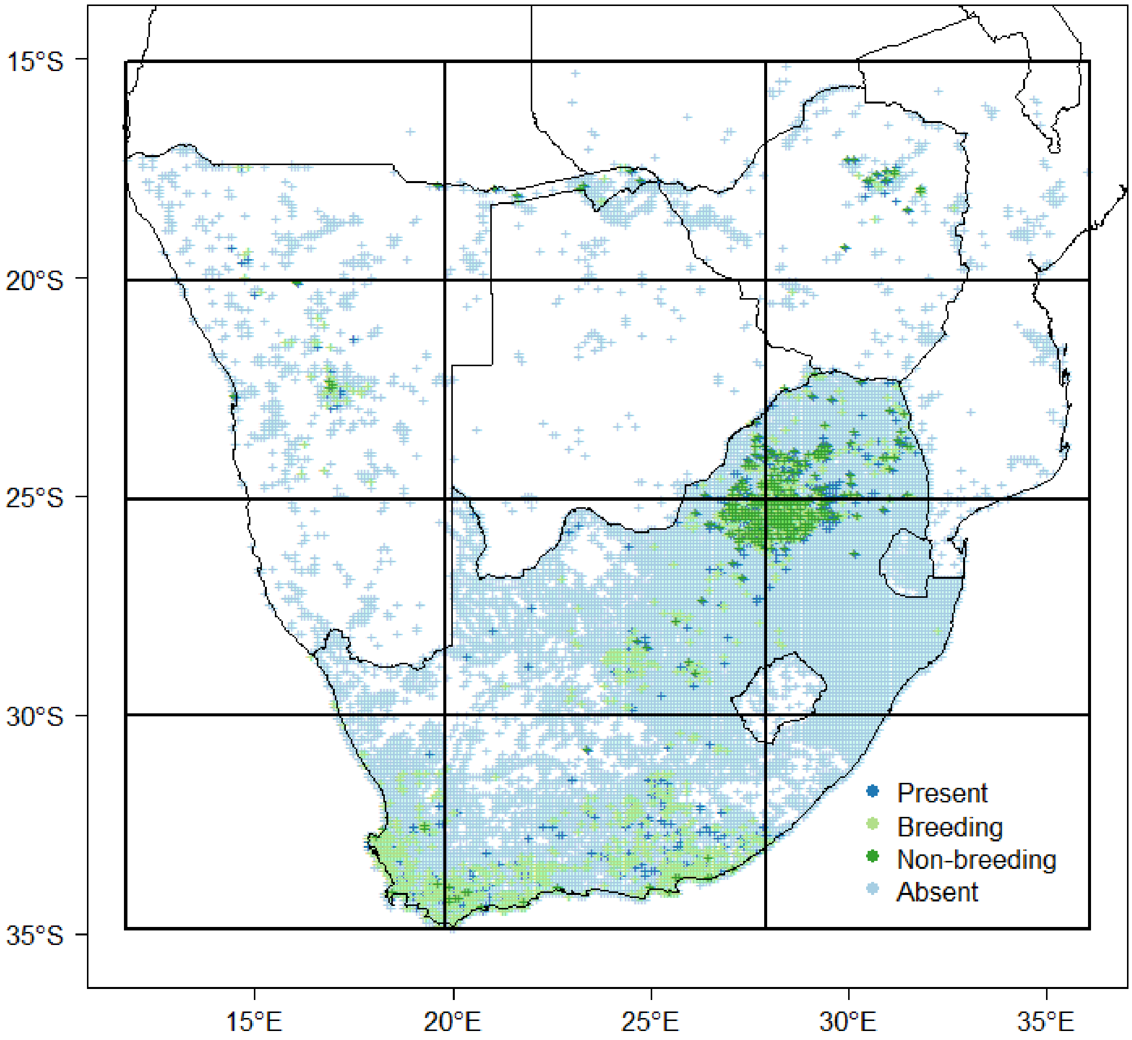
A weakness of models fitted to the Pearl-breasted Swallow's entire range is that, because the species is migratory (Maclean, 1993), it does not actually experience the full range of environmental variables upon which the model is built. For example, the birds may be present in an area where the maximum temperature of the warmest month is exceedingly high, but the bird is only present during the coolest months of the year.

To avoid this problem, I investigated ways to temporally partition the Pearl-breasted Swallow data. One option is to look exclusively at areas where the species is resident, as in these places it will experience the whole year's environmental variation. Alternatively, breeding season models might be interesting if the mechanism for range limitation is an effect on breeding success (see Chapter 7). Occurrence data from SABAP2 are available by month, so it is possible to separate records temporally (SABAP2, 2016). The Pearl-breasted Swallow is reported to breed in all months between August and April, with a peak generally between October and December (Turner, 2004). In the Cape, the main region in which it is migratory, it is present from August to April but nests from September to January (Schmidt, 1959).

I subdivided the Pearl-breasted Swallow occurrence data into 1) breeding season occurrences (September to January); and 2) non-breeding season occurrences (May to July). I also attempted to identify "resident" locations, where birds had been recorded in all or most months. However, only five squares contained records from all 12 months, and only 101 squares contained records from at least 6 months. Since records from only 6 months could not be considered representative of a "resident" site, and 101 presence points is not enough to build a robust model, I did not follow this idea further. Instead, given that the birds tend to migrate to breed, the non-breeding season dataset was used to provide an approximation to the species' resident range.

I plotted out the presence, breeding, and non-breeding season datasets. On a broad scale, the breeding season data covered most of the areas in the presence dataset, meaning that a model built using this data would replicate (with a smaller sample) the full species model. However, the non-breeding season records covered some of the areas in the full presence dataset (e.g. north of the Highveld in South Africa), whilst having few or no records in other areas (e.g. around the Cape) (Figure 6.1), making it useful for comparison. I therefore fitted a second set of distribution models using only the non-breeding season records as presence locations. Owing to the smaller number of non-breeding records, the panels used for *k*-fold cross-validation were enlarged and reduced in number to six, to ensure presence locations occurred in every panel.

Figure 6.1: Rectangles indicating the panels used for *k*-fold cross-validation of Pearl-breasted Swallow models, with species records from any time of year (dark blue), the breeding season (light green), the non-breeding season (a proxy for where it is resident, dark green) and absence data (grey) from SABAP2.



6.3 Results

6.3.1 Temperature patterns within the White-tailed Swallow's range

Maximum Temperature

Splitting both the measured temperature values, and those predicted by the linear regression of temperature on date and site (Section 3.5.3), by the presence or absence of White-tailed Swallows revealed that birds were absent from sites with the highest temperatures (Figure 6.2). This was also the case when comparing predicted values for sites in the hot and cool seasons separately, although the difference was more marked in the hot season (Figure 6.3). However, White-tailed Swallows were not recorded in many locations which were as cool as those where the species was recorded.

I calculated the mean predicted temperature at each site in each season and then, having checked for equal variance and normal errors, conducted t-tests to compare presence and absence sites in the cool season, and Wilcoxon tests to compare them in the hot season (as the hot season data were not normally distributed). Although the mean temperature at the presence sites was always lower than at the absence sites, the difference was only significant for the 3pm dataset in the cool season (Table 6.1).

Table 6.1: Tests of differences in temperature between White-tailed Swallow presence and absence sites in each season.

Dataset	Mean temperature ± S.D.		Test	Stat	DF	P-value
	Presence sites	Absence sites				
3pm hot	27.2 ± 4.8	29.3 ± 6.1	Wilcoxon	54	-	0.340
3pm cool	24.2 ± 2.0	25.2 ± 2.7	Student's t	2.66	200	0.008 *
11am+3pm hot	26.1 ± 4.2	27.2 ± 5.2	Wilcoxon	48	-	0.650
11am+3pm cool	22.9 ± 1.6	23.5 ± 2.3	Student's t	1.69	200	0.093

Figure 6.2: Measured 3pm temperatures at sites where White-tailed Swallows were seen (blue), where they were not recorded on bird transects (red), and where they were not seen at non-transect sites (black). Points represent recorded temperatures on each day throughout the year. 1 = 1st Jan.

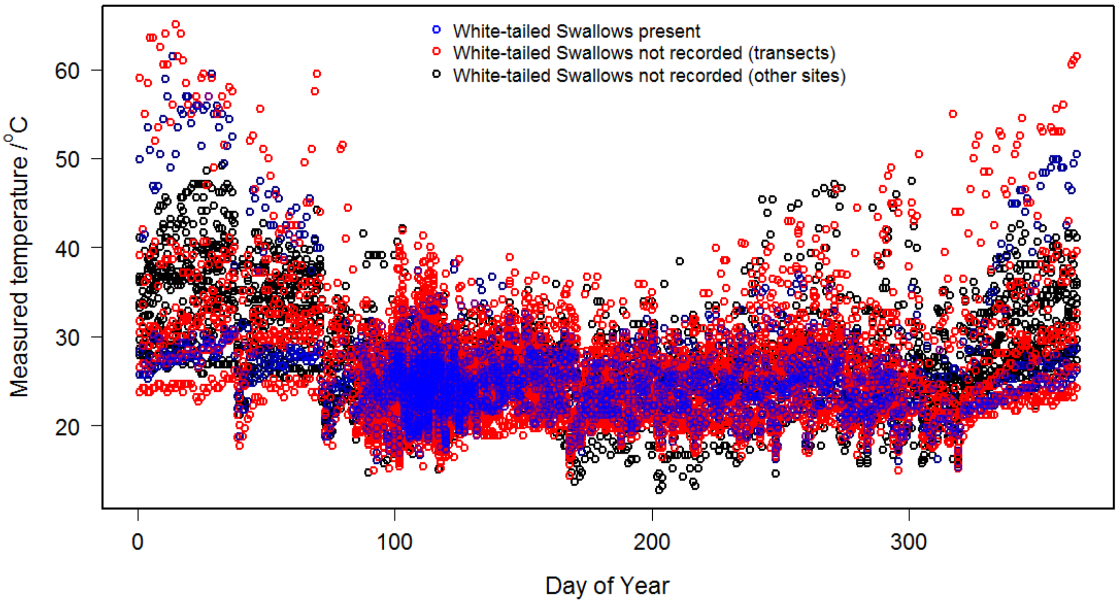
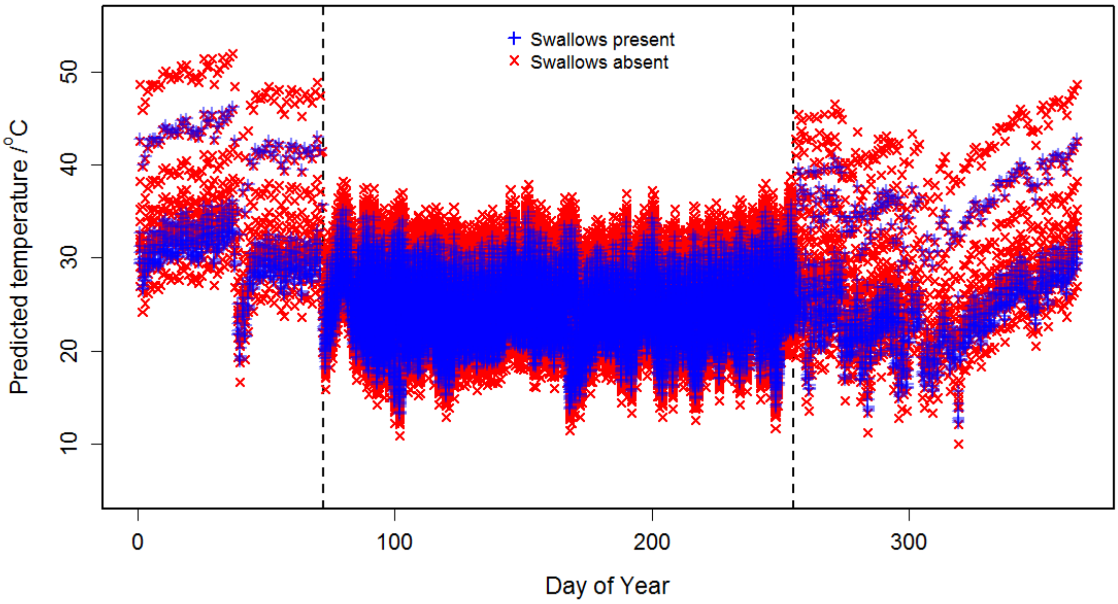


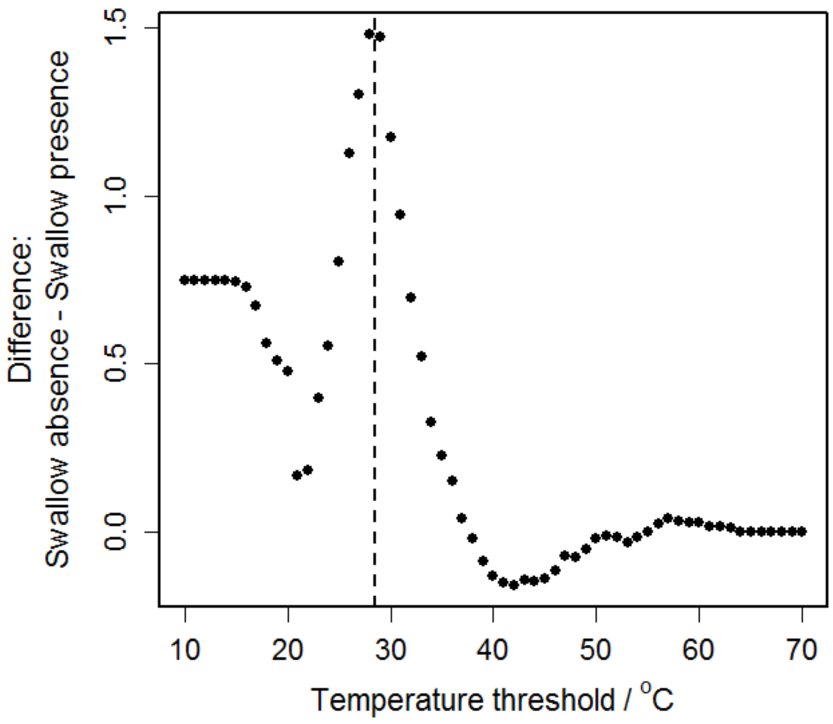
Figure 6.3: Predicted 3pm temperatures at sites where White-tailed Swallows were seen (blue), and where they were not recorded on bird transects (red). Models were fitted separately to data from cool (between the dashed lines) and hot (outside the dashed lines) seasons. Points represent predicted temperatures on each day throughout the year. 1 = 1st Jan.



Temperature thresholds

Rather than responding to maximum temperatures alone, birds may be affected by the frequency of extreme weather events (Cunningham et al., 2013a). I calculated the number of days per month where temperatures at each site exceeded a moving threshold from 10°C to 70°C, at 1°C intervals. I then calculated the mean of this for presence and absence sites, and the difference between the means at each threshold. The maximum difference between the means, of 1.5 days, occurred at 28.5°C (Figure 6.4).

Figure 6.4: The difference between White-tailed Swallow presence and absence sites in the mean number of days per month (from March 2013–May 2015) which exceeded temperature thresholds from 10 to 70°C. The dashed line shows the temperature, 28.5°C, at which the greatest difference occurred.



6.3.2 White-tailed Swallow response to local temperatures

No effect of temperature was found on any of the metrics of White-tailed Swallow occurrence and density at transect sites: presence, bird or group density, or group size. Owing to the small number of transects on which White-tailed Swallows were recorded, the sample size for these models was very small, which makes detecting significant effects difficult. However, all models indicated non-significant negative effects of temperature on White-tailed Swallow presence and density at a site.

6.3.3 Effects of temperature and habitat on the global distribution of the White-tailed and Pearl-breasted Swallows

Environmental comparison

Histograms of environmental variables demonstrated that there was close overlap in the ranges of some variables found in areas occupied by White-tailed and Pearl-breasted Swallows. Little rainfall in the dry season, low tree cover, and a high percentage of non-tree vegetation are all typical of the savannah habitat occupied by the two species. However, across all ten variables, the environment occupied by the White-tailed Swallow is greatly restricted compared to that occupied by the Pearl-breasted Swallow (Figure 6.5). Most noticeably, whereas the White-tailed Swallow is not present where maximum temperatures rise above 30–35°C, the Pearl-breasted Swallow still occurs in areas with higher temperatures than this.

The range of environmental variables in localities where the Pearl-breasted Swallow is resident was lower than for the whole year in its migratory range, which is to be expected if it is assumed that migration is a strategy to track favourable environments that occur in different places, and avoid less favourable environments. However similar patterns were seen, most pertinently the same trend in maximum temperature, with both resident and migrant Pearl-breasted Swallow records coming from areas where temperatures exceed 30°C. The biggest difference in a single variable between plots was in the dry season precipitation, where the Pearl-breasted Swallow’s resident range was much more comparable with the White-tailed Swallow’s range than the Pearl-breasted Swallow’s migratory areas were, albeit that the White-tailed Swallow’s range was still wetter. The most striking difference across all plots was in annual temperature range and temperature seasonality, where the White-tailed Swallow’s environment barely matched that of the Pearl-breasted Swallow at all (Figure 6.6; Figure 6.7).

Figure 6.5: Histograms of the environmental variables (see Table 3.4) in locations where White-tailed Swallows (blue) and Pearl-breasted Swallows (red) have been recorded at any time of year.

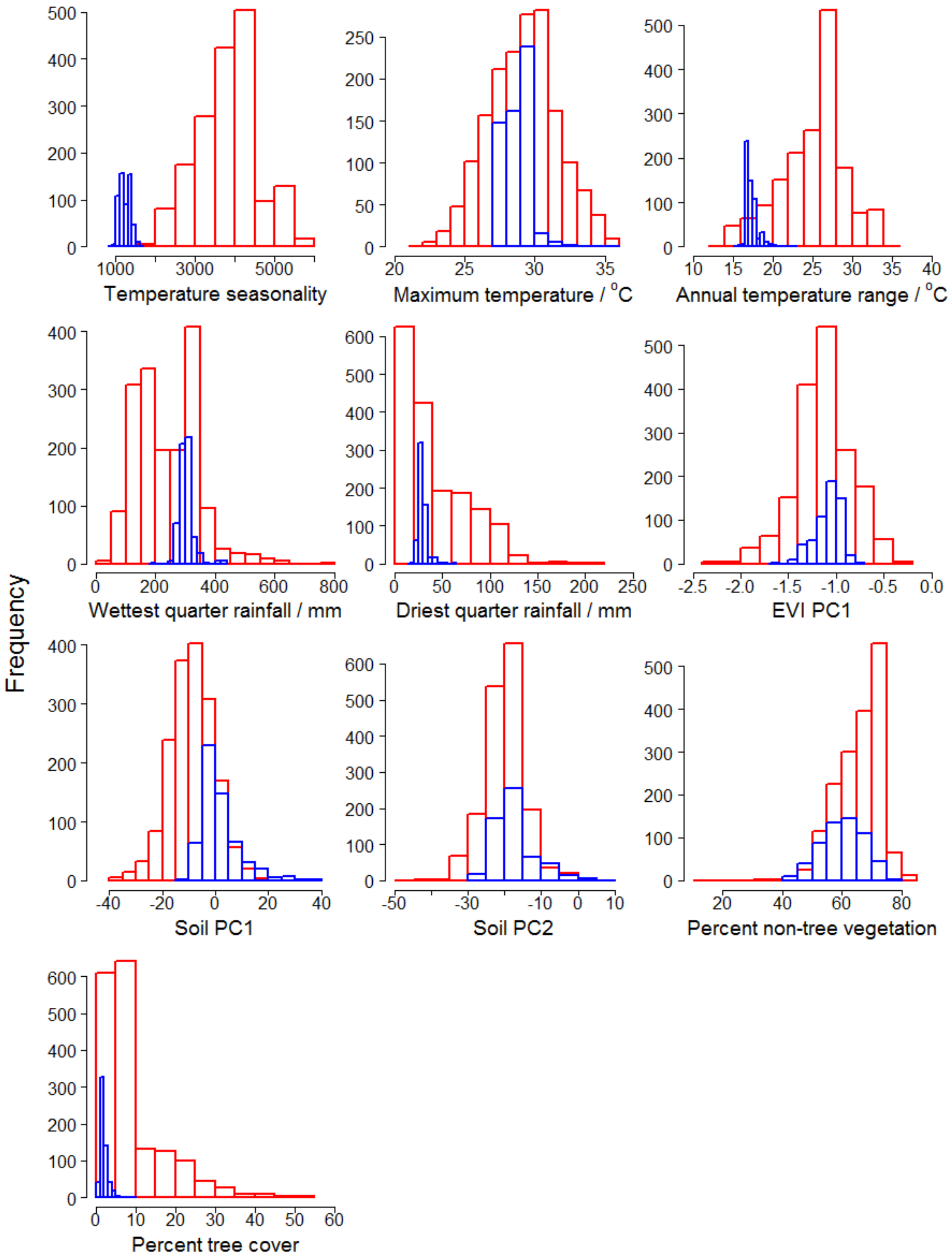


Figure 6.6: Histograms of the environmental variables (see Table 3.4) in locations where White-tailed Swallows are present (blue) and Pearl-breasted Swallows are resident (green).

