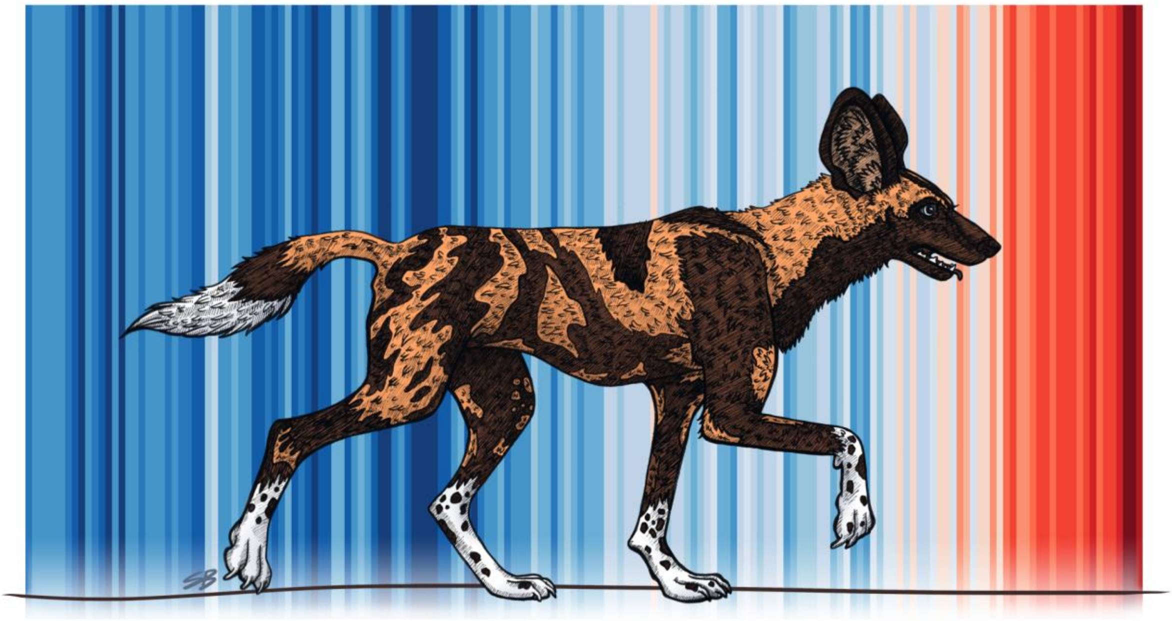
The Impact of Climate Change on a Tropical Carnivore: From Individual to Species



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Declaration

I, Daniella Rabaiotti, confirm the work presented in this thesis is my own. The research was supported by NERC through the London NERC DTP.

All data analysis data visualisation and modelling was done by Daniella Rabaiotti. Tim Coulson provided training in individual based modelling. Mike Croucher assisted in code optimisation for the individual based model.

All chapters of this thesis were written by Daniella Rabaiotti, with guidance and comments from Rosie Woodroffe and Richard Pearson. Tim Coulson provided comments on Chapter 4, and Rosemary Groom, J.W. McNutt and Jessica Watermeyer provided comments on Chapter 3.

Data from Laikipia, Kenya, on wild dog survival and movements were collected by Rosie Woodroffe and the Kenya Rangelands Wild Dog and Cheetah Project. Data on wild dog mortality in Savé Valley, Zimbabwe were collected by Rosemary Groom and the Savé Valley team at the African Wildlife Conservation Fund. Data on wild dog mortality in the Okavango, Botswana, were collected by J.W. McNutt and the Botswana Predator Conservation Trust. Data on wild dog distributions were provided by the Rangewide Conservation Programme for Cheetah and African Wild Dogs.

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Abstract

Climate change is impacting species globally. Predicting which species will be impacted, where, when, and by how much, is vital to conserve biodiversity in a warming world. In this thesis, I evaluate the likely impacts of climate change on an endangered species, the African wild dog, *Lycaon pictus*, for which direct impacts of high ambient temperature on behaviour and recruitment have previously been identified.