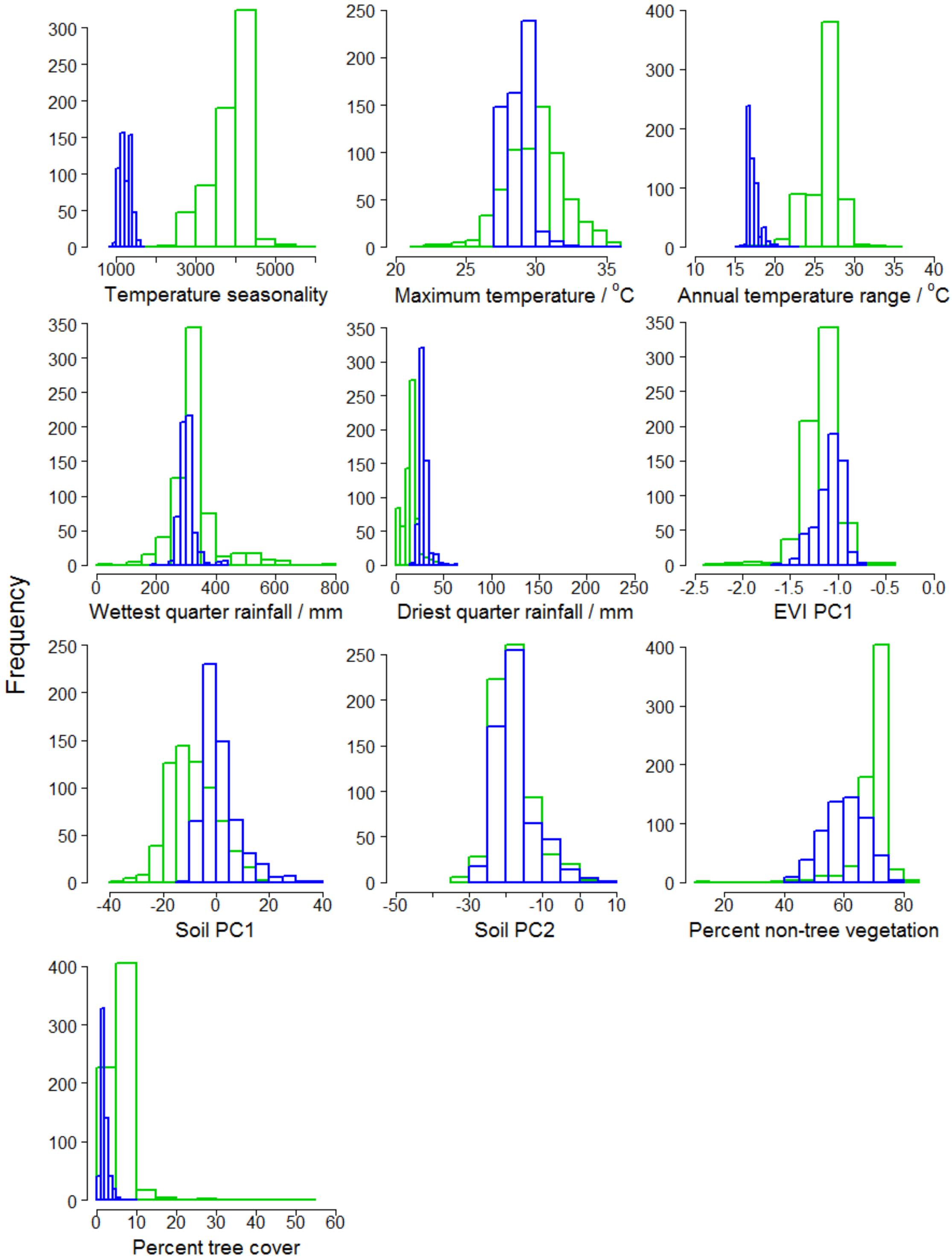
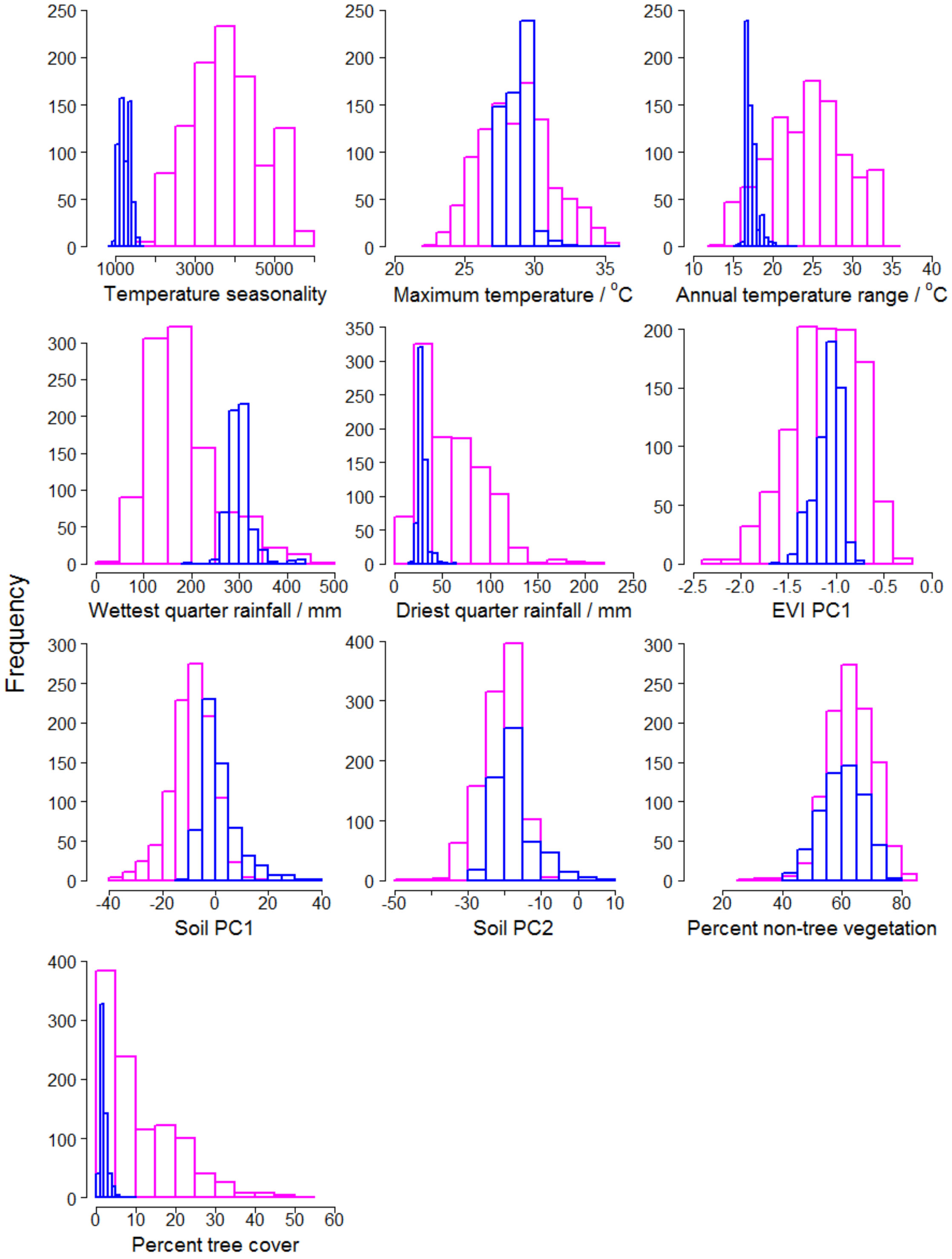


Figure 6.7: Histograms of the environmental variables (see Table 3.4) in locations where White-tailed Swallows are present (blue) and migratory populations of Pearl-breasted Swallows breed (pink).



White-tailed Swallow distribution models

K-fold cross-validation AUC scores for each model algorithm were used to assess which techniques performed best, and were compared to AUC scores produced when models were fitted using all data (Table 6.2). As expected, AUC scores were higher when all available data were used to fit a single model than under *k*-fold partitioning. AUC scores generally dropped when fewer variables were used in the model, in particular when habitat variables alone were modelled. Random Forests (RF) and MaxEnt were the top two algorithms rated by AUC for all models fitted to all data. However, differences among algorithms indicated by the more robust *k*-fold models were less clear, with no "best" algorithms distinguishable based on 95% confidence intervals (e.g. Figure 6.8). Generalised Linear Models (GLM), MaxEnt and Multiple Adaptive Regression Splines (MARS) had the highest *k*-fold AUC scores for all data, climate- and habitat-only, respectively.

Table 6.2: White-tailed Swallow SDM AUC scores for each model algorithm for all variables, climate-only and habitat-only variables. For each variable set, results are compared for predictions based upon models fitted to all the data and *k*-fold validation in which the prediction for each location in based only upon data from other locations. Letters correspond to model groups whose 95% C.I.s overlapped.

Model	All predictors k-fold	All predictors All data	Climate only k-fold	Climate only All data	Habitat only k-fold	Habitat only All data
RF	0.618 a	0.997 a	0.566 a	0.997 a	0.576 a	0.999 a
GLM	0.671 a	0.750 d	0.619 a	0.652 c	0.551 a	0.660 b
BRT	0.530 a	0.832 c	0.567 a	0.800 b	0.547 a	0.688 b
GAM	0.606 a	0.841 c	0.601 a	0.773 b	0.572 a	0.673 b
FDA	0.579 a	0.714 d	0.554 a	0.676 c	0.547 a	0.618 c
MARS	0.637 a	0.762 d	0.570 a	0.676 c	0.588 a	0.625 c
MAXENT	0.595 a	0.898 b	0.627 a	0.829 b	0.553 a	0.713 b

To assess variable importance, the algorithms with *k*-fold AUC scores greater than 0.6 from all predictor models (GLM, MARS, RF and GAM) were re-fitted with each variable left out for another *k*-fold run. Delta AUC scores were calculated by subtracting the *k*-fold AUC for the models with the variable missing from the *k*-fold AUC for the maximal model. Maximum temperature of the warmest month and percent tree cover produced the highest delta AUC scores for the top three algorithms (GLM, MARS and RF), whilst dry season precipitation was most important under GAM (Figure 6.9).

Figure 6.8: White-tailed Swallow *k*-fold AUC estimates with 95% C.I.s (dashed lines) for each algorithm for models that used all predictor variables.

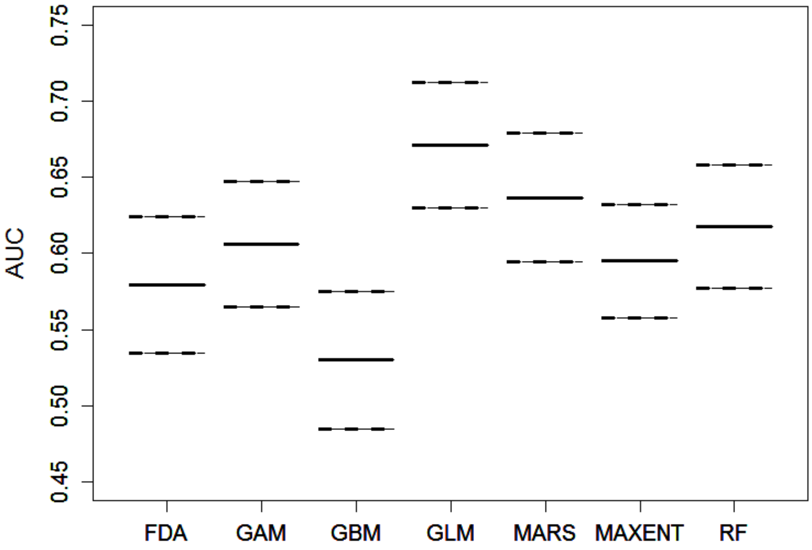
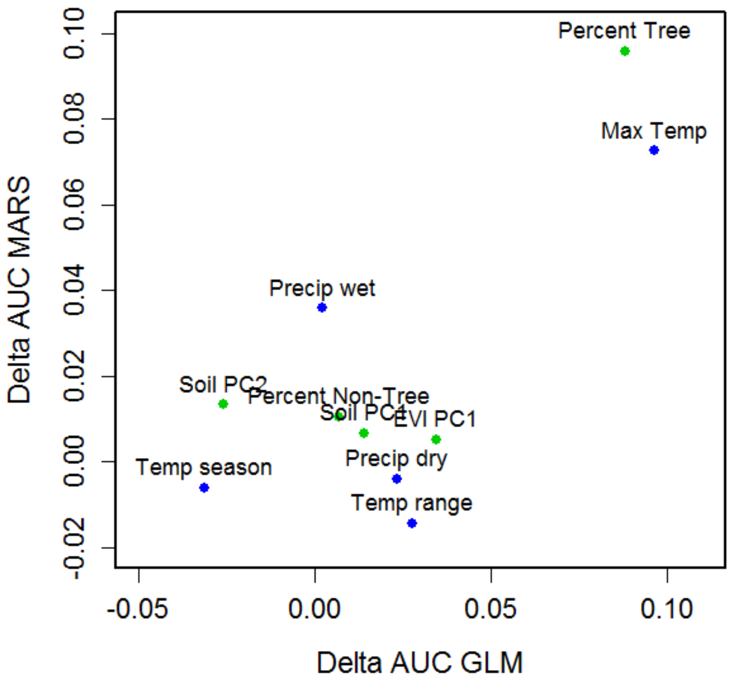


Figure 6.9: Delta AUC scores for each variable under GLM and MARS algorithms. Climatic variables are shown in blue, and habitat variables in green. Maximum temperature of the warmest month (Max Temp) and percent tree cover (Percent Tree) are the two most important variables in both models.



Response plots from the best four model algorithms indicated strong temperature (30–35°C) and tree cover (10%) thresholds, above which White-tailed Swallows did not occur (Figure 6.10; Figure 6.11).

Figure 6.10: The response of probability of White-tailed Swallow occurrence to each environmental variable. Lines show the predicted response to each variable according to the GLM (black), MARS (red), RF (green) and GAM (blue) algorithms, with all other variables held at their mean.

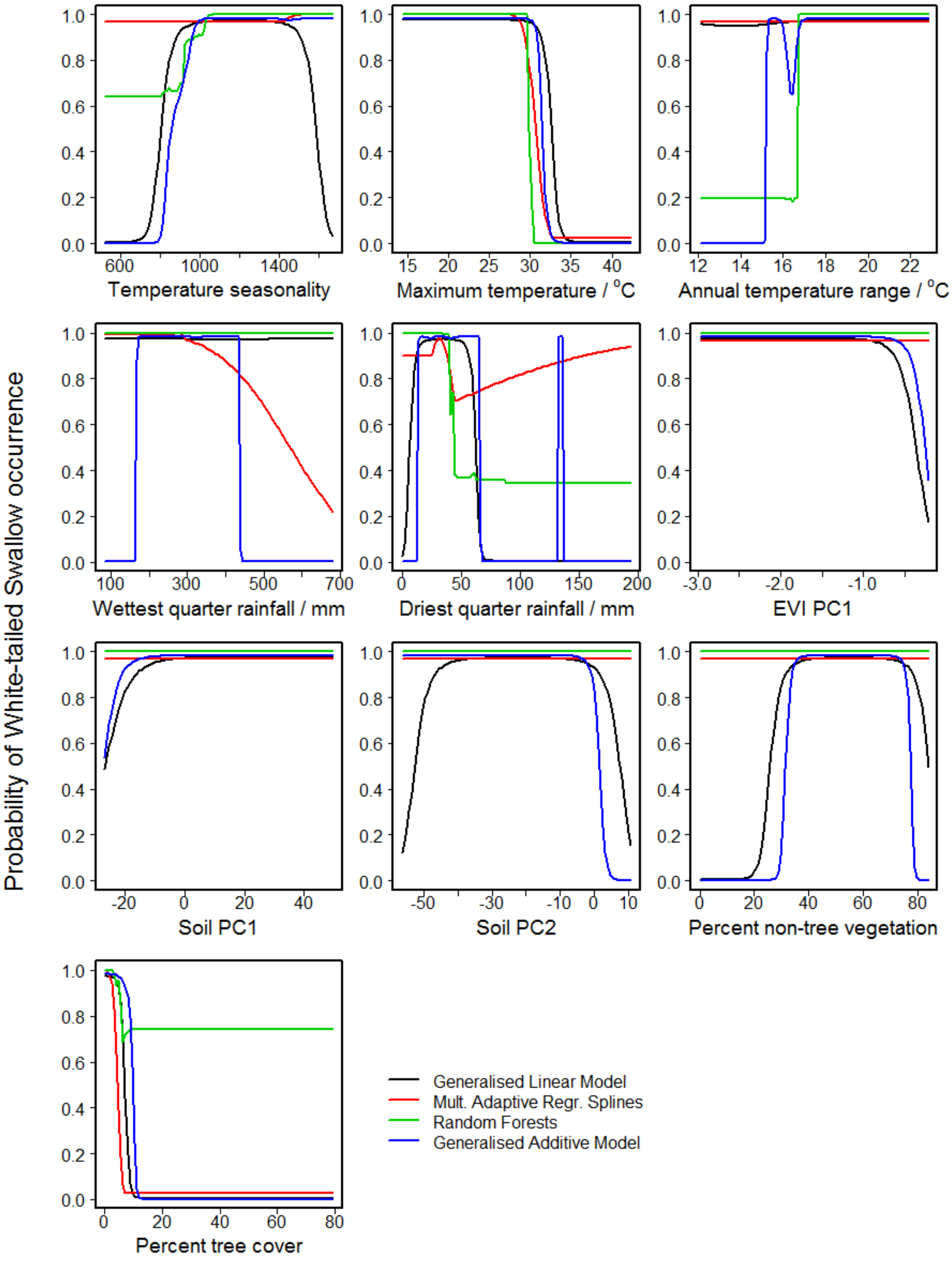
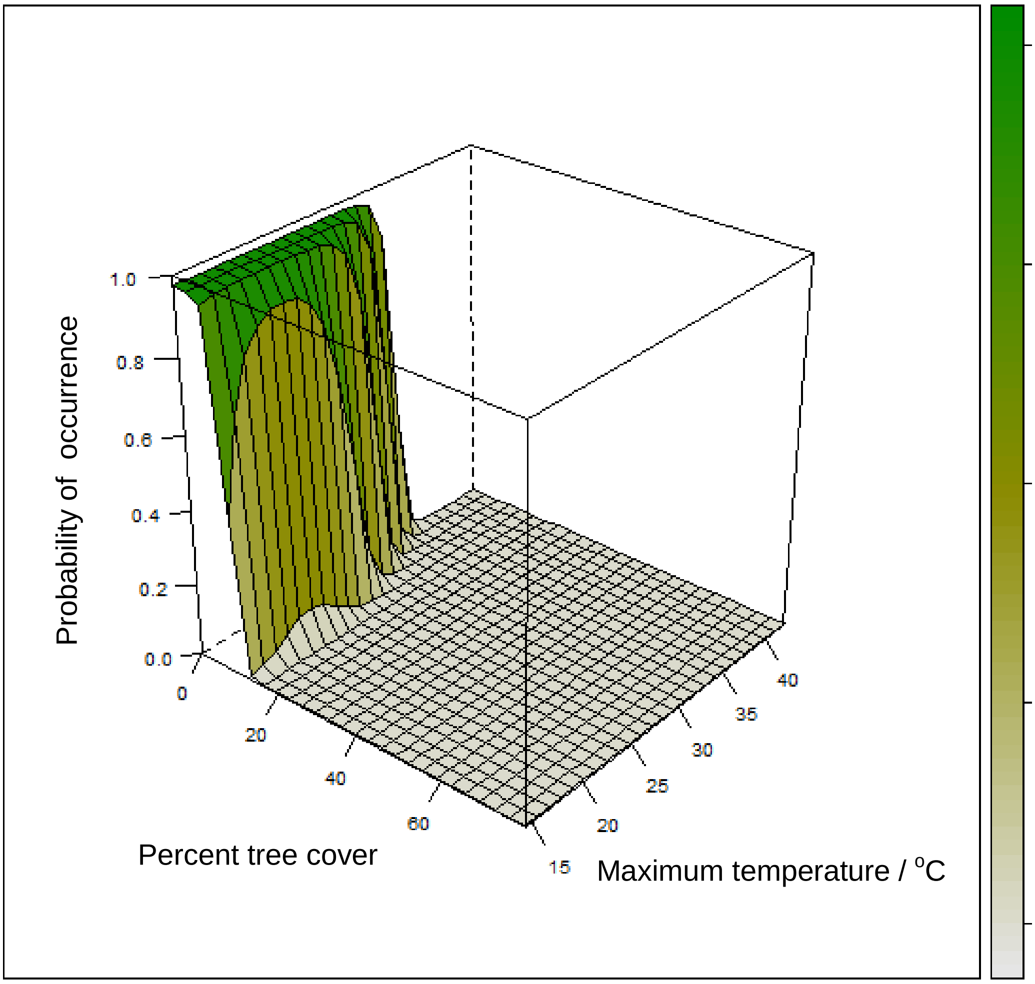
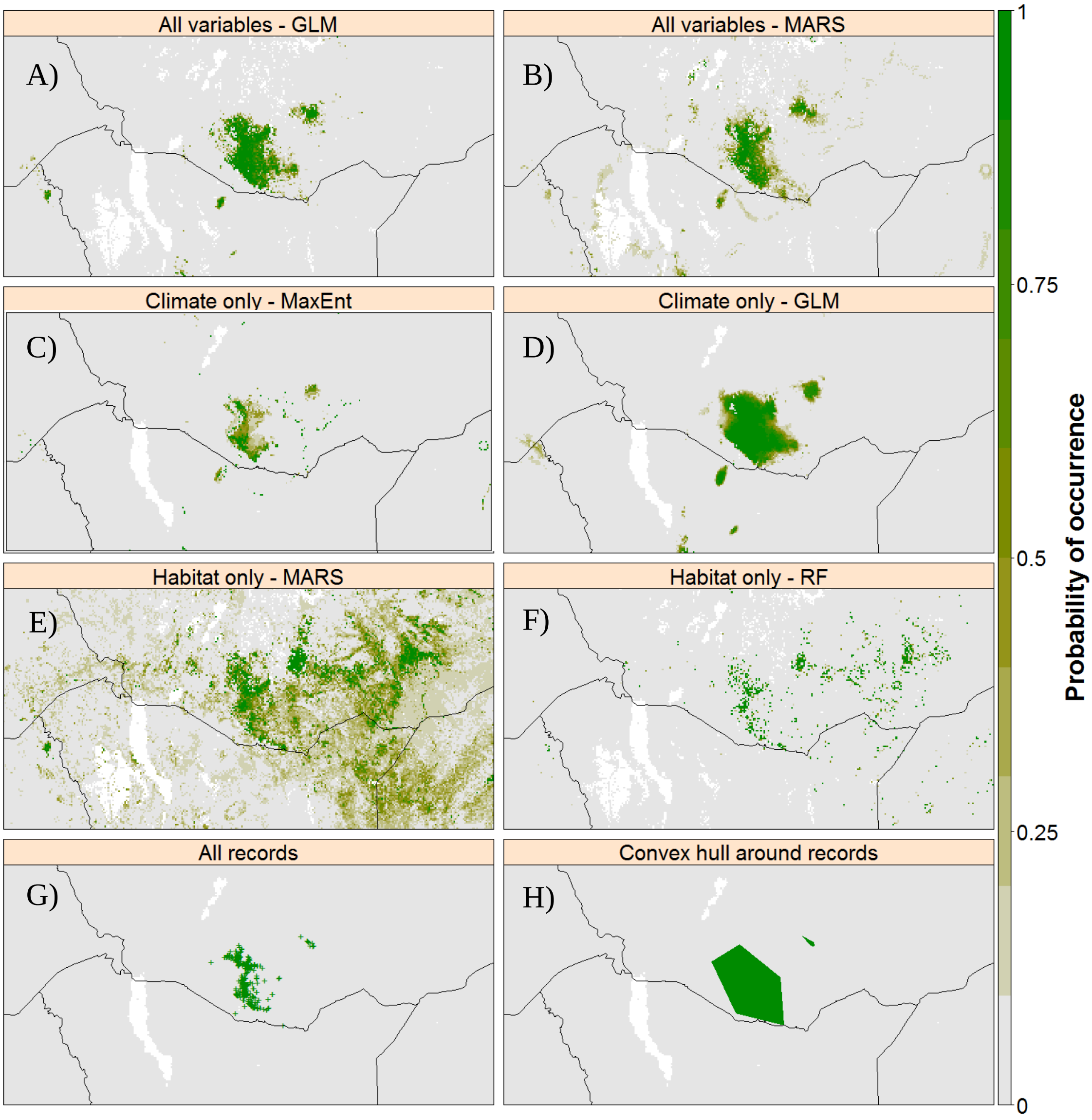


Figure 6.11: Response surface for White-tailed Swallow probability of occurrence against the two most important variables, maximum temperature and tree cover, according to the best fitting GLM model. All other model variables are held at their mean.



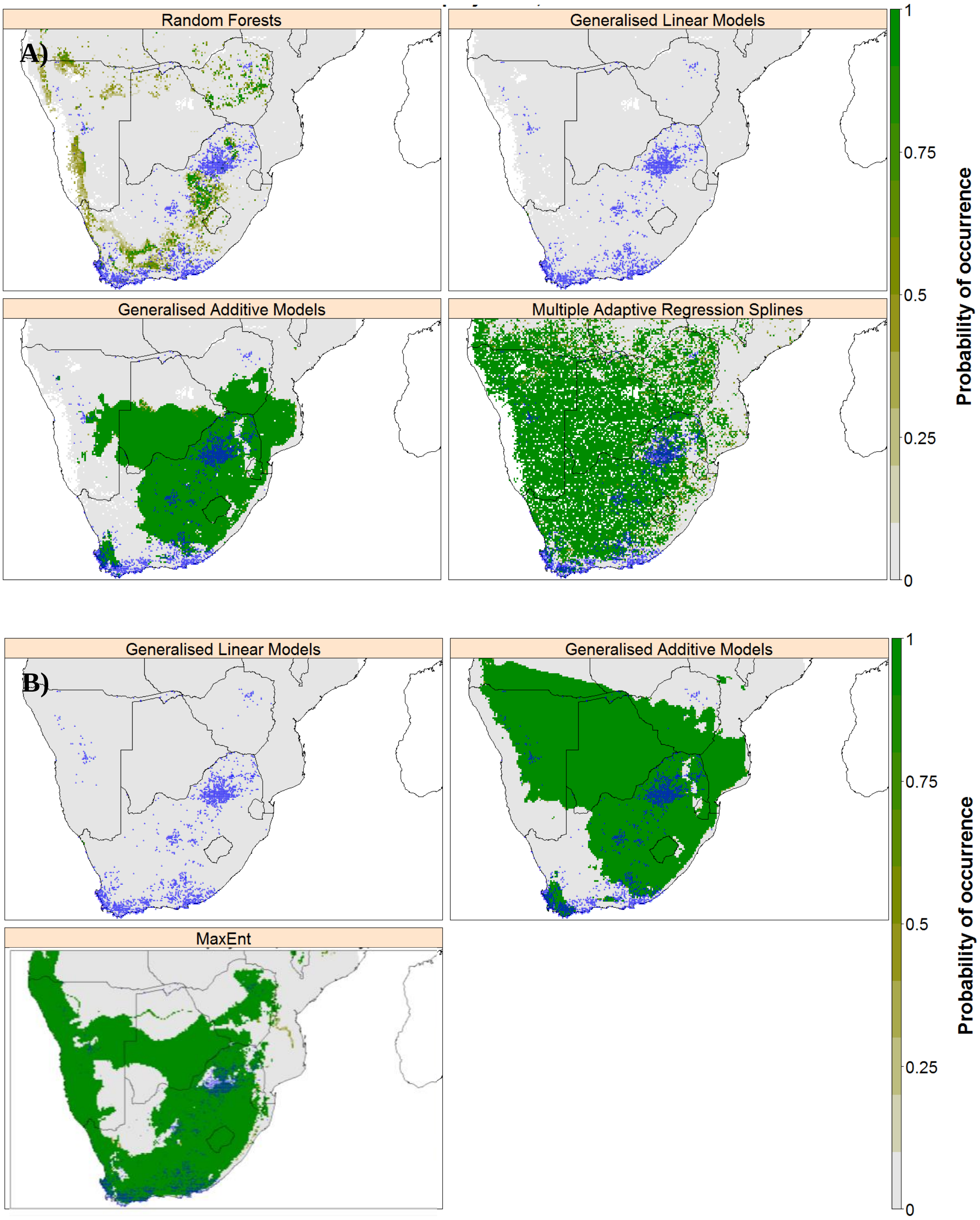
I used the models fitted to all species data, selecting the top two model algorithms for each set of environmental variables, to produce six simulations of the White-tailed Swallow's range under current environmental conditions. The models fitted to all ten variables (Figure 6.12; *A*, *B*) produced the best predictions of the White-tailed Swallow's true range (Figure 6.12; *G*, *H*), with the climate-only models performing reasonably (Figure 6.12; *C*, *D*) and the habitat-only models poorly (Figure 6.12; *E*, *F*).

Figure 6.12: Simulations of the White-tailed Swallow's current range using models fitted to all White-tailed Swallow records, with climate and habitat predictor variables (*A*, *B*), climate variables alone (*C*, *D*), and habitat variables alone (*E*, *F*). Simulations are presented for the two best-performing model algorithms with each set of predictor variables, assessed by *k*-fold cross-validation. The simulations are compared with all species records (*G*), and the convex hull fitted around the outermost species records (*H*).



Simulations based upon the top four models built with all ten environmental variables (Figure 6.13; *A*) and the top three climate-only models for the White-tailed Swallow in Ethiopia (Figure 6.13; *B*) failed to predict the Pearl-breasted Swallow's distribution in southern Africa. In southern Africa, five and four variables, respectively, were outside of the range for Ethiopia.

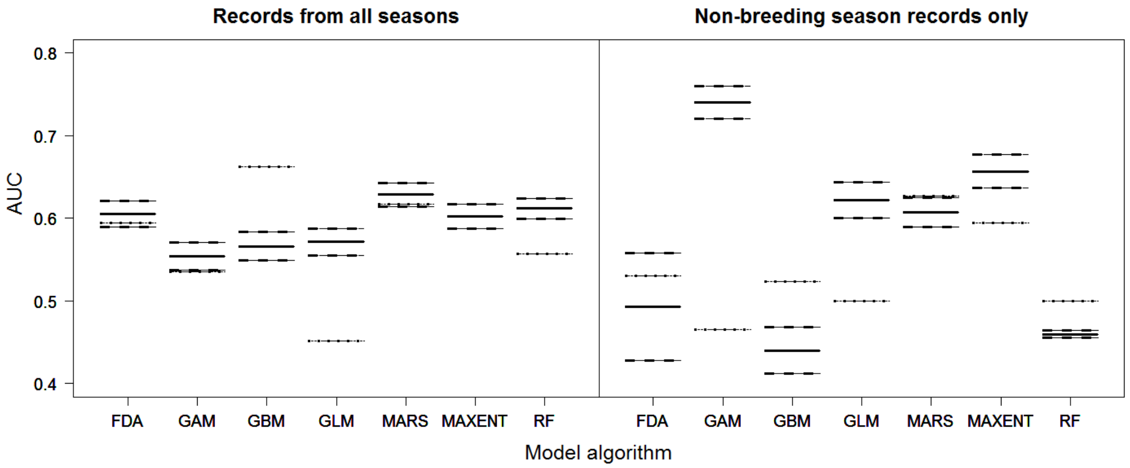
Figure 6.13: Simulations of the potential range of the White-tailed Swallow in southern Africa under current conditions, based upon the best models (*k*-fold AUC > 0.6), fitted to *A*) climate and habitat variables and *B*) climate variables alone for Ethiopia. Simulations use environmental data for southern Africa. Blue dots indicate Pearl-breasted Swallow records (SABAP2, 2016).



Pearl-breasted Swallow distribution models

The best performing models, with a *k*-fold AUC score greater than 0.6, were MARS, RF, FDA and MaxEnt for models fitted to species records from all seasons, and GAM, MaxEnt, GLM and MARS for the non-breeding distribution. There was more variation in the AUC scores for the non-breeding season models (Figure 6.14). The non-breeding season GAM was the best model overall, and the only one to achieve a ‘useful’ AUC value above 0.7 (Swets, 1988). As expected, the ability of the Pearl-breasted Swallow model simulations to predict the species’ true distribution was therefore poor, with the general tendency to over-predict occurrence (Figure 6.15).

Figure 6.14: Pearl-breasted Swallow model *k*-fold AUC estimates (solid lines) with 95% C.I.s (dashed lines). Dotted lines indicate the AUC scores for prediction of the White-tailed Swallow occurrence data using the simulations from the Pearl-breasted Swallow models.



Unlike the White-tailed Swallow, the fitted responses to each environmental variable under the different models were varied, with no clear response to one or two predictors for either model set (Figure 6.16). Most notably there was no response to maximum temperature and a positive, rather than the White-tailed Swallow’s negative, response to percent tree cover in both the full year (Figure 6.16; *A*) and non-breeding season models (Figure 6.16; *B*).

Figure 6.15: Simulations of the Pearl-breasted Swallow's range under the best models, assessed by *k*-fold AUC, fitted to *A*) records from all seasons and *B*) non-breeding season records only. Blue dots show the Pearl-breasted Swallow records from SABAP2 used to fit the models.

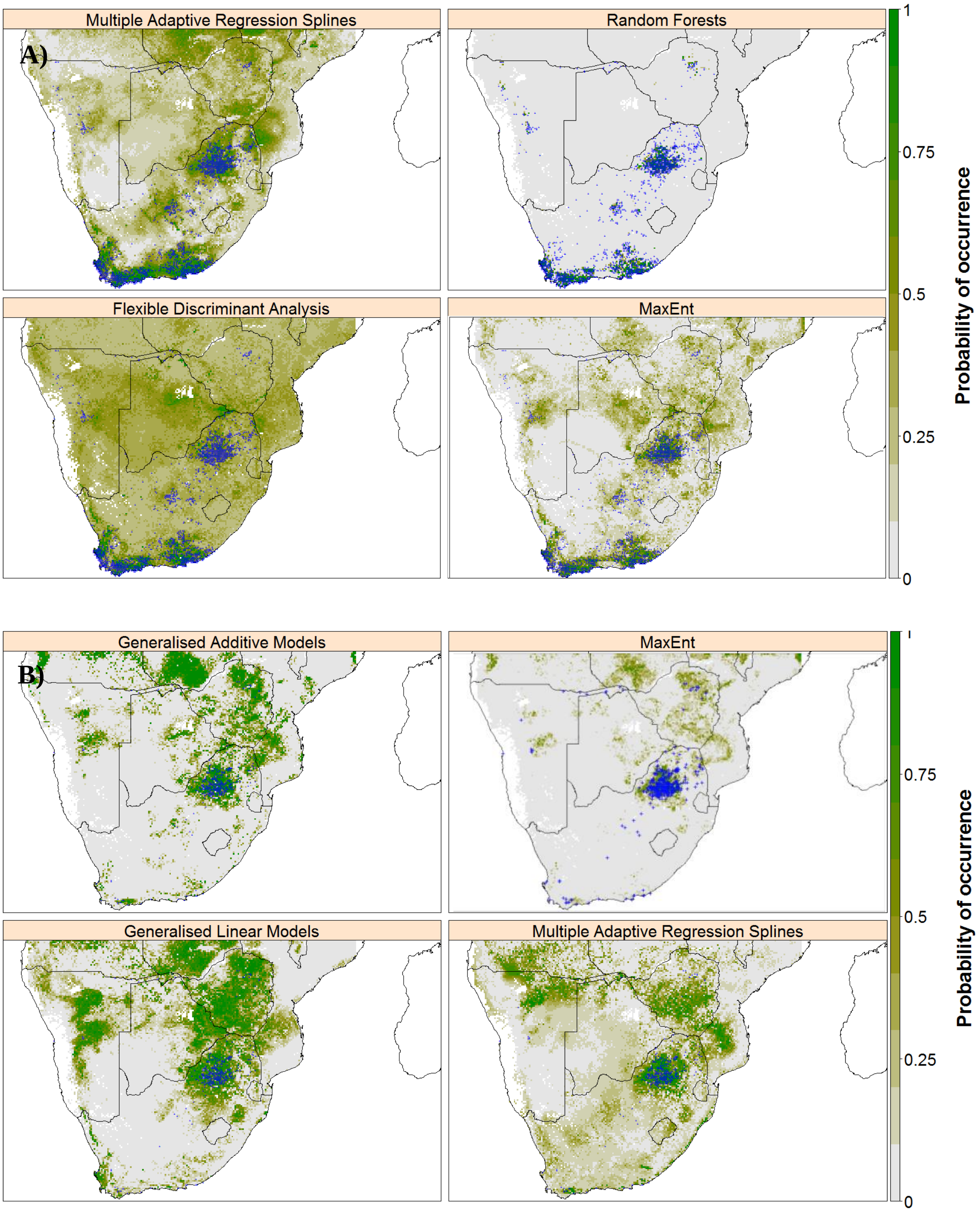
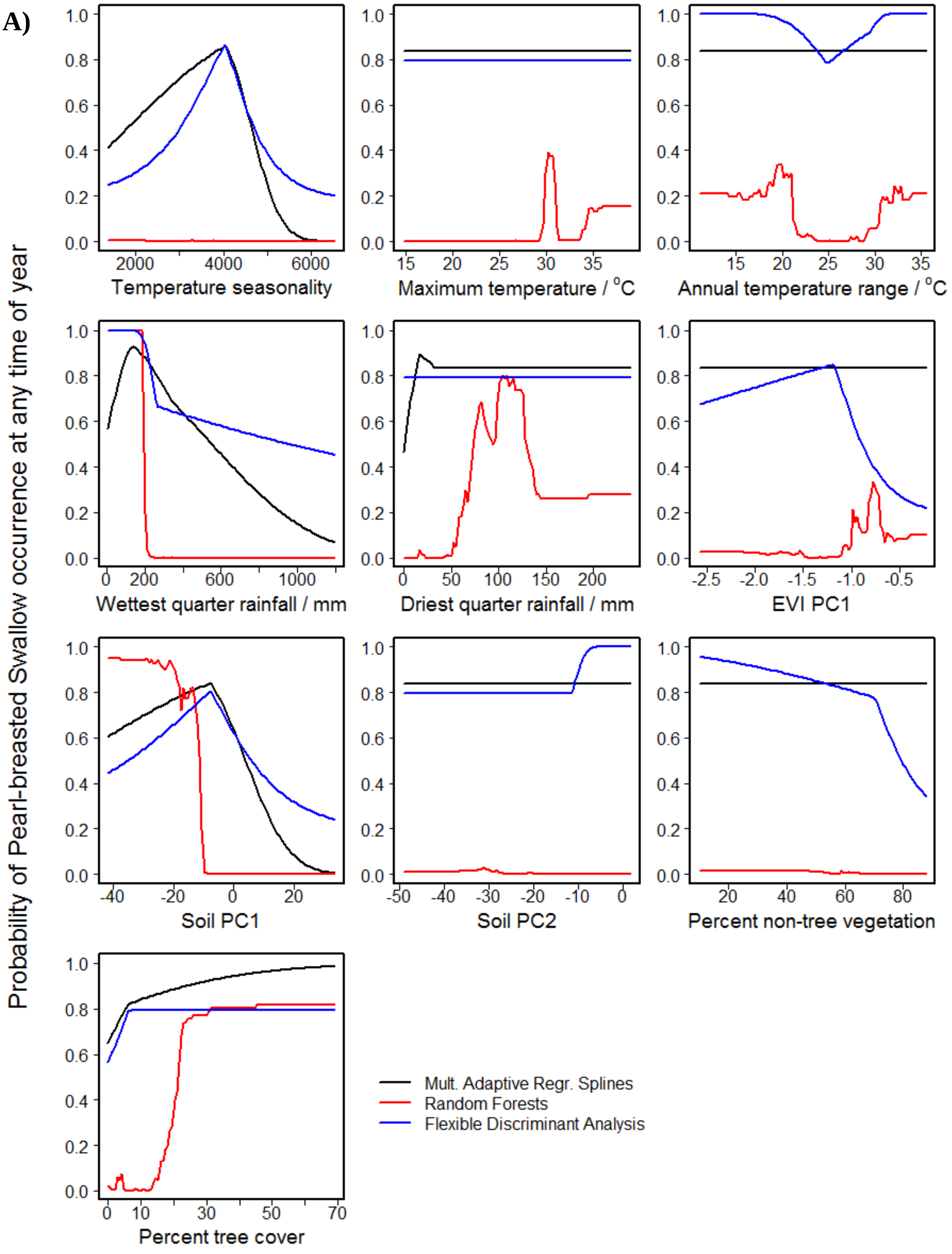
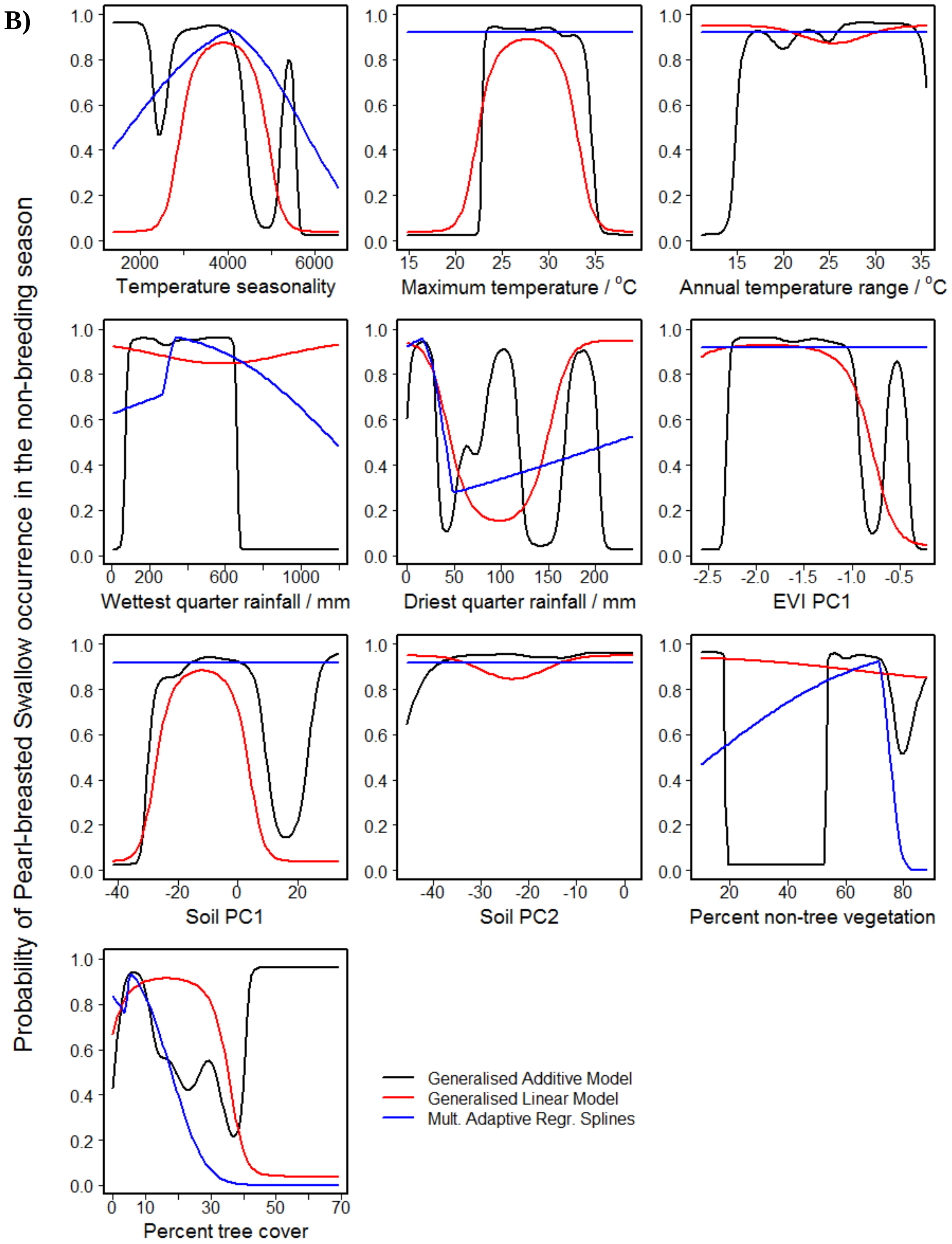


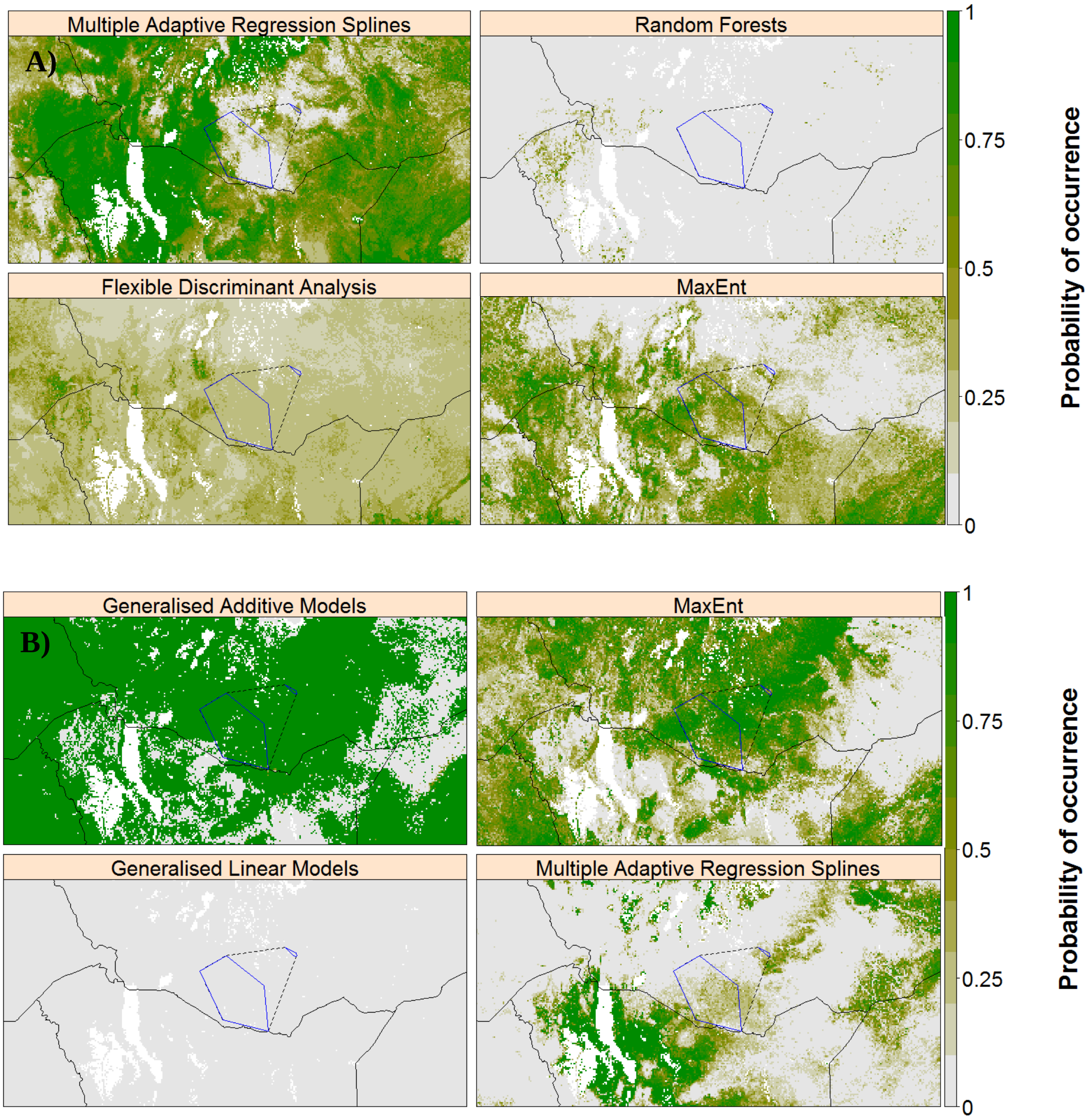
Figure 6.16: The response of probability of Pearl-breasted Swallow occurrence to each environmental variable. Lines show the predicted response to each variable according to the top three algorithms, assessed by *k*-fold AUC, with all other variables held at their mean. Responses for models fitted with *A*) records from all seasons and *B*) from the non-breeding season only.





Range simulations under current conditions based upon the best Pearl-breasted Swallow models failed to predict the range of the White-tailed Swallow in Ethiopia (Figure 6.17), and the AUC scores, calculated using each model's ability to predict the White-tailed Swallow occurrence data, were very low (Figure 6.14).

Figure 6.17: Simulations of the potential range of the Pearl-breasted Swallow in Ethiopia, based upon the best models (*k*-fold AUC > 0.6), fitted to *A*) records from all seasons and *B*) non-breeding season records only. Blue polygons show the known range of the White-tailed Swallow, dashed lines show the total range if the species' two populations are assumed to be continuous.



6.4 Discussion

Plots of site temperatures against White-tailed Swallow presence and absence suggested that White-tailed Swallows are absent from the sites with the highest temperatures in both the hot and cool season, although the pattern was less clear than for the Bush-crow (Chapter 4). Site definition is presumably less clear for the Swallow, as individuals must range further than Bush-crows (Bladon et al., 2016).

Analysis of my transect data found no effect of temperature on White-tailed Swallow occurrence, density or group size, however the sample of transects on which birds were recorded was small, which makes it difficult to detect significant effects. All estimates of the effect of temperature were negative, which suggests perhaps that with a much larger sample, a negative effect of temperature on the species might be detectable.

Regardless of the model algorithm chosen, the species distribution models found a strong negative effect of maximum temperature of the warmest month on the presence of White-tailed Swallows, with temperatures greater than 30–35°C associated with their absence. In addition to this, White-tailed Swallows are only found in areas with less than 10% tree cover. This suggests that, like the Bush-crow, the White-tailed Swallow's global distribution is determined directly or indirectly by temperature, with its within-range occurrence further influenced by the availability of suitable habitat (Donald et al., 2012; Chapter 4).

The White-tailed Swallow's close genetic affiliation to the Pearl-breasted Swallow (Dor et al., 2010) suggests that their ecological niches might be similar and that they might constitute a pair of recently derived ecologically equivalent replacement species (Moreau, 1966; Spottiswoode et al., 2013). However, comparison of the environmental variables within the two species' ranges found that whilst a few variables were broadly similar, others differed markedly. Simulated potential distributions for southern Africa based upon the White-tailed Swallow distribution models failed to predict the Pearl-breasted Swallow's distribution, and simulated potential distributions for Ethiopia based upon the Pearl-breasted Swallow distribution models failed to predict the White-tailed Swallow's distribution. In fact, most Pearl-breasted Swallow models greatly over-predicted the White-tailed Swallow's range, which is to be expected given that the comparative histograms generally showed that the Pearl-breasted Swallow inhabits a much broader range of environments than the White-tailed Swallow.

Interestingly, the Pearl-breasted Swallow models themselves showed no consistent response to any environmental variable, which presumably led to the model's inability to accurately predict the Pearl-breasted Swallow range.

6.5 Conclusions

The White-tailed Swallow's range showed a strong correlation with a distribution model in which the most important variables were maximum temperature of the warmest month and percent tree cover. The species was absent from sites at which the highest temperatures were recorded, and non-significant negative trends in its probability of occurrence and site density were detected from transect data, despite a small sample size. This suggests that, like the Bush-crow, its restricted-range is climatically determined (Donald et al., 2012; Chapter 4).

Comparison with the lack of response to temperature of its sister taxon, the Pearl-breasted Swallow, suggests that either 1) the White-tailed Swallow's restricted distribution is driven by an indirect effect of temperature, such as on food availability or predation pressure, from which the Pearl-breasted Swallow does not suffer, or 2) the direct physiological inability of White-tailed Swallows to cope with temperature is determined by recently evolved genetic differences between the two species (Dor et al., 2010).

One way to test between direct and indirect effects is to look for an effect of temperature on individual White-tailed Swallows. This could be manifested in a variety of ways, such as an impact on foraging ability (Cunningham et al., 2015; du Plessis et al., 2012; Chapter 5) or an effect on the growth or survival of young birds (Cunningham et al., 2013b; Salaberria et al., 2014). The latter possibility is investigated in Chapter 7.

7 THE EFFECT OF TEMPERATURE ON THE GROWTH AND BREEDING SUCCESS OF THE WHITE-TAILED SWALLOW AND ETHIOPIAN SWALLOW

"He is like Abba Raaree, the Father of the Swallows."

7.1 Introduction

The global distribution of the White-tailed Swallow is well described by a species distribution model, in which maximum temperature of the warmest month is the most influential climatic variable (Chapter 6). The species is restricted to areas with relatively low maximum temperatures, however the mechanism which drives this limitation is unclear. There are a number of potential mechanisms, such as a direct impact of temperature on physiology (Oswald et al., 2008; Tieleman and Williams, 1999), foraging ability (Cunningham et al., 2015; du Plessis et al., 2012; Chapter 5) or breeding success (Cunningham et al., 2013b; Salaberria et al., 2014), or an indirect effect via a competitor, prey or predator species (Araújo and Luoto, 2007; Hersteinsson and MacDonald, 1992; Mason et al., 2014b).

Environmental conditions, including temperature, can have a strong effect on breeding success (Bolger et al., 2004). In general, it may be expected that, within limits, warm conditions will be more favourable to young birds than cool conditions (Webb, 1987). Experimental heating of Tree Swallow *Tachycineta bicolor* nests resulted in higher body mass and condition of nestlings, better maintenance of female condition (Pérez et al., 2008) and higher nestling growth and survival rates (Dawson et al., 2005), whereas experimental cooling led to extended incubation periods, lower nestling body mass, and impaired immune responses (Ardia et al., 2010). Nestlings experiencing cooler temperatures also showed increases in corticosterone secretion, which is associated with both energy mobilisation (for thermoregulation) and stress (Lobato et al., 2008). Increases in nest temperature can also improve success by reducing the energetic demands on the parents when providing food for the chicks and brooding eggs and chicks, enabling greater investment later in the nestling stage (Reid et al., 2000). In particular, higher nest temperatures during the incubation phase allow adults more time to forage and maintain condition, as eggs do not cool as quickly (Hepp et al., 2015).

For very young birds, environmental temperatures are particularly influential before their thermoregulatory capacity has developed. O'Connor (1975a) demonstrated that the thermolytic capacity (the ability to dissipate heat from the body) of young nestlings, including those of Barn Swallows *Hirundo rustica* and House Martins *Delichon urbicum*, develops earlier than their thermogenic capacity (the ability to generate heat), suggesting that chicks might be more resilient to higher temperatures than to lower ones. He also found that the chicks' thermoneutral zone (the ambient temperatures at which they are able to maintain body temperature without resorting to evaporative cooling) increases systematically with age, demonstrating an increasing tolerance of higher temperatures during development (O'Connor, 1975b). Moreover, House Martin chicks develop their thermoregulatory capacity earlier than do Blue Tits *Parus caeruleus* or House Sparrows *Passer domesticus*, via higher rates of fat deposition and earlier feather emergence (O'Connor, 1975a). This early development enables House Martin chicks to survive longer foraging trips made by their parents in times of food shortage (O'Connor, 1978).

However, negative impacts of higher temperatures have been demonstrated in a number of species. High environmental temperatures lead to reduced provisioning rates by adults and direct physiological costs to Common Fiscal *Lanius collaris* chicks, leading to reduced growth rates (Cunningham et al., 2013b). High nest temperatures also negatively impact nestling growth, condition and survival of Spotless Starling *Sturnus unicolor* chicks (Salaberria et al., 2014). In nests of Eastern Kingbirds *Tyrannus tyrannus* exposed to direct sun, the nestlings lose mass on hot days (Murphy, 1985).

High temperatures can have a negative impact in themselves, but they can also be associated with exposure to highly variable temperatures and it may be this variation that affects the birds. Blue Swallows *Hirundo atrocaerulea* select nesting sites which offer temperature regimes more stable than ambient temperatures (Wakelin et al., 2013), presumably to reduce the range of temperatures to which chicks are exposed before their thermoregulatory capacity is fully developed, and to minimise the energetic trade-off between growth and thermoregulation (Dawson et al., 2005). Blue Swallows, like White-tailed Swallows, have a narrow geographical range and a limited climatic distribution, and Wakelin et al. (2013) suggest that the species may be strongly influenced by microclimate. However, there has been no investigation of the impact of temperature regime on Blue Swallow breeding success. In extreme cases, climatic variation can lead to near total breeding failure (Bolger et al., 2004).

The effects of environmental stressors on development can also have delayed impacts. McCarty (2001) found that fledgling mass of Tree Swallows *Tachycineta bicolor* is not affected by short periods of delayed growth, but return rates in subsequent years are affected, suggesting a negative effect on post-fledging survival. Temperature during the nestling period can also be an important predictor of post-fledging survival (Greño et al., 2008). An impact of environmental conditions on breeding success may not, therefore, be detected within the breeding season itself (Hepp et al., 2015). These environmental factors may affect chick growth and survival either directly, by impacting the chicks themselves, or indirectly, by impacting the adults’ ability to care for their offspring.

A number of factors other than temperature are known to affect the growth rate and survival of chicks, such as the timing of egg-laying or hatching within a season, clutch size and the presence of hatching asynchrony (Bryant, 1978; Zach, 1982). Such effects can be subtle and varied. Timing can affect the food supply, which in Tree Swallows correlates with growth rates (McCarty, 2001). Alternatively, earlier breeders may lay better quality eggs, which hatch heavier chicks; and differences in hatchling weight are a strong predictor of survival in House Martins (Bryant, 1978). Hatching asynchrony in Tree Swallows leads to more young fledging, but a decreased chance of the youngest chicks surviving (Zach, 1982).

The impacts of any of these factors on nestlings can be manifest in a number of different ways, from weight gain to primary feather growth (Cunningham et al., 2013b; Salaberria et al., 2014), and survival to fledging to first-year post-fledging survival (Dawson et al., 2005; McCarty, 2001). Effects on nestling performance, such as growth rate, do not necessarily correlate well with other effects such as those on survival (Zach and Mayoh, 1982), suggesting that which aspects of growth and survival are protected from environmental influences, and which remain labile under sub-optimal environmental conditions may vary between species.

Previous work studying the growth of young birds found that the logistic function provides a better fit than other growth functions for weight gain in altricial birds (O’Connor, 1984; Ricklefs, 1979, 1973), because of their faster growth rate when compared to precocial birds (Ricklefs, 1984, 1973). Specifically, logistic curves provide the best fit for Tree Swallow *Tachycineta bicolor* weight (Zach and Mayoh, 1982).

Ricklefs (1979) suggested that early maturation, rather than weight gain, is most strongly influenced by natural selection. The early development of thermoregulatory capacity, via fat deposition, is also important for hirundine chicks to survive longer foraging trips by their parents (O’Connor, 1978). Whilst weight gain may be prioritised under environmental stress, this may result in primary feather growth being detrimentally affected. The Gompertz growth equation provides the best fit for Tree Swallow *Tachycineta bicolor* primary feather growth (Zach and Mayoh, 1982).

The nesting behaviour of the White-tailed Swallow was described by Bladon et al. (2015), the key finding being the importance of traditional village huts as a nesting location (Bladon et al., 2015). A number of hirundine species, including four in the genus *Hirundo*, occupy larger ranges that entirely overlap that of the White-tailed Swallow (Redman et al., 2009). Of these, the most abundant in the Yabello region is the Ethiopian Swallow *Hirundo aethiopica* (BirdLife International, 2016c), which occupies similar habitat to the White-tailed Swallow (Turner, 2004), associates with people (Ash and Atkins, 2009), and builds similar open-cup nests in village huts (Bladon et al., 2015; Fry et al., 1992).

Ethiopian Swallow nesting behaviour has been previously described in Kenya, where most records come from large, substantial buildings. Its nest is up to 100mm wide, 80mm deep and 130mm high, lined with rootlets, dry grass, hairs and feathers. The eggs are white, tinged faintly pink, with chestnut blotches, and clutch size ranges from one to four eggs. One egg is laid per day, before the female begins a 14-day incubation period. Fledging is recorded at 21 and 25 days, with the young often continuing to roost at the nest for a further week (Grant and Lewis, 1984). The nest is re-lined before the second brood is laid, and it is known to breed twice, or occasionally three times, per season as is common in swallows (Grant and Lewis, 1984; Turner, 2004). In Ethiopia, nesting has been recorded in buildings and trees, under bridges, and down wells. Sixteen previous Ethiopian nest records come from all months between April and October (Ash and Atkins, 2009).

In this chapter, I investigate some of the potential mechanisms by which the climatic range-restriction of the White-tailed Swallow may occur. I examine effects of temperature on nestling survival and also on nestling growth rates, which provide an accessible indicator of chick performance (McCarty and Winkler, 1999b). The comparable nesting locations and wider geographical range of the Ethiopian Swallow (BirdLife International, 2016c, 2016b), make it an ideal control species for studying factors affecting the breeding success of the White-tailed Swallow.

7.2 Methods

7.2.1 Finding and recording nests

Villages across the north-west of the White-tailed Swallow's range were searched for swallow nests. Villagers were asked whether they had swallows ("*raaree*") nesting in their huts (Figure 2.21 and Figure 2.22), and all nests of White-tailed or Ethiopian Swallows were recorded. Local people do not distinguish between swallow species, so the word "*raaree*" did not bias sampling. Using roads as transects, an effort was made to find nests along transects running from within to outside the range, and to find Ethiopian Swallows nesting beyond the limit of the White-tailed Swallow's distribution.

An iButton (Maxim Integrated, DS1921G-F5) was left on the ceiling joist next to each nest to measure nest temperature, and a second unit was left to record ambient temperature in a nearby tree, in a comparable location to those used for transects, as described in Section 3.5.1. iButtons were left recording from the time the nest was found until after the chicks had fledged or died.

The lining and contents of each nest were recorded and photographed. Empty nests, and those containing eggs, were revisited weekly until an estimated laying or hatching date was determined from changes in the number of eggs, and each nest was visited as soon as possible after hatching. Nests with chicks were revisited every two to seven days to record progress, with extra visits focussed on nests where the exact hatching date, and therefore chick age, was known, to aid calibration of age estimates at all other nests. Feather growth on the femoral, caudal, dorsal, tail, primary, nape, crown and breast tracts were recorded with reference to Fernaz et al. (2012) as well as whether the eyes and ears were open or closed, to aid post-hoc age estimation (Section 7.2.2).

Once the chicks' eyes were visibly open, at around seven days of age (Fernaz et al., 2012), chicks were deemed safe to handle. On subsequent visits, the brood was removed from the nest and chicks were individually inspected for feather growth, weighed using a plastic cone attached to a Pesola balance, and the growth of the 9th primary (total length and emerged length) was measured. Standard photographs of the head, spread wing, belly and tail of each chick were taken. Chicks were uniquely marked using a permanent black marker on one or both legs before the whole brood was replaced in the nest. Broods were not handled once projected total 9th primary length for any chick was over 54mm for White-tailed Swallow and 58mm for Ethiopian Swallow, to avoid the risk of chicks 'exploding' from the nest (i.e. leaving the nest prematurely). Nests were revisited until found empty, at which point villagers were asked about when the chicks had fledged.

7.2.2 Estimating chick ages

After the completion of fieldwork, photographs of the broods were inspected in detail. Beginning with broods apparently seen within the first two days of hatching, based upon size and development and, with reference to Fernaz et al. (2012), the age of each brood was estimated based on known laying dates and the appearance of the chicks the first time they were seen. For the first two days after hatching, White-tailed and

Ethiopian Swallow broods were considered together, but descriptions of their respective growth patterns thereafter are provided in Section 7.3.1.

Chicks with wet, clumped down, heads bent over and very small gapes were regarded as having hatched that day, and these birds often appeared to have some orange colour still in the femur/stomach. Those with drying down were regarded as being later on the day of hatching or one day old. By one day old, the gape had widened noticeably.

On the second day, chicks appeared completely naked but for dark, visible stippling under the skin of the wing, where the primary feathers would appear (Fernaz et al., 2012), and the gape was thicker. This was supported by anecdotal evidence that the egg shells had fallen out of one nest two days before the chicks were observed; without this information the estimate may have remained as one day old, but the key difference between this and other nests (where the beak was not visible) was the appearance of the primary stipples.

Some evidence suggested that eggs do not always hatch on the same day (Schmidt, 1959). Four nests (two of each species) were observed with fewer than the eventual total number of chicks hatched, and in another brood there was a striking difference in age between the two chicks. Therefore, when there was an obvious difference in age between the chicks the first time a brood was seen, two hatching dates were assigned. In all but one case this occurred within the first two days after hatching. A number of other nests showed no obvious difference between chicks when they were first seen, but later had one chick that was consistently less developed, and quite possibly a day younger, than the others. However, these broods were only assigned a single hatching date for two reasons. First, this variation later in development may be caused by differences in growth rate, not hatching date, especially given the lack of variation on earlier visits. Second, in some nests the difference between chicks became blurred again, because the smaller chicks “caught up” and the leg markings became indistinct. The fact that this uncertainty arose suggests that counting back apparent hatching dates in older chicks may be unreliable. For the purposes of age description it is therefore worth bearing in mind that in any nest one (or two) chick(s) may be a day younger than the rest of the brood, and so appear underdeveloped. Age differences within broods were subsumed in analyses of growth rate where means are taken.

7.2.3 Chick survival

I fitted binomial regression models in which the number of nestlings that (a) survived to fledging or (b) died/disappeared before fledging within a brood was the dependent variable for that brood. Five uncorrelated preliminary explanatory variables were investigated: mean maximum daily nest temperature, mean maximum daily ambient temperature (means taken across the nestling period), brood size at hatching, hatching date and species. The sample size of 29 nests meant that not all single terms and two-way interactions could be included, so I inspected plots of each variable against fledging success to select the most likely terms for inclusion in the maximal model. This suggested that there could be a quadratic effect of ambient temperature, and that the two temperature terms and hatching date had different effects on the two species. These terms, along with the two brood size by temperature interactions, were fitted in a maximal model.

The model was over-fitted, so to further investigate the likely importance of each term, I fitted all possible models from within the maximal model using the '*dredge*' function (Barton, 2015) in R (R Core Team, 2016), and compared them using AIC_c. Comparison of all models within four AIC_c points of the minimum AIC_c model suggested that ambient temperature and its quadratic term were the most important variables (included in all models), whilst the least important term was nest temperature (Table A2). Additionally, combining data from the two species required interactions containing the species term, which added complexity to the model, so I decided to fit models for the two species separately.

I fitted new maximal models containing three single terms (ambient temperature, brood size and hatching date) and a quadratic effect of ambient temperature to data for each species. Model selection was carried out by successively removing non-significant terms, and comparing models using a likelihood-ratio test (Crawley, 2005).

The age of some nests was known, either because the nest had been found during construction (and therefore was known to be in its first year), or because villagers reported that the birds had used the nest before. This was often corroborated by the blackened appearance of the nest (Bladon et al., 2015). To test whether nest age affected the timing of breeding, I performed a Welch Two Sample *t*-test on the White-tailed Swallow nest hatching dates, grouping nests as “First year” and “Later year”.

7.2.4 Weight gain

Model form

I fitted logistic growth curves to chick weight data by non-linear least-squares regression, using the logistic equation: $W_t = \frac{A}{1 + (A/W_0 - 1) * e^{(K * t)}}$

where: W_t = weight at age t

A = asymptotic weight

W_0 = the weight at t = 0

K = a constant proportional to the overall growth rate

t = age of the brood, in days since hatching

The influences of four factors (temperature experienced at the nest, brood size, hatching date and ambient temperature) on growth rate were investigated by fitting K as:

$$K = v_0 + v_1 * Nest.T + v_2 * Brood + v_3 * Hatch + v_4 * Ambient.T$$

where: $Nest.T$ = a function of the temperature experienced at the nest

$Brood$ = a function of the brood size of the nest

$Hatch$ = the date on which the brood hatched

$Ambient.T$ = a function of ambient temperature

v_0, v_1, v_2, v_3 and v_4 = constants

Since it was not safe to handle very small chicks, data were only collected from day six onwards. It was therefore necessary to obtain an independent estimate of the starting weight of the chicks, which was not estimated from the data. The value of W_0 was fixed, using the fresh weight of Pearl-breasted Swallow *Hirundo dimidiata* (1.4g) and Ethiopian Swallow (1.7g) eggs (Schoenwetter, 1969) and the conversion rate for fresh egg weight to chick hatching weight (0.73) for Great Tits (Schifferli, 1973). This gave values for chick weight at hatching (W_0) of 1.022g (White-tailed Swallow) and 1.241g (Ethiopian Swallow).

The final equation used was therefore:

$$W_t = \frac{A}{(1 + (A/W_0 - 1) * exp\,(v_0 * t + v_1 * (Sum.T/2) + v_2 * Sum.Br + v_3 * Hatch + v_4 * Sum.Amb))}$$

where: $W_t =$ weight at age t

A = asymptotic weight

W_0 = weight at hatching, 1.022g or 1.241g

t = age of the brood, in days since hatching

$Sum.T$ = sum of maximum temperatures on each half day experienced at the nest since hatching

$Sum.Br$ = sum of brood size on each day since hatching

$Hatch$ = date on which the brood hatched

$Sum.Amb$ = sum of maximum ambient temperatures on each half day since hatching

Where brood size changed between visits (i.e. when chicks died), it was assumed that this had occurred half-way between the two visits.

Data truncation

Nestling birds, and in particular hirundines, grow to weights beyond their final adult weight before undergoing a period of weight recession prior to fledging (O’Connor, 1977; Ricklefs, 1968). In order to fit a logistic growth curve to weight data, it is therefore necessary to truncate the dataset at an age which best estimates the maximum weights of the broods. The logistic model given above was fitted (using the ‘*gnls*’ function (Pinheiro et al., 2007) in R (R Core Team, 2016)) to datasets truncated at each half day from 12.0 to 16.0 days, as from visual inspection of the data these ranges included the maximum recorded weight for every brood. Lower truncation ages were excluded to avoid unnecessarily reducing the dataset on which comparisons could be made. The models were compared by calculating the residual sum of squares (RSS) for each model on the data points which were included in all models (i.e. up to 12.0 days only), with the lowest RSS value being preferred. The asymptote estimate for each model was checked to ensure that it was within a sensible range given the raw data.

Truncation of the White-tailed Swallow data at 12.0 days gave the lowest RSS value, but there was a local minimum at 13.0 days. Inspection of the data suggested that weight did not decrease from 12.0 to 13.0 days, so 13.0 days was chosen as it retained more data. Maximal fixed effects models with different random effects structures were fitted to the 13.0 day data, and the minimum AIC_c was given by the model with a random effect of nest fitted on the asymptote.

Truncation of the Ethiopian Swallow data at 12.0 days gave the lowest RSS value, but visual assessment of the data showed that weights were still increasing past this point. A local minimum RSS occurred at 15.0 days, which also better matched the apparent maximum weights attained, and produced a more sensible asymptote, therefore 15.0 days was chosen for truncation. Maximal models were fitted to the 15.0 day data with different random effects structures. The model with a random coefficient of nest fitted on age provided the best fit to the data.

7.2.5 Ninth primary growth

Model form

I fitted Gompertz growth curves to chick weight data by non-linear least-squares regression, using the Gompertz equation:

$$L_t = A * exp\,(-b * exp\,(-(K * t)\,)\,)$$

where: L_t = total length of the 9th primary at age t

A = asymptotic 9th primary length

b = the feather length at t = 0, as a proportion of A

K = a constant proportional to the overall growth rate

t = age of the brood, in days since hatching

The influences of four factors (temperature experienced at the nest, brood size, hatching date and ambient temperature) on feather growth rate were investigated by fitting K as:

$$K = v_0 + v_1 * Nest.T + v_2 * Brood + v_3 * Hatch + v_4 * Ambient.T$$

where: $Nest.T$ = a function of the temperature experienced at the nest

$Brood$ = a function of the brood size of the nest

$Hatch$ = the hatching date of the nest

$Ambient.T$ = a function of ambient temperature

v_0, v_1, v_2, v_3 and v_4 = constants

Since swallows' feathers do not finish growing until after fledging, it was not possible to obtain data right up to the asymptotic feather length. This makes feather length model fitting less reliable than weight modelling (Zach and Mayoh, 1982). To constrain model fitting, it was therefore necessary to obtain an independent estimate of the asymptotic feather length, which was not estimated from the data. The value of A was fixed for White-tailed Swallows, using the mean 9th primary length of the specimens kept at the Natural History Museum's collection in Tring, 7.9cm (n = 9).

The final equation used was therefore:

$$L_t = A * exp\,(-b * exp\,(-(v_0 * t + v_1 * (Sum.T/2) + v_2 * Sum.Br + v_3 * Hatch + v_4 * Sum.Amb)\,)\,)$$

where: L_t = total length of the 9th primary at age t

A = asymptotic 9th primary length, 7.9cm

b = the feather length at t = 0, as a proportion of A

t = age of the brood, in days since hatching

$Sum.T$ = sum of maximum temperatures on each half day experienced at the nest since hatching

$Sum.Br$ = sum of brood size on each day since hatching

$Hatch$ = date on which the brood hatched

$Sum.Amb$ = sum of maximum ambient temperatures on each half day since hatching

Where brood size changed between visits (i.e. when chicks died), it was assumed that this had occurred half-way in between the two visits.

Model selection

As multiple visits were made to each nest to record chick weight and primary length, it was necessary to control for repeated measures on each nest. The following procedure was conducted for both weight gain and primary growth models. Using the '*nlme*' function (Pinheiro et al., 2007) in R (R Core Team, 2016), I fitted models with a random coefficient of 'Nest' on each parameter (given in the equations above) in turn, as well as on each combination of parameters up to a maximum of three. All models were fitted by maximum likelihood (ML), as restricted maximum likelihood (REML) does not make sense for non-linear mixed effects models (Bates, 2009). ML also allows fixed effects to be compared by likelihood-ratio tests, whereas REML does not (Gurka, 2006). To assess the most appropriate random effects structure, the AIC_c values for each model were compared and the model with minimum AIC_c selected (Burnham and Anderson, 2002; Zuur et al., 2009). Models with random effects structures that failed to converge were considered to be over-parameterised, and were left out from this analysis (Sofaer et al., 2013). Once the most suitable random effect structure had been selected, model simplification was conducted. Fixed effect terms were sequentially removed from the maximal model, and their significance tested using likelihood-ratio tests. The predicted growth curves arising from the minimal and maximal selected model were compared with model-averaged predictions across all fitted random effects structures (Burnham and Anderson, 2002).

7.2.6 Nest and ambient temperatures

To test whether White-tailed Swallow nests experience higher temperatures than Ethiopian Swallow nests, I conducted a two-sided Welch two-sample *t*-test on the mean maximum nest temperatures from the two species' nests.

To investigate whether there was any change in environment through the breeding season, I used the maximum recorded ambient temperatures on each day from my standardised tree locations (Section 3.5) to assess how external temperatures varied over the brooding and fledging period.

First, I fitted a simple linear regression using temperature data from April to June 2014, at sites where the breeding study was conducted, with date fitted as a continuous variable. I then repeated the analysis using data from both 2013 and 2014, and from all sites from which I had collected data between April and June. I did not include data from 2015, because there were no data after early May. To account for differences between years, I fitted a maximal model with effects of year, date and a quadratic effect of date, and the interactions between year and date, and year and the quadratic term.

7.3 Results

In total, 28 White-tailed Swallow and 10 Ethiopian Swallow nests were found across the north-west of the White-tailed Swallow's known range. Despite a good deal of searching, no Ethiopian Swallow nests were found outside of the White-tailed Swallow's reported breeding range along roads to the north and west. However, four White-tailed Swallow nests were found outside their previously known breeding range, close to the edge of the area of modelled climatic suitability (Chapter 6). Most nests were found prior to laying, or with eggs, giving good coverage of the entire breeding cycle. Five of the White-tailed Swallow nests proved not to be active, and of the remaining 23, four failed to fledge any chicks. One of the Ethiopian Swallow nests was destroyed by children, but the adults rebuilt and the new nest was recorded. The failed attempt was not included in analyses. One nest failed to hatch, but the other nine all fledged at least one chick.

7.3.1 Comparison of chick development

I studied the physiology of White-tailed and Ethiopian Swallow chicks on each day of growth from hatching to fledging. Details for both species at 0 and 1 day old are presented in Section 7.2.2, and descriptions thereafter are provided in Table 7.1. A summary of the raw data is presented in Table A3.

Table 7.1: Comparison of the growth patterns of White-tailed and Ethiopian Swallow broods on each day after hatching.

Day	White-tailed Swallow	Ethiopian Swallow
0-1	See Section 7.2.2.	See Section 7.2.2.
2	Naked apart from darkening on wings where primaries, and in some chicks secondaries, will appear. Stippling on the dorsal tract and tail is visible in a couple of chicks, and the ear sometimes begins to form a depression. The gape is thicker, and the egg tooth is still visible.	Chicks still appear completely naked though slightly bigger.
3	Wings: Primary pins are just breaking. Visible stippling elsewhere on the wing. Body: Visible stippling on dorsal tract and tail. Slight stippling on the femoral tract and crown of some chicks. Ears: Each forms a depression, and is open properly in some chicks. Beak: Gape has noticeably widened again. Egg tooth has disappeared.	Wings: One chick had primary and secondary pins emerging; wings dark with stippling in others. Body: Femoral pins beginning to emerge on most chicks. Stippling on the dorsal tracts in most chicks, and on the crown and face in some. Ears: One chick had the ears open, but they formed a depression in other chicks.
4	Wings: Primary pins emerged, secondaries are emerging in some chicks. Body: Dorsal tract is distinct or emerging. Femoral tract or tail may be in pin. In some chicks, the crown and face also have visible stippling. Ears: Open. Beak: Gape slightly larger than three days, but not enough so to be used for ageing if otherwise unknown.	Only one chick seen. Wings: Primaries and secondaries in pin. Body: Femoral tracts in pin. Some stippling on the nape. Ears: Depression
5	Wings: Primaries and secondaries in pin Body: Dorsal and femoral tracts emerging. Tail in pin or visible. Head: Face in pin or visible. Crown and nape visible. Eyes: One chick opened slightly when begging.	Wings: Primaries and secondaries in pin. Body: Femoral tracts in pin, stippling on dorsal tract. In one well advanced brood the dorsal tract was in pin and all the other pins were longer. Head: Stippling is obvious on the crown, nape and face. Ears: Open.

6	Body: Chicks appear darker. Two more advanced chicks had noticeably longer dorsal and tail pins (white is appearing on them), and the femoral tract unsheathing. Head: Face in pin in all and the crown in most chicks. Eyes: Closed, except in a single chick.	Body: Dorsal and tail pins have emerged. Head: Face is beginning to pin. Eyes: Open slightly when begging.
7	Body: Dorsal and femoral tracts are unsheathing in some chicks, body more covered in pins. Head: Nape and crown nearly fully in pin. Eyes: Open when begging.	Wings: Primary and secondary pins about to emerge. Body: Femoral tracts unsheathing in some chicks. Dorsal pins about to emerge. Tail in pin. Overall impression is a much greater coverage of pins. Head: Crown and face in pin in about two thirds and nape in half of chicks. Eyes: Slightly open in one brood.
8	Wings: Beginning to unsheathe in one brood. Body: Femoral tracts unsheathed, and some caudal, dorsal and tail tracts are unsheathing. White pins on the breast form two distinct tracts, and were unsheathing in one brood. Head: Nape and crown in pin. Eyes: Mostly open	Wings: About to unsheathe, secondary coverts have started to. Body: Femoral and caudal tracts unsheathed. Pins on the breast form two white tracks down either side. Head: Nape, crown and face are all in pin. Eyes: Open.
9	Wings: Unsheathing in most chicks, especially primaries. Body: Femoral and breast tracts are near fully unsheathed. All other feathers are unsheathing. Head: Nape unsheathing in some chicks.	All feathers have started to unsheathe except on the crown and face, and black feathers are beginning to cover the gap in the breast. The flanks appear very fluffy.
10	Wings: Unsheathed Body: Unsheathed Head: Nape, and to a lesser extent crown, beginning to unsheathe in some chicks. Face in pin.	Head: Red appearing in forecrown pins (Redman et al., 2009). Crown starting to unsheathe in some chicks. Nape unsheathing in some chicks. Face is in pin.
11	Body: Top of the breast is feathered all the way across. Head: Nape and crown feathers are emerging in two thirds of chicks. Face only unsheathing in one chick.	Body: Feathers cover nearly all the way across the top of the breast, but a wedge of bare skin remains on the belly. Head: Crown unsheathing in about 50% of chicks. Nape still in pin in some. Face in pin.

		Huge variation between and within broods.
12	Body: Thin strip of bare skin remaining down the breast, with a bulge at the belly. Head: Nape and crown feathered, face unsheathing in two thirds of chicks.	Only a single chick seen. Body: Strip of bare skin on the belly Head: Crown unsheathed. Pins remain only on the face.
13	Fully feathered except for the belly, some pins still visible on the back, wings and face.	Head: Face unsheathing in one chick. Body: Thin strip remains uncovered on the belly.
14	Wings: Still noticeable gaps. Body: A thin slither of belly remains feather free. Head: Still some pins visible on the face.	Wings: Primaries nearly complete in some broods. Head: Face unsheathing. Body: Small patch of skin on the belly and a thin strip of dark feathers up the breast. Larger patches remain on chicks with less developed wings.
15	Wings: Primaries complete in most chicks. Body: Belly almost covered. White is now visible on the tail in some chicks (Bladon et al., 2015; Redman et al., 2009), paralleling wing development. Head: A few pins remain above the beak and in front of the eye.	Wings: Nearly complete. Body: Small patch of belly remains bare. Tail feather sheathes still obvious in one brood, though the white patches are appearing (Redman et al., 2009). Head: Pins remain only in front of the eyes.
16	Breast and wing fully feathered in some chicks, secondaries still have some gaps in others.	Development of one brood appeared complete. White patches obvious in the tails of two chicks. One chick still had some gaps in its secondaries. The breast was fully covered.
17	Feathering complete in some broods, a few pins remain in front of the eye and slight gaps in wing of others. Care should be taken when handling, as chicks are restless. Two broods fledged.	Some pins remain on the face. Some chicks had white patches in the tail.
18	Development seems complete, some broods judged too big to handle. Breast fully feathered in all chicks. Two chicks fledged.	White patches on the tail visible in all chicks. One brood was deemed too large to handle.
19	Development complete. Too large to handle. Five broods fledged.	No nests seen.
20	Seven broods fledged.	Too large to handle. Two broods fledged.

21	Three broods fledged.	Four broods fledged (inc. three seen flying in and around their nest hut).
22	No broods left.	Three broods fledged.

7.3.2 Chick survival

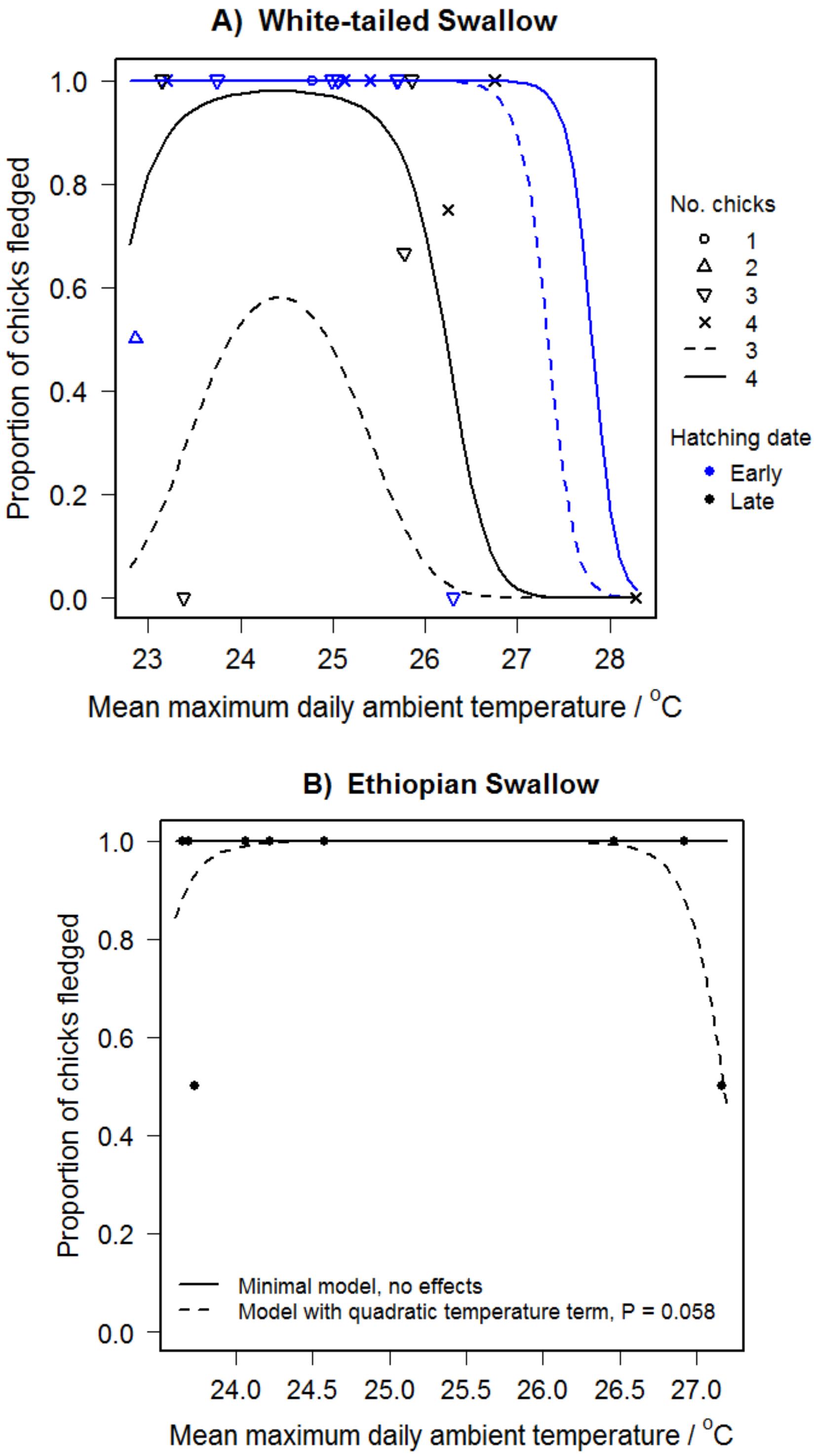
Ambient temperature had a quadratic effect on White-tailed Swallow fledging success (deviance = 9.72, d.f. = 2, P = 0.008), with survival increasing at low temperatures, but decreasing at higher temperatures. Fledging success was higher from larger broods (deviance = 8.73, d.f. = 1, P = 0.003). Broods which hatched later had lower fledging success (deviance = 10.79, d.f. = 1, P = 0.001) (Figure 7.1, *A*).

The smaller sample size for the Ethiopian Swallow meant that hatching date could not be included, but results from preliminary models with both species suggested that hatching date had no effect on Ethiopian Swallow chick survival. The model with temperature squared and brood size still failed to converge, so I fitted the two simpler models (brood size and temperature, and temperature and temperature squared). Both favoured reduction to a model containing temperature alone, which had no effect on fledging success. However, the quadratic temperature term was close to significance (deviance = 5.69, d.f. = 2, P = 0.058), suggesting that temperature may also have a quadratic effect on Ethiopian Swallow success (Figure 7.1, *B*). White-tailed Swallows had lower fledging success than Ethiopian Swallows, although the difference arose because of the late season rather than early season nests (Table 7.2).

Table 7.2: Summary of swallow brood hatching and fledging success. Differences in the number of broods arose because some nests were not seen at the egg stage, and others failed to hatch any chicks.

		Mean ± S.D. (*n*)			
Species	**Hatching month**	**Eggs per clutch**	**Percent hatched**	**Chicks per brood**	**Percent fledged**
White-tailed	All	3.53 ± 0.51 (*19*)	86 ± 22 (*19*)	3.09 ± 0.83 (*21*)	80 ± 37 (*20*)
Ethiopian	All	3.00 ± 1.25 (*10*)	85 ± 34 (*10*)	2.70 ± 1.42 (*10*)	89 ± 22 (*9*)
White-tailed	April	3.53 ± 0.52 (*15*)	82 ± 23 (*15*)	3.00 ± 0.87 (*17*)	91 ± 27 (*16*)
Ethiopian	April	3.00 ± 1.55 (*6*)	75 ± 42 (*6*)	2.50 ± 1.76 (*6*)	90 ± 22 (*5*)
White-tailed	May	3.50 ± 0.58 (*4*)	100 ± 0 (*4*)	3.50 ± 0.58 (*4*)	35 ± 41 (*4*)
Ethiopian	May/June	3.00 ± 0.82 (*4*)	100 ± 0 (*4*)	3.00 ± 0.82 (*4*)	88 ± 25 (*4*)

Figure 7.1: The response of proportion of chicks fledged to ambient temperature, brood size and hatching date for *A*) White-tailed and *B*) Ethiopian Swallow broods. Points show data for individual nests. Lines show predicted responses in *A*) for broods of different sizes and with early vs. late hatching dates, and in *B*) for the models with and without ambient temperature retained.



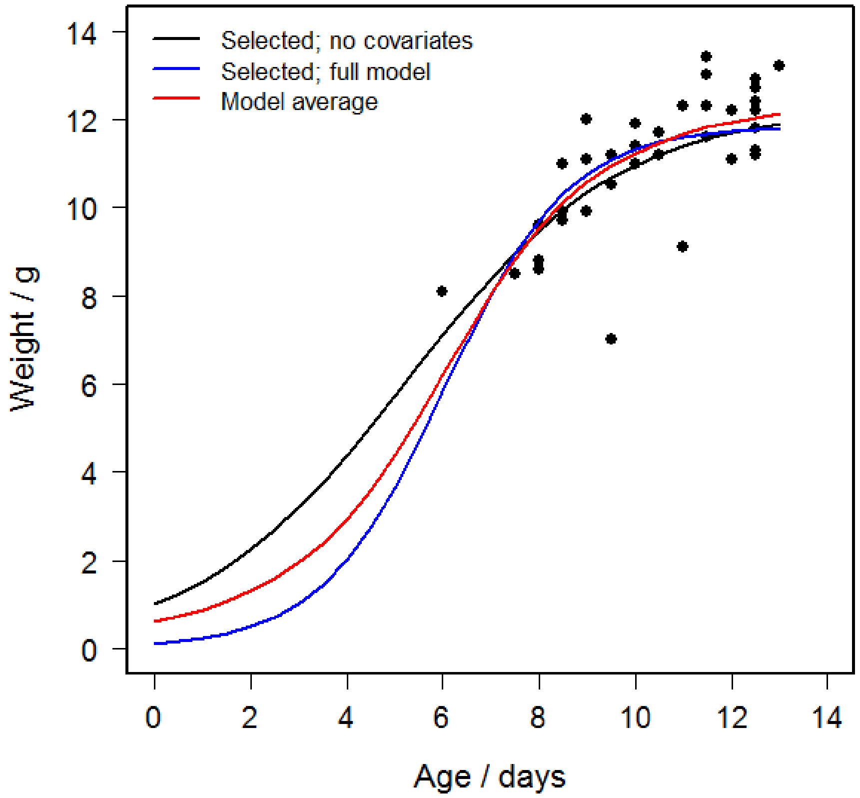
White-tailed Swallow chicks hatched significantly earlier in older than first-year nests (t = 3.87, d.f. = 21.0, P < 0.001), even when the data were restricted to only include nests for which I was certain of their age grouping (t = 5.24, d.f. = 2.4, P = 0.024).

7.3.3 Weight gain

White-tailed Swallow

There were no effects of covariates on White-tailed Swallow chick weight gain. Inspection of the diagnostic plots indicated that the assumptions of normality of errors and random effects were satisfied. Predictions from the minimal model with no covariates were broadly similar to those from the maximal model, and the model averaged predictions across all fitted random effects models (Figure 7.2).

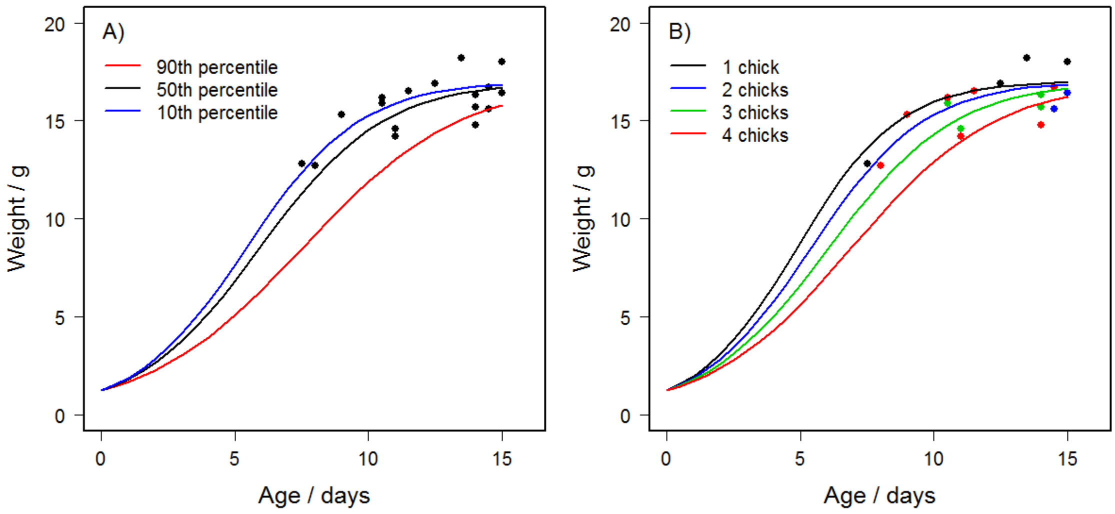
Figure 7.2: White-tailed Swallow weight gain predictions from models fitted with the selected random effects structure (random effect of nest on the asymptote) with all (blue) and no (black) covariates, and the model averaged predictions across all fitted random effects structures (red). Points show data for brood means.



Ethiopian Swallow

There was a negative effect of both nest temperature (likelihood-ratio = 6.58, d.f. = 1, P = 0.010) and brood size (likelihood-ratio = 6.97, d.f. = 1, P = 0.008) on Ethiopian Swallow chick weight gain (Figure 7.3). Inspection of the diagnostic plots indicated that the assumptions of normality of errors and random effects were satisfied.

Figure 7.3: The response of Ethiopian Swallow weight gain to variation in *A*) nest temperature and *B*) brood size. Points show data for brood means. Lines show predicted growth curves from the minimal model, with a random effect of nest on age, for broods *A*) experiencing different temperature regimes and *B*) of different sizes.



7.3.4 Ninth primary growth

White-tailed Swallow

An initial model was fitted with no random effects, with nest temperature, brood size and hatching date as covariates, and with all parameters estimated. This model estimated the asymptote as 7.3cm, below the mean length of 7.9cm measured from adult specimens (*n* = 9). I therefore tried fixing the value of the asymptote at 7.9cm in the random effects models.

However, models fitted with random effects and with the asymptote fixed appeared to be over-constrained, as there was little or no variation in each of the parameter estimates, and the values of AIC and log-likelihood were identical between a number of models. To test whether this was an effect of fixing the asymptote, or the chosen fixing value, I re-fitted the models with asymptote fixed at the maximum recorded 9th primary length, 6.2cm. However, this produced the same problem, with most AIC and log-likelihood estimates being identical. It was therefore necessary to fit the models with the asymptote estimated instead.

The model with a random coefficient of nest fitted on nest temperature produced the minimum AIC_c value. However, three other models were all within two AIC_c points of this model, so I compared their predictions graphically. All were similar, so I used the model with minimum AIC_c for fixed effects simplification.

There were no covariate effects on the 9th primary growth of White-tailed Swallow chicks. The nest temperature term had to be retained in the model due to its presence in the random effects structure, but it was not significant. Inspection of the diagnostic plots indicated that the assumptions of normality of errors and random effects were satisfied. The asymptote estimate arising from the selected model was 7.51cm, which was still smaller than 7.9cm, the mean length of the Natural History Museum specimens. Under-estimation of the asymptote is a common problem when fitting growth curves to feather lengths, since data for primary lengths post-fledging are rarely available (Zach and Mayoh, 1982). Predictions from the minimal and maximal models, and the model-averaged predictions were nearly identical (Figure 7.4).

Ethiopian Swallow

The model with a random effect of nest fitted on brood size had the smallest AIC_c value, and this was used for fixed effects selection. Fixing of the asymptote was not tried for these data, to keep the models comparable with those for White-tailed Swallow. There was a negative effect of hatching date on Ethiopian Swallow chick 9th primary growth (likelihood-ratio = 4.98, d.f. = 1, $P = 0.026$; Figure 7.5). The effect of brood size was not significant, but the term had to be retained due to its presence in the random effects structure. Inspection of the diagnostic plots indicated that the assumptions of normality of errors and random effects were satisfied. Predictions from the minimal and maximal models, and the model-averaged predictions, were nearly identical.

Figure 7.4: White-tailed Swallow 9th primary growth predictions from models fitted with the selected random effects structure (random effect of nest on the nest temperature covariate) with all (blue) and no (black) covariates, and the model averaged predictions across all fitted random effects structures (red). Points show data for brood means.

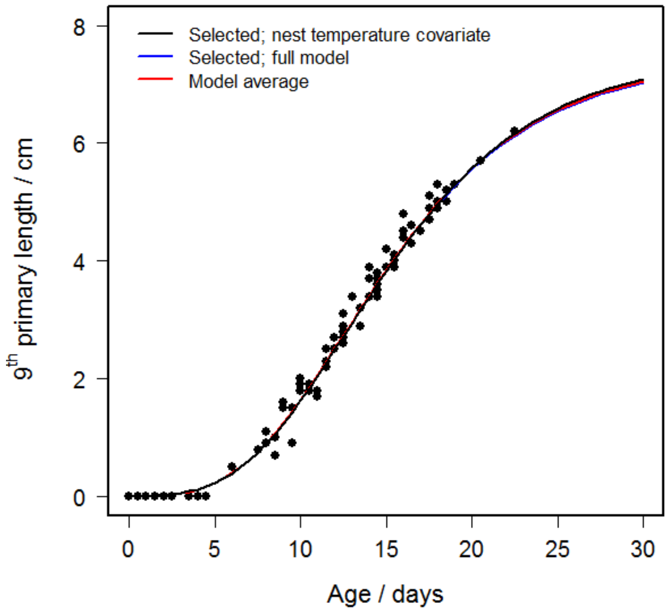
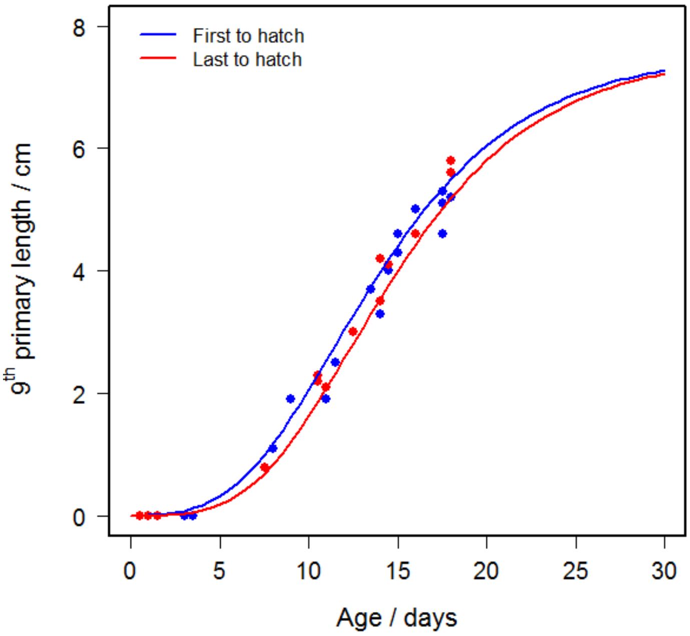


Figure 7.5: The effect of hatching date on Ethiopian Swallow chick 9th primary growth. Points show data for brood means. Lines show predicted growth curves from the minimal model, with a random effect of nest fitted on brood size, for broods which hatched earliest (blue) and latest (red) in the season.

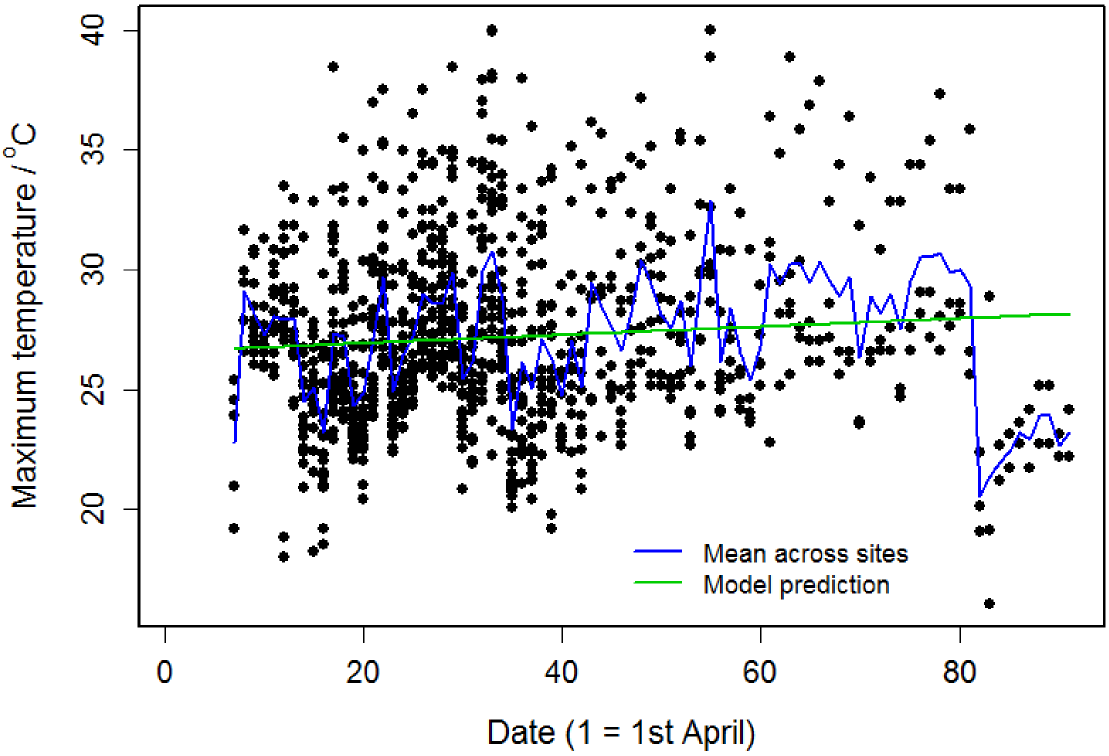


7.3.5 Nest and ambient temperatures

The mean maximum daytime temperatures recorded at White-tailed Swallow nests (mean = 28.3°C) were higher than those recorded at Ethiopian Swallow nests (mean = 25.1°C, *t* = 4.86, d.f. = 23.52, P < 0.001).

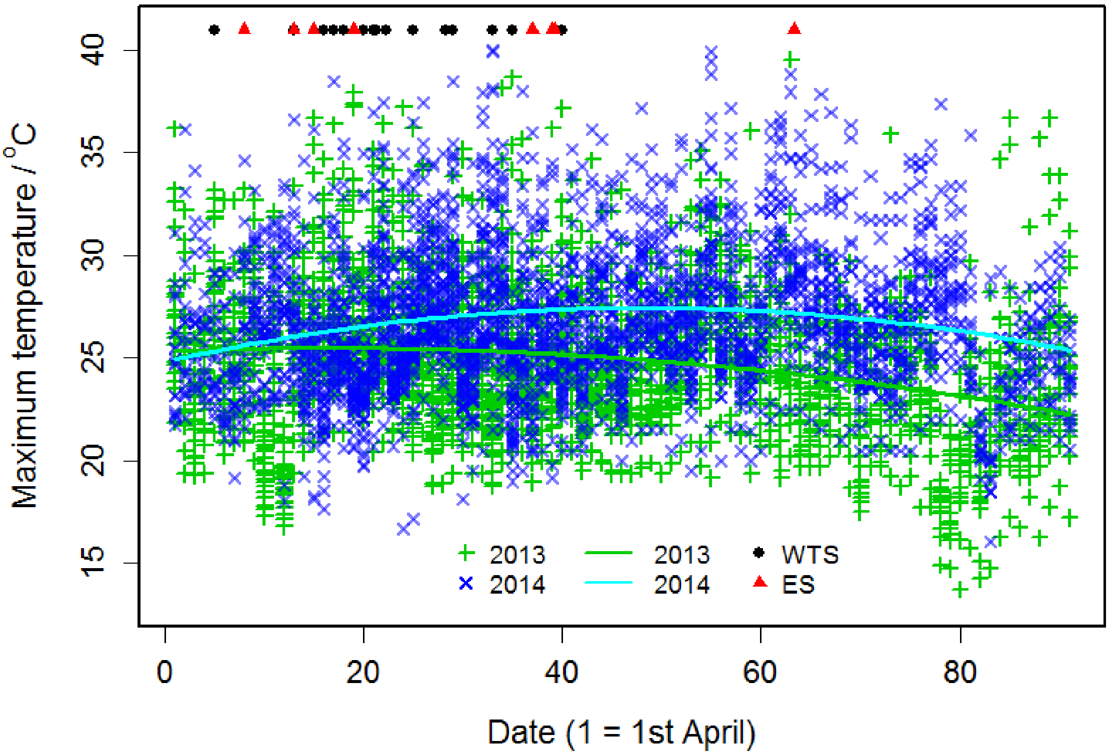
At sites in the north-west of the range in 2014, ambient temperature increased with date (F = 6.31, d.f. = 1000, P = 0.012; Figure 7.6).

Figure 7.6: Maximum daily ambient temperatures from April to June 2014, from sites in the north-west of the White-tailed Swallow's range, where the nesting study was conducted. Points show data from individual sites on each date. The blue line represents the mean maximum temperature on each day, while the green line represents the predictions of a simple linear regression of temperature on date.



The two year, all site, model found a significant interaction between year and the quadratic effect of date (F = 57.84, d.f. = 2, P < 0.0001). May and June temperatures were significantly higher in 2014 than in 2013, while temperatures in April were much more comparable between years (Figure 7.7). In 2014 temperatures appeared to peak in May, whereas in 2013 temperatures declined from April through to June.

Figure 7.7: Maximum daily ambient temperatures from April to June 2013 and 2014 from all sites. Points show data from individual sites on each date. Lines show predicted temperatures from the model, split by year. Points at the top indicate hatching dates for White-tailed Swallow (black circles) and Ethiopian Swallow (red triangles) nests.



7.4 Discussion

Hatching date was a strong predictor of White-tailed Swallow survival, with later nests having much lower fledging success. In some other species earlier breeders lay better quality eggs and therefore achieve higher fledging success due to more efficient pairing and nest building (Bryant, 1978). This is confounded by the fact that older, more experienced birds, or those in better condition, tend to breed earlier (Hepp and Kennamer, 1993; Winkler and Allen, 1996), although laying date does not necessarily affect fledging success (Stutchbury and Robertson, 1988). A negative effect of hatching date on chick growth rate is seen in Tree Swallows (McCarty and Winkler, 1999b), and this was observed in my study in the 9th primary growth of the Ethiopian Swallow, although there was no significant effect of this variable on chick survival for this species.

White-tailed Swallow nests which were built in previous years contained eggs and hatched chicks earlier than nests built in the year of study. It may be assumed that older nests are indicative of birds re-using their previous structures, and therefore nest age would be a proxy for parental age, a strong predictor of breeding time in Tree Swallows (Winkler and Allen, 1996). Alternatively, nest re-use may result from high-quality birds taking the best nesting sites, which would also be expected to result in earlier breeding and greater breeding success. In other species, removing or reducing the cost of nest building can have a positive effect on levels of parental care and subsequent nestling growth rates (Moreno et al., 2010). Differences in parental experience or quality, egg size, or allocation of resources could therefore explain the difference in chick survival between early and late White-tailed Swallow broods. However, Ethiopian Swallows did not show this reduction in survival through the season and, moreover, were recorded with second broods, which were not observed in any of the White-tailed Swallow nests (Bladon et al., 2015). This suggests that environmental conditions late in the season were no longer suitable for White-tailed Swallow breeding.

Ambient temperature had a quadratic effect on White-tailed Swallow chick survival, with chicks having increasing survival rates from low to moderate temperatures but decreasing survival rates at the highest ambient temperatures. In other species, parental provisioning rates are negatively associated with temperature (Luck, 2001), which over the course of a season could lead to negative effects on chick growth and survival. Moreover, ambient temperatures increased as the 2014 breeding season progressed, suggesting that this might have caused the reduction in White-tailed Swallow nestling survival later in the season. There was variation in temperature between the two field seasons, with higher temperatures in May and June 2014 than in 2013. This could be related to the duration of the rainy season. Unfortunately, nesting data were not collected in 2013 so breeding success is unknown.

The decline in White-tailed Swallow chick survival occurred at ambient temperatures ranging from 26–28^{o}C. This is considerably lower than the “maximum temperature of the warmest month” threshold of around 35^{o}C found in the distribution models, which is to be expected given that the breeding season falls within the cooler part of the year (Chapter 6). These two temperature measures are derived from different sources, and are therefore not directly comparable, but it is interesting to note that their predicted effects on the White-tailed Swallow occur at broadly comparable temperatures.

There was no effect of ambient temperature on White-tailed Swallow weight gain or primary growth, suggesting that the decrease in survival was not mediated through reductions in growth rate. In altricial birds, the development of features required for precocity, such as primary feather growth, is prioritised, and therefore may be preserved even under more stressful developmental conditions (Ricklefs, 1979).

There was no effect of nest temperature on White-tailed Swallow weight gain or primary feather growth. Most White-tailed Swallow nests were found in human occupied huts which contained fires (Bladon et al., 2015), and therefore temperature in the hut was probably driven mostly by human activity, rather than environmental factors. The White-tailed Swallow nests experienced higher temperatures than the Ethiopian Swallow nests, and if temperature negatively affected White-tailed Swallow chick growth, it would be expected that adult birds would select cooler nesting sites as an initial response. Alternatively, parental foraging efficiency might be negatively affected by high ambient temperatures, as I observed in Bush-crows (Chapter 5). This would necessitate extended foraging trips, and warmer huts may help to buffer eggs and nestlings against excessive cooling and its associated costs (Hepp et al., 2015). Ethiopian Swallows, on the other hand, did show a reduction in weight gain at higher nest temperatures, but this was not reflected in chick survival rates. Ethiopian Swallow nests were predominantly found in store huts which did not contain fires (Bladon et al., 2015), and were consistently cooler than huts containing White-tailed Swallow nests. Ethiopian Swallows may select these cooler nesting sites in order to reduce the negative effect of temperature on chick growth rates.

7.5 Conclusions

The negative effect of high ambient temperatures on White-tailed Swallow chick survival, coupled with the rise in ambient temperatures and reduction in survival rates through the breeding season, suggest that the species' temperature determined range (Chapter 6) could be partly driven by decreased chick survival at high ambient temperatures. This may be mediated by the parents' inability to care for their young (Luck, 2001), which effectively restricts the species' breeding range. Despite decreases in Ethiopian Swallow growth rate at higher temperatures, there was no reduction in survival, and Ethiopian Swallows produced a number of second broods later in the season when White-tailed Swallows were no longer nesting. Taken together, this provides compelling evidence that a reduction in breeding success at high environmental temperatures may drive the White-tailed Swallow's climatic range-restriction.

Further work should compare the prey selection and feeding rates of White-tailed and Ethiopian Swallow parents at different ambient temperatures. A difference in diet, together with different responses of the preferred prey items to temperature, could drive the White-tailed Swallow's range restriction if its primary prey species does not occur, or is less abundant, at higher temperatures. Conversely, interspecific differences in feeding rates at the nest at high temperatures, with no difference in dietary composition, would further support the evidence presented here that the White-tailed Swallow's restricted range is a consequence of the adult birds' reduced foraging ability at higher ambient temperatures, leading to reduced nestling survival.

8 CONSEQUENCES OF CLIMATIC CHANGE FOR THE CONSERVATION OF RANGE-RESTRICTED SPECIES

Qaaqaa fi raaree, jirta?

8.1 Introduction

In Chapters 4 and 6, I used species distribution models (SDMs) to show that the maximum temperature of the warmest month, dry season precipitation and percent tree cover are associated with the probability of occurrence of the Ethiopian Bush-crow and White-tailed Swallow. The use of SDMs to describe and understand the environmental limits of species' current ranges is an important topic in population ecology, but SDMs also have potential practical value in offering the possibility to predict species' responses to future changes, which can assist conservation planning (Pearce-Higgins and Green, 2014). Models that successfully predict the current distribution of a species using a small number of bioclimatic variables can be used to simulate the potential future range under different projected climate scenarios (Huntley et al., 2006).

The effects of climate change on a range of taxa have been discernible over recent decades, and include range shifts and changes in local density, changes in phenology, morphology and behaviour, and shifts in genetic frequencies (Root et al., 2003; Walther et al., 2002).

Investigation of climate change impacts on species’ ranges is a prolific research area, with a large number of published studies based upon future projections using SDMs. In Europe, the mean change in location of centroids of the potential ranges of all breeding birds is 258–882 kilometres by the end of this century, whilst the mean future potential range extent is 72–89% of their current area (Huntley et al., 2008). However, focus on poleward shifts alone may underestimate the impacts of climate change, as species’ responses can be multidirectional, especially in the tropics (VanDerWal et al., 2012). In Africa, therefore, directional changes will vary, with southern species predicted to become more restricted to the Cape, whilst inhabitants of others biomes, including in the Horn of Africa, are projected to decrease their range extent, particularly as arid areas expand (Huntley et al., 2006). In South Africa two Fynbos endemics, the Cape Rock-jumper *Chaetops frenatus* and Protea Canary *Serinus leucopterus*, whose ranges are limited by temperature, have suffered over 30% reductions in both range extent and reporting rates since the late 1980s, declines which are consistent with a loss of potential range indicated by recent climate change and climate envelope models (Lee and Barnard, 2015).

Range shifts in response to climatic change are facilitated by two processes, “cold-edge” expansion and “warm-edge” contraction, which lead to changes in local density (Cahill et al., 2012), and evidence for these effects has been found in taxa other than birds. Since 1975, climate change in Mexico has led to 12% of local lizard populations going extinct, and this proportion is estimated to equate to around 4% of populations worldwide (Sinervo et al., 2010). Long-term climate trends in North America explain local extinction patterns in American Pika *Ochotona princeps*, a species which seems to be primarily affected by chronic heat stress (Beever et al., 2011, 2010). Warm-edge contraction, therefore, can have a severe effect on reducing species’ ranges.

Cold-edge expansions are dependent on the availability of suitable habitat in areas of newly suitable climate, and for many species, especially those with already restricted ranges or specific habitat requirements, this is likely to be limited. This has led to various predictions of extinction rates ranging from 0–54%, with a meta-analysis derived mean of 7.9% (Urban, 2015). There is a great degree of uncertainty associated with different baseline data, climate change scenarios and global circulation models

(GCMs) (Baker et al., 2016; Buisson et al., 2010; Dormann et al., 2008), but the overall pattern across species and models is one of population declines and range contractions. Given ongoing climatic change, and the lagged effects which accrue, many species could already be committed to extinction by 2050 (Thomas et al., 2004). For example, in South Africa two species of lark are projected to suffer complete potential range loss by 2055 under two out of three GCMs considered (Huntley and Barnard, 2012).

In addition to the uncertainty associated with a diverse range of future scenarios, another unknown factor is species' ability to respond. Projected changes in potential distributions are expected to occur rapidly, in some cases at rates an order of magnitude higher than during the late Quaternary (Huntley et al., 2006). Whilst species are responding by shifting their distributions (Lehikoinen et al., 2013; Parmesan and Yohe, 2003), there is evidence that in birds this is not keeping pace with climatic change, so species are increasingly not occupying all of their climatically-determined niche (Devictor et al., 2008). However, a cross-taxa meta-analysis suggests that mean latitudinal range shifts are sufficient to track temperature changes, but the true rate varies greatly between species (Chen et al., 2011).

Range shifts are not the only way in which species can respond to changes. Evolutionary change might allow species to adapt to their new environment rather than track the movement of their current environment, and could be an important response mechanism (Visser, 2008). High seasonal temperatures are associated with increased body size in White-plumed Honeyeaters *Ptilotula penicillatus*, and a 23-year population-wide increase in body size appeared to be driven largely by rising temperatures (Gardner et al., 2014). By contrast, populations of Alpine Chamois *Rupicapra rupicapra* and Soay Sheep *Ovis aries* have exhibited long-term reductions in body size, driven by ecological responses to increasing temperatures (Mason et al., 2014a; Ozgul et al., 2009). However, adaptation is likely to occur only under slower rates of change (Huntley et al., 2010) or, at least, adaptation to higher rates of change is likely to be insufficient even if it does occur (Visser, 2008). Moreover, evidence for genetic adaptation tends to come from the centre of species' ranges (where genetic variation is higher), and involves shifts to higher frequencies of pre-existing heat-tolerant genotypes, rather than development of novel forms (Parmesan, 2006). Parmesan concludes that there is little evidence that species' absolute climatic tolerances will evolve enough to conserve their current geographic distributions.

An important limit on the scope of a species to change its climatic niche by evolutionary change in response to climate change is that there is often a replacement or competitor species with existing adaptations to a different climate. These competitor species can supplant the focal species at the warm edge of the focal species' range, which is the cold edge of the competitor's range. An example is the replacement of Arctic Fox *Alopex lagopus* by Red Fox *Vulpes vulpes* in the boreal zone (Hersteinsson and MacDonald, 1992).

For species which exhibit direct physiological intolerance of high temperatures, climate change also threatens to increase the frequency and severity of heatwave events (Meehl and Tebaldi, 2004), which can lead to high mortality rates even in areas which are still generally climatically suitable (McKechnie and Wolf, 2009).

Changes in individual species' ranges will inevitably have consequences for community composition, with high species turnover expected to occur within broad geographic regions (Hole et al., 2009). This will affect biotic interactions, leading to further detrimental effects on some species (Pounds et al., 2006), and will make careful conservation planning, over large spatial scales, increasingly important to ensure that species' requirements are met in newly suitable areas (Hole et al., 2011).

The severity of climate change impacts on species' populations can be predicted, to some degree, by species' traits (Foden et al., 2013). Habitat specialists, for example, are declining faster than generalists, species with high natal dispersal are declining slower than species with low dispersal, and the lower the thermal maximum within a species' range, the more negative its population trend (Jiguet et al., 2007). The Ethiopian Bush-crow (Chapters 4 and 5) and White-tailed Swallow (Chapters 6 and 7) exhibit traits, such as restricted ranges and narrow environmental tolerances, that make them particularly susceptible to climate change (Foden et al., 2009; Huntley et al., 2006). Investigating the projected impacts of local climate change on these species is, therefore, important for assessing their long-term conservation prospects.

In this chapter, I combine my climate-only species distribution models for the Ethiopian Bush-crow and White-tailed Swallow, built in Chapters 4 and 6, with projected future climate scenarios in my study region, to predict how the potential climatic range of the two species will be affected by climate change. It is expected that, given the close correlation between the two species' distributions and regional temperature patterns, climate change induced temperature rises will negatively impact their potential ranges. However, the complex orography of the region means that increases in temperature may not be uniform or universal, offering hope that some areas could remain climatically-suitable in the mid-term. Understanding the potential impact of climate change on the species' range boundaries is a key component of developing conservation management plans for them in the newly formed Yabello National Park (Ethiopian Wildlife Conservation Authority, 2016).

8.2 Methods

In addition to the current climatic data used for model building in Chapters 4 and 6, the WorldClim database (Hijmans et al., 2005) contains future projections of the same bioclimatic variables under a range of different GCMs and Representative Concentration Pathways (RCPs) (Meinshausen et al., 2011; Vuuren et al., 2011) into two time periods: 2050 (average for 2041–2060) and 2070 (average for 2061–2080). These can be used to project SDMs, built under current conditions, into the future, to assess species' potential ranges under different scenarios. I downloaded projections under six GCMs (Table 8.1) and all four RCPs for the two time periods available on WorldClim (Hijmans et al., 2005).

Table 8.1: Global Circulation Models (GCMs) used for projections.

GCM	Developers	Reference
BCC-CSM1-1	Beijing Climate Center, Beiijing	T. Wu (2012)
CCSM4	National Center for Atmospheric Research, Boulder, Colorado	Meehl et al. (2012); Vertenstein et al. (2014)
HadGEM2-ES	Hadley Centre for Climate Science and Services, Exeter	Collins et al. (2008)
IPSL-CM5A-LR	Institut Pierre Simon Laplace, France	Dufresne et al. (2013)
MIROC-ESM	Center for Climate System Research, Tokyo	Hasumi and Emori (2004)
MRI-CGCM3	Meteorological Research Institute, Japan	Yukimoto et al. (2012)

The four RCPs (RCP2.6, RCP4.5, RCP6.0, RCP8.5) are compiled to cover a range of possible radiative forcing values for 2100, from 2.6 to 8.5 W/m^2 (Vuuren et al., 2011), taking account of multi-gas emission scenarios. The lowest, RCP2.6, assumes that atmospheric greenhouse gas concentrations peak before 2050, and decline thereafter, whilst the others assume progressively higher and later stabilisation of concentrations. The best-estimate global mean surface temperature increases range from 1.5^{o}C to 4.5^{o}C by 2100, relative to pre-industrial levels (Meinshausen et al., 2011). Together the four RCPs represent the range of scenarios considered possible by the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report (IPCC, 2014).

The choice of GCM and modelling technique can have a significant impact on climate change predictions, an effect which becomes more marked the further into the future projections are run (Buisson et al., 2010). This effect tends to outweigh differences arising from the initial dataset used or climate change scenario (i.e. RCP) selected (Buisson et al., 2010; Dormann et al., 2008). However, projections of future range changes are more consistent for species with restricted environmental requirements (Buisson et al., 2010), such as the Bush-crow and White-tailed Swallow

I used my *k*-fold cross-validated AUC comparison of species distribution models built on current climate data for the Ethiopian Bush-crow (Chapter 4) and White-tailed Swallow (Chapter 6) to select the model algorithms which produced the highest AUC scores when projected over each species' current distribution (Boosted Regression Trees (BRT) and Random Forests (RF) for the Bush-crow, and MaxEnt, Generalised Linear Models (GLM) and Generalised Additive Models (GAM) for the Swallow). I projected these under the six GCMs, four RCPs and two time periods downloaded from WorldClim (Hijmans et al., 2005) to assess the potential impacts of climate change on the two species. Previous studies have advocated the use of the RF algorithm as a method which provides robust predictions of range shifts under climate change (Elith et al., 2006; Lawler et al., 2006).

The goodness-of-fit statistic, kappa, is a measure of the agreement between observed and predicted data, once agreement due to random chance has been removed. Kappa can be calculated for each threshold used to convert continuous probability of occurrence into presence-absence predictions, and the maximum value of kappa indicates the best threshold to use for a given model (Elith et al., 2006). To determine the projected future range sizes of the Bush-crow and Swallow, I first calculated maximum kappa for the current range simulations according to each model algorithm. I used the threshold which yielded maximum kappa under current conditions to convert the probability of occurrence for each future scenario into binary presence-absence scores in each cell, and summed the area of the cells where the species' presence was predicted. I took the mean area across all six GCMs and the projected model algorithms for each species, to produce the mean potential climatically suitable area under each RCP/time period scenario. By subtracting the remaining climatically suitable area under each scenario from the current simulated range size (based on maximum kappa) for the best fitting climate-only models, I calculated the mean percent loss of climatically suitable range under each scenario for each species.

8.3 Results

There was a lot of variation between the predicted potential ranges for each species under different GCMs for a given RCP and time period. However the same trend, a severe decline in projected suitable area, was observed across RCPs under each GCM as predicted temperatures increase (Figure 8.1; Figure 8.2). Under all scenarios both species' potential ranges are projected to severely contract, in some cases leading to a total loss of suitable area by 2070.

Summarised across models, and depending on which RCP is realised, the species are projected to suffer 85–96% (Bush-crow) and 56–79% (Swallow) loss of potential range by 2050, and 90–100% (Bush-crow) and 68–84% (Swallow) loss by 2070, relative to the current mean climatically suitable area according to the best climate-only models for each species (Chapters 4 and 6). Such decreases will leave remaining areas which are likely to be too small to support viable populations (Table 8.2).

Figure 8.1: Projected current and future potential range for the Ethiopian Bush-crow based upon climate-only SDMs. Predictions for the four IPCC RCPs are presented in two time periods, 2041–2060 and 2061–2080. Each panel represents the mean probability of occurrence under each scenario, averaged across six GCMs and the two best performing model algorithms (RF and BRT) under current conditions, according to *k*-fold AUC cross-validation. The blue polygon shows the convex hull fitted around the Bush-crow's current distribution.

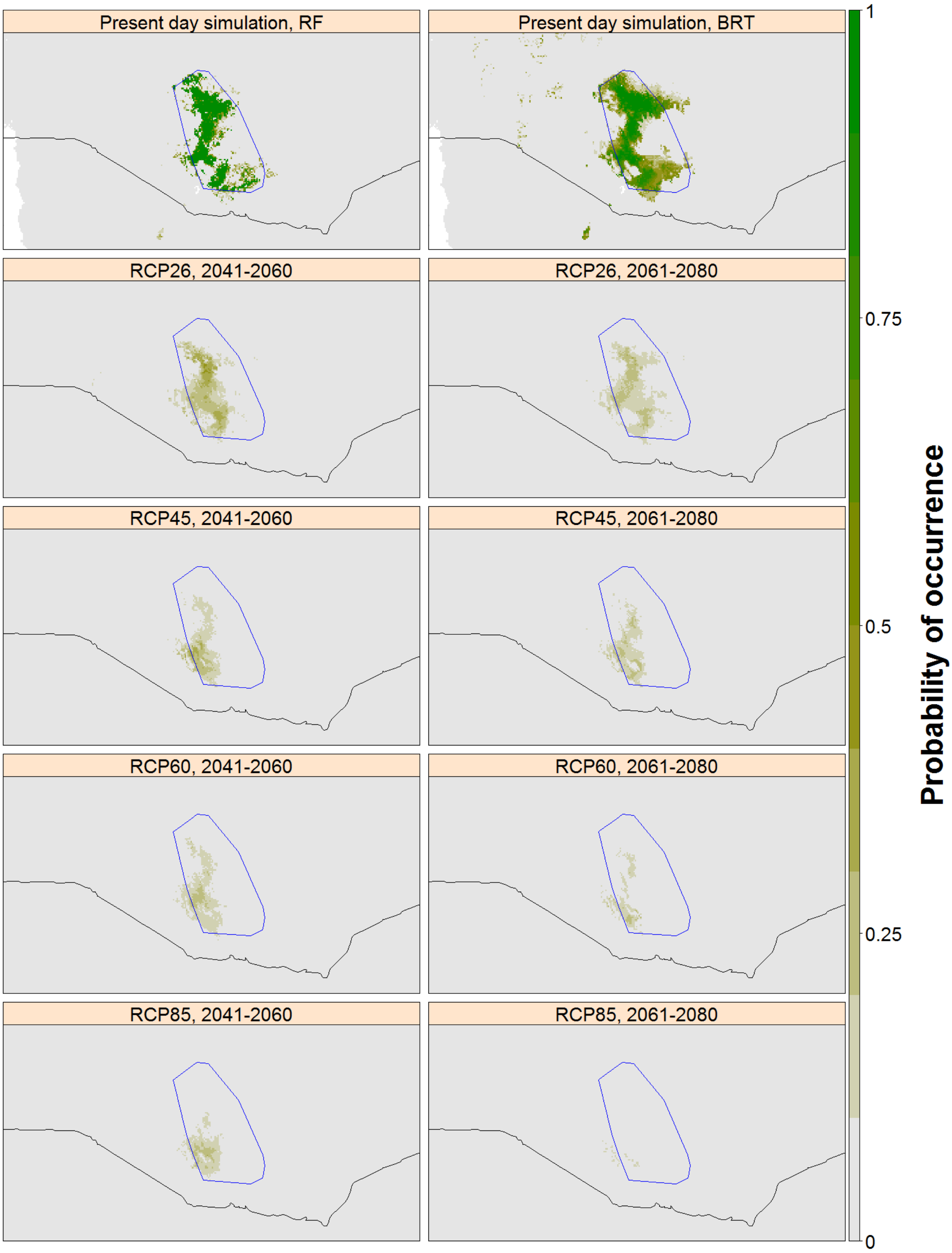


Figure 8.2: Projected current and future potential range for the White-tailed Swallow, based upon climate-only SDMs. Predictions for the four IPCC RCPs are presented in two time periods, 2041–2060 and 2061–2080. Each panel represents the mean probability of occurrence under each scenario, averaged across six GCMs and the three best performing model algorithms (MaxEnt, GLM and GAM) under current conditions, according to *k*-fold AUC cross-validation. The blue polygon shows convex hulls fitted around the White-tailed Swallow's current distributions in the core range and on the Liben Plain, whilst the dashed line shows the complete hull if these two populations are considered to be continuous.

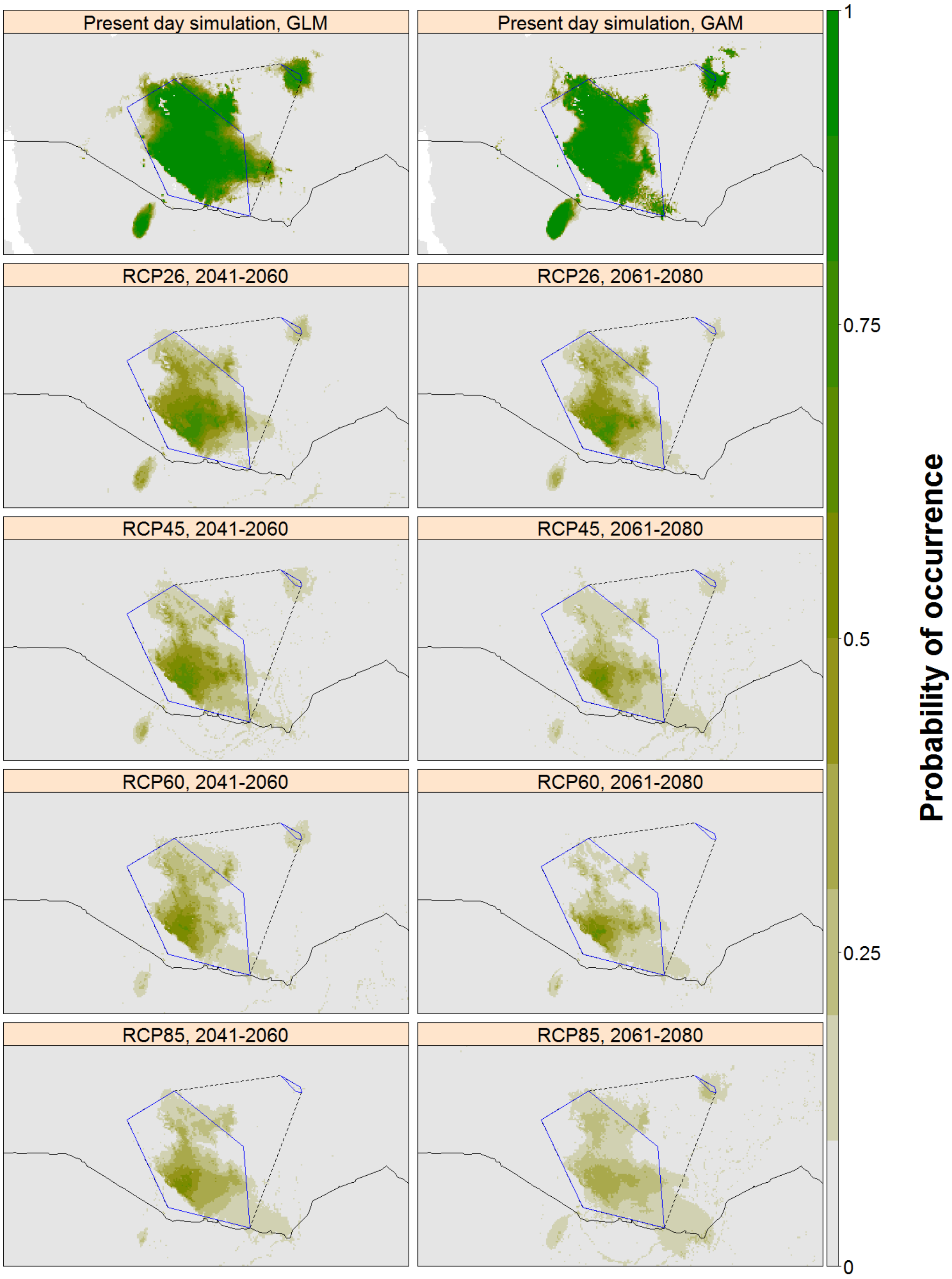


Table 8.2: The area of mean current and future potential Ethiopian Bush-crow and White-tailed Swallow ranges based upon climate-only SDMs. Current ranges are the mean area of suitable climate according to the best two (Bush-crow) and three (Swallow) model algorithms (Chapters 4 and 6). Future ranges are averaged across projections from the same algorithms and six GCMs under each Year/RCP scenario. Percentages are calculated relative to the mean simulated current range.

	Ethiopian Bush-crow			White-tailed Swallow		
Scenario	Potential range / km²	Percent left	Percent loss	Potential range / km²	Percent left	Percent loss
Current	3495	-	-	8311	-	-
Year 2050, RCP 2.6	522	14.9	85.1	3642	43.8	56.2
Year 2050, RCP 4.5	263	7.5	92.5	2218	26.7	73.3
Year 2050, RCP 6.0	202	5.8	94.2	1761	21.2	78.8
Year 2050, RCP 8.5	136	3.9	96.1	1713	20.6	79.4
Year 2070, RCP 2.6	342	9.8	90.2	2664	32.1	67.9
Year 2070, RCP 4.5	173	4.9	95.1	1583	19.0	81.0
Year 2070, RCP 6.0	65	1.9	98.1	1274	15.3	84.7
Year 2070, RCP 8.5	5	0.2	99.8	1367	16.4	83.6

8.4 Discussion

Despite the uncertainty inherent in species distribution modelling and subsequent projection of potential ranges under future climate scenarios, numerous studies have found that climate envelope models fitted to species' distributions in one time period can predict likely changes in range boundaries and population trends in future periods (Araújo et al., 2005; Green et al., 2008; Gregory et al., 2009; Stephens et al., 2016; Tingley et al., 2009). Such analyses give confidence that the patterns of projected future change for other species are reasonable.

The greatest uncertainty in projections tends to arise from the choice of modelling technique and baseline climate data used in model fitting, and of GCM used for model projections (Baker et al., 2016; Buisson et al., 2010; Dormann et al., 2008). In Chapters 4 and 6, I investigated a suite of modelling techniques, and here selected those with the highest predictive capacity under current conditions, preferring to use methods which performed well using the *k*-fold cross-validation method. Given that the results were validated using data independent of and spatially separate from the data used for model fitting (Chapters 4 and 6), I consider that the models are likely to be reasonably robust.

Climate-only models make projections about species' potential future ranges with greater confidence than those incorporating non-climate variables because, for all the uncertainty in future projections of climate, the uncertainty in predictions of future change in land cover and other human impacts is much larger (Pearce-Higgins and Green, 2014). For my study region, it was possible only to project the climate-only models, because predicting future non-climate variables largely determined by human populations and economic and technological development, especially in comparable layers to those used for model building, was not possible. Since climatic factors were the strongest predictors of current Bush-crow and Swallow occurrence (Chapters 4 and 6), these models are likely to represent the maximum potential distribution of each species under each climate scenario, with further restrictions imposed by habitat availability and human land-use (Pearce-Higgins and Green, 2014).

My projections of potential range reductions under a selection of GCMs for the Ethiopian Bush-crow and White-tailed Swallow, whilst varying in severity between individual models, are very consistent in their overall predictions. The outcomes for both species are bleak, with severe loss of potential range under all GCMs and RCPs, even by 2050. Many scenarios resulted in a total loss of suitable climate by 2070, particularly for the Bush-crow. Even under the most optimistic RCP scenario, RCP2.6, which requires strong mitigation strategies to be employed urgently (IPCC, 2014), the Bush-crow is projected to lose 85% of its potential range by 2050, and 90% by 2070, whilst the Swallow is projected to lose 56% and 68% in the same periods. Studies which have modelled changes in the reporting rate of species, which is a proxy for local abundance, as well as their extent, have found that reporting rates are often predicted to decline even in areas of persistence, indicating that models of range extent alone are likely to overestimate future population sizes (Huntley and Barnard, 2012). Given the negative effects of temperature on Bush-crow density found in Chapter 4, it is likely that decreases in population size within the remaining suitable areas will also occur.

In temperate regions, wide-ranging species which show a strong response to temperature are currently able to shift their ranges polewards and at least partially track their preferred climate (Chen et al., 2011; Parmesan and Yohe, 2003), although this response is more common in habitat generalists (Warren et al., 2001). Such shifts occur because of two processes: cold-edge expansion and warm-edge contraction (Cahill et al., 2012). Necessarily, however, this relies on the species having a “cold-edge” to its range. For the Ethiopian Bush-crow and the White-tailed Swallow this is not the case, as their potential range is projected to contract from all sides, with little change in their projected range centroids.

Previous documented extinctions in which climate change has been implicated have been driven by biotic interactions leading to species’ declines (e.g. Pounds et al. (2006)), and to date none appear to have been driven solely by intolerance of high temperatures (Cahill et al., 2012). Although this is not proven for the Ethiopian Bush-crow and White-tailed Swallow, the evidence built prior to and throughout this thesis suggests that they may be examples of species principally limited by climate (Donald et al., 2012; Jones et al., in review; Chapters 4–7). For the Ethiopian Bush-crow, the behavioural responses to high ambient temperatures are suggestive of a direct mechanism (Chapter 5), although the mechanism is less clear for the White-tailed Swallow (Chapter 7).

Given the Ethiopian Bush-crow’s and White-tailed Swallow’s strong responses to climate variables alone (Chapters 4 and 6), there may be little that can be done by management to prevent or limit their decline. However, the rate might be slowed if suitable habitat can be retained and perhaps managed to increase its carrying capacity within the last pockets of climate suitability (Borghesio and Giannetti, 2005; Pearce-Higgins and Green, 2014). This type of conservation response to climate change has been termed *compensatory*, because it reduces a negative effect of climate change by improving demographic rates through a different mechanism, unrelated to the climate-related effect that induced or threatens a decline. By contrast *counteracting* interventions seek to prevent climate change from having its effect by blocking the mechanism (Green and Pearce-Higgins, 2010). For example, if Alpine Chamois *Rupicapra rupicapra* decline because of warming only because domestic sheep *Ovis aries* arrive and outcompete them, careful livestock management to limit the spread of sheep might counteract the effect of climate change on the Chamois (Mason et al., 2014b).

Another corvid, the Pied Crow *Corvus albus*, was found to have a strong association with temperature. Its distribution has tracked changes in its temperature envelope across

South Africa, rather than showing adaptation to, or persistence in areas with, higher temperatures (Cunningham et al., 2016). Other species exhibiting strong responses to temperature have also reduced their range sizes, indicating an inability to respond physiologically to rising temperatures (Lee and Barnard, 2015).

Two African bird species (Rudd's Lark *Heteromirafra ruddi* and Botha's Lark *Spizocorys fringillaris*) are already projected to suffer complete range loss by 2055 under two out of three GCMs considered (Huntley and Barnard, 2012). The Ethiopian Bush-crow and White-tailed Swallow must be added to this list of species which are almost certainly committed to extinction by climate change.

With more detailed understanding of species' responses to climate change and habitat availability, especially with respect to population dynamics and dispersal, models of species' potential future distributions are likely to become more realistic (Anderson et al., 2009; Huntley et al., 2010; Kearney and Porter, 2009), and could incorporate the predicted frequency of severe weather events, such as heatwaves, which might threaten species' populations (McKechnie and Wolf, 2009). Such detailed data are not yet available for the Bush-crow and Swallow, but with added evidence of strong negative responses to increased temperatures and a severe reaction to climate change projected, the species should become model systems for furthering our understanding of species' distributions, for testing our models' ability to predict future changes, and for assessing whether there is scope for conservation interventions to reduce the negative impacts of climate change.

9 CONCLUDING REMARKS

"If you cut down the big dadacha, there is no shade for a gaadaa meeting."

In this thesis I have investigated the effects of temperature on two range-restricted Ethiopian endemic birds, the Ethiopian Bush-crow and White-tailed Swallow, at three scales. Firstly, using species distribution models fitted to global climatic and habitat data, I have shown that the species' ranges are described by a climate envelope, primarily described by maximum temperature of the warmest month. The results were robust to stringent *k*-fold cross-validation, and to the use of multiple modelling techniques. Secondly, using data on bird abundance, temperature and habitat collected at a local scale, I have found a negative effect of temperature on Bush-crow density and group size, and negative trends in Swallow abundance. Finally, through studies of Bush-crow behavioural responses, and Swallow breeding success, I have uncovered mechanisms by which the two species might be directly affected by temperature.

For the Bush-crow, this occurs in its foraging behaviour, as foraging effort and food intake rates decline as temperatures rise, and the birds switch their foraging techniques to favour methods which yield higher success rates, and larger prey items. Juvenile birds are more severely affected than adults, becoming less active and moving to the shade at lower temperatures than adult birds.

In the White-tailed Swallow, breeding success is impacted by ambient temperatures, with later hatching broods, which grew up during warmer weather, showing a much lower fledging success than earlier hatching nests.

To reinforce these results, I have shown that three sympatric, but wider ranging, species do not show the same responses to temperature. White-crowned and Superb Starling foraging behaviour is unaffected by temperature and, although these two species are less active than Bush-crows, they also begin panting and seek shade at much higher temperatures than Bush-crows. This is indicative of a higher upper critical temperature, above which the birds begin to suffer from heat stress. Moreover, their ranges show no response to temperature patterns, instead being described by the amount of wet season precipitation. This provides compelling evidence that the Bush-crow's range is determined by its physiological intolerance of high temperatures.

Despite showing some negative effects of nest temperature on their growth rates, Ethiopian Swallows do not suffer a reduction in survival as ambient temperatures rise and the breeding season progresses. Indeed, this species continued to produce second broods after the White-tailed Swallow had stopped breeding. Interestingly, the White-tailed Swallow's sister species, the Pearl-breasted Swallow, does not show the same environmental limitation as the White-tailed Swallow. It inhabits a much broader climatic range, and neither species' distribution models were able to predict the other's occurrence.

Finally, I used future climate projections to investigate the potential impacts of climate change on the Ethiopian Bush-crow and White-tailed Swallow. Foden et al. (2013) proposed that species have three dimensions of vulnerability to climatic change: sensitivity, exposure, and low-adaptive capacity. The strong association of the range boundaries of the Ethiopian Bush-crow and the White-tailed Swallow with temperature thresholds (Chapters 4 and 6), and the negative effects of temperature on behaviour and breeding success (Chapters 5 and 7), demonstrate that they are sensitive to climate, especially high temperatures. The projections of future climatic change for southern Ethiopia, combined with species distribution modelling results (Chapter 8), indicate that both species will be exposed to biologically significant change. The species' current restricted ranges, and the lack of movement of the centroids of their future potential ranges, indicate that neither species can respond by changing the location of their distribution. The evidence from my studies of Bush-crow foraging and thermoregulatory behaviour indicates that there may be a direct effect of high temperature on this species which would be indicative of a low adaptive capacity. This puts them in the highest bracket of vulnerability suggested by Foden et al. (2013, fig. 1): species for which specific research and interventions are required.

The Ethiopian Bush-crow and the White-tailed Swallow are currently listed respectively as Endangered and Vulnerable, assessments which were based on their restricted range sizes, and apparent declines in Bush-crow counts (BirdLife International, 2016a, 2016b; Borghesio and Giannetti, 2005). No information was previously available on their likely responses to climate change. In light of their severe climatic limitation, and the changes projected to occur across their current area of occupancy in the coming 25 to 65 years, the true threat to their survival is significantly higher than previously thought, and I would recommend updating their RedList assessment to reflect this.

Understanding species’ responses to climate change is fundamental to our ability to protect them. The global ranges of most species are determined by a number of factors, which interact at each edge of the focal species’ range, making it difficult to determine which factor is most important. It is unusual, if not unique, to find not one but two species, both members of otherwise common taxonomic families, restricted to a tiny global range by their response to temperature alone. For these reasons, the Ethiopian Bush-crow and White-tailed Swallow provide fascinating study species. They offer the opportunity to better understand how temperature, and therefore climate, can affect species physiologically, behaviourally and geographically. By monitoring their population responses to current climate warming, by far the largest threat to their survival, we also have the opportunity to test the speed at which these species respond to adverse climatic changes. Moreover, with careful monitoring targeted in areas predicted by climate simulations to experience the fastest and slowest changes in temperature, we may be able to test, in real time, the ability of our climate simulation models to predict biologically meaningful changes on the ground. Whilst there may be little we can do to prevent the extinction of the Ethiopian Bush-crow and White-tailed Swallow in the wild, the insights they offer us into species’ responses to climate change may support the conservation of other species around the world.

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11 APPENDICES

APPENDIX 1: ADDITIONAL TABLES

Table A1: Observers who have kindly contributed observations documented in Chapter 1, with initials used to credit them in the text.

Observer	Initials
Andrew Bladon	AJB
Jarso Denge	JD
Kai Gedeon	KG
Mengistu Wondafrash	MW
Merid Gabremichael	MG
Nigel Collar	NJC
Paul Dolman	PD
Paul Donald	PFD
Sam Jones	SEIJ
Simon Busuttil	SB
Steve Rooke	SR
Till Töpfer	TT
Yilma Dellelegn	YD

Table A2: Models of Swallow chick survival within four AIC_c points of the minimum AIC_c model.

Model	Intercept	Brood size	Hatch date	Nest Temp	Amb. Temp	(Amb. Temp)^2	Species	Brood by Nest Temp	Brood by Amb. Temp	Hatch date by Species	Nest Temp by Species	Amb. Temp by Species	df	log-Likelihood	AIC_c	Δ AIC_c	AIC_c weight
25	-315.10				25.551	-0.514							3	-24.25	55.69	0.00	0.211
57	-329.88				26.863	-0.541	+						4	-23.16	56.43	0.74	0.146
26	-338.36	0.574			27.332	-0.551							4	-23.39	56.88	1.18	0.117
27	-338.44		-0.024		27.452	-0.551							4	-23.81	57.72	2.03	0.077
58	-367.26	0.635			29.798	-0.602	+						5	-22.22	57.77	2.07	0.075
29	-305.92			-0.139	25.152	-0.506							4	-23.85	57.82	2.12	0.073
154	-301.75	10.663			23.106	-0.440			-0.402				5	-22.42	58.18	2.49	0.061
59	-357.77		-0.029		29.161	-0.587	+						5	-22.64	58.62	2.93	0.049
28	-358.79	0.588	-0.024		29.004	-0.584							5	-22.92	59.18	3.49	0.037
315	-315.99		0.004		25.686	-0.517	+			+			6	-21.19	59.33	3.64	0.034
30	-332.88	0.566		-0.137	27.231	-0.549							5	-23.03	59.40	3.71	0.033
61	-335.53			0.043	27.228	-0.548	+						5	-23.14	59.62	3.93	0.030
1081	-340.41				27.657	-0.556	+					+	5	-23.16	59.65	3.96	0.029
316	-371.77	1.014	0.003		30.109	-0.609	+			+			7	-19.34	59.69	4.00	0.029

Table A3: Summary table of White-tailed and Ethiopian Swallow growth patterns.

Numeric values represent means across all chicks seen on that day. Letters represent modal traits: presented singly if they represent more than 75% of chicks (e.g. V); with a second trait if the modal trait was seen in 50-75% of chicks (e.g. VP); and separated by a "/" if two were equally numerous (e.g. V/P). N = pins not visible; V = pins visible under the skin; P = in pin; U = pins unsheathed; No = eyes/ears not open, breast not fully feathered; Yes = eyes/ears open, breast fully feathered; Wb = eyes open only when begging; D = ear forming a depression.

Species	**Age / days**	**Weight / g**	**Femoral**	**Caudal**	**Total 9th primary length**	**Emerged 9th primary length**	**Secondaries**	**Ear**	**Tail**	**Dorsal**	**Crown**	**Face**	**Nape**	**Eye**	**Breast**
WTS	0	-	N	N	N	-	N	No	N	N	N	N	N	No	-
WTS	1	-	N	-	N/V	-	N	No	N	N	N	N	N	No	-
WTS	2	-	N	N	V	-	VN	N/D	NV	N	N	N	N	No	-
WTS	3	-	N	N	VP	-	V	DY	N/V	VN	N	N	N	No	-
WTS	4	-	NVP	N	P	-	VP	Yes	V/P	VP	VN	VN	NV	No	-
WTS	5	-	P	-	P	-	P	Yes	PV	PV	V	V	VN	No	-
WTS	6	8.1	PU	P	P	-	P	Yes	P	P	PV	P	VP	NY	No
WTS	7	8.5	UP	P	0.8	0.0	P	Yes	P	P	P	P	P	YN	No
WTS	8	9.5	U	UP	1.0	0.0	P	Yes	P	PU	P	P	P	Yes	No
WTS	9	10.7	U	U	1.5	0.1	UP	Yes	UP	U	P	P	P	Yes	No
WTS	10	11.7	U	U	1.9	0.3	U	Yes	U	U	P	P	PU	Yes	No
WTS	11	11.7	U	U	2.2	0.6	U	Yes	U	U	UP	P	UP	Yes	No
WTS	12	12.1	U	U	2.8	1.2	U	Yes	U	U	U	UP	U	Yes	No
WTS	13	12.3	U	U	3.3	1.6	U	Yes	U	U	U	U	U	Yes	No
WTS	14	12.1	U	U	3.6	2.2	U	Yes	U	U	U	U	U	Yes	No
WTS	15	12.2	U	U	4.0	2.6	U	Yes	U	U	U	U	U	Yes	No
WTS	16	11.8	U	U	4.5	3.1	U	Yes	U	U	U	U	U	Yes	NY
WTS	17	11.5	U	U	4.8	3.5	U	Yes	U	U	U	U	U	Yes	YN
WTS	18	11.5	U	U	5.1	3.8	U	Yes	U	U	U	U	U	Yes	Yes
WTS	19	11.2	U	U	5.3	3.9	U	Yes	U	U	U	U	U	Yes	Yes

WTS	20	8.5	U	U	5.7	4.5	U	Yes	U	U	U	U	U	Yes	Yes
WTS	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WTS	22	9.6	U	U	6.2	5.0	U	Yes	U	U	U	U	U	Yes	Yes
ES	0	-	N	-	V	-	N	No	-	N	N	-	N	No	-
ES	1	-	N	N	V	-	VN	No	-	N	N	N	N	No	-
ES	2	-	N	-	-	-	-	No	-	N	N	-	N	No	-
ES	3	-	VP	-	V	-	V	YN	-	VN	NV	V	N	No	-
ES	4	-	P	-	P	-	P	D	-	-	-	-	V	No	-
ES	5	-	P	-	P	-	P	Yes	-	PV	V	V	V	No	-
ES	6	-	PU	-	P	-	P	Yes	P	P	V	VP	V	WbN	-
ES	7	12.8	UP	U	P	-	P	Yes	P	P	PV	PV	PV	No	No
ES	8	12.7	U	U	1.1	0.0	P	Yes	P	P	P	P	P	Yes	No
ES	9	15.4	U	U	1.9	0.3	U	Yes	U	U	P	P	UP	Yes	No
ES	10	15.8	U	U	2.2	0.5	U	Yes	U	U	PU	P	UP	Yes	No
ES	11	15.2	U	U	2.2	0.6	U	Yes	U	U	UP	P	UP	Yes	No
ES	12	16.9	U	U	3.0	0.9	U	Yes	U	U	U	P	U	Yes	No
ES	13	17.3	U	U	3.6	1.8	U	Yes	U	U	U	P	U	Yes	No
ES	14	15.7	U	U	3.8	2.1	U	Yes	U	U	U	U	U	Yes	No
ES	15	16.9	U	U	4.4	2.8	U	Yes	U	U	U	U	U	Yes	No
ES	16	15.4	U	U	4.9	3.4	U	Yes	U	U	U	U	U	Yes	Yes
ES	17	15.0	U	U	5.0	3.5	U	Yes	U	U	U	U	U	Yes	YN
ES	18	14.6	U	U	5.7	4.2	U	Yes	U	U	U	U	U	Yes	Yes