Wild dogs hunt mainly in daylight, and I show they are unlikely to be able to adapt to a warming climate by hunting at night. I found nocturnal hunting was constrained by the availability of moonlight, and by the need to guard pups in the den, restricting the use of cooler night-time hours.

I also show high ambient temperatures are associated with increased adult mortality, appearing to increase mortality due to human causes and disease, which is linked to human pressures through transmission from domestic dogs.

Having quantified the impacts of ambient temperature on key vital rates, I develop an Individual-Based Model to project the likely effects of climate change on population growth. I show that population projections for this species are sensitive to the emissions scenario and population size, with population collapse predicted for smaller populations under the worst-case scenario.

Finally, I use my Individual-Based Model to make spatially explicit predictions of population changes throughout the species' remaining range. My model predicts that populations in cooler coastal regions will suffer the smallest population declines, along with populations located in East Africa. Predicted threat status of the species was dependant on the emissions scenario.

My study shows how behavioural and demographic data can be used to inform conservation planning in a changing climate. My findings also inform efforts to incorporate climate change impacts into assessments of species' threat status by the IUCN Red List.

Impact statement

Climate change is one of the biggest threats to species globally. In contrast with most other threats to species, protected areas provide little protection against climate change, which is slower and more difficult to reverse than threats such as habitat loss. Identifying how species will respond as temperatures rise, and where they are most likely to persist, will be vital to implementing conservation actions that ensure the survival of species under future climatic conditions.

Whilst current methods of assessing species vulnerability work well with limited data, and can be used across high numbers of species, for those species where extensive data exist, focused, data driven models of the species' responses to climate change may shed new light on climate change threats. The need for detailed, species specific models is especially acute for endangered species, which are often already range-limited due to other threats such as habitat loss or invasive species.

This thesis presents novel evidence of climate change threats to the endangered African wild dog at individual, population, and species-wide level. Through identifying the drivers of temperature impacts on adult mortality it indicates that conservation interventions designed to mitigate other risks such as disease can also buffer the species from the effects of high temperatures. Similarly, through highlighting areas where the species is predicted to experience the highest and lowest level of climate-driven population declines the results of this thesis provide a valuable tool for conservationists to use when planning conservation actions for the species.

By highlighting the ability of data-driven individual based model to assess future Red List Criteria for species this thesis also highlights ways in which predictions of climate change impacts on species can be used alongside the Red List Framework to predict species' threat level. It also highlights some concerns with how these kinds of models are integrated into red listing.

The methods used in this thesis are unique, but readily adaptable to other species, or even multi-species systems. They provide an example that can be followed for other species for which large datasets exist, which include many culturally and economically important species which are likely to be a priority for climate change mitigation actions in the future.

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Chapter 1 Introduction

1.1. *Predicting climate change impacts on species*

Climate change is widely accepted as one of the greatest threats to species globally (Barros et al., 2014). Changes in temperature and rainfall influence many species' ability to survive and reproduce. As the Earth warms and the climate becomes more variable, declines in population sizes and species richness, coupled with shifts in distribution, are predicted to occur globally, across a wide variety of flora and fauna (Walther et al., 2002). Increasingly, climate change is not just a future threat to species but a current threat, with impacts already observed in numerous species, and a number of species extinctions attributed to climate change (Wolfe et al., 2005; Parmesan, 2006; Pounds et al., 2006; Welbergen et al., 2008; Waller et al., 2017).

Predicting the impact of climate change on species will be key in informing future conservation policy and practice. By identifying which species will be most impacted by climate change, where species will be most impacted by climate change and how species will be impacted by climate change, conservation interventions can be implemented which mitigate the impacts of changing temperature and rainfall regimes on wildlife. Interventions could potentially be implemented in the species' current range through actions aimed at improving species' capacity to cope with less favourable conditions, for example through supplementary feeding (Correia et al., 2015), increased shelter or creating buffers around the species' current habitat (Heller and Zavaleta, 2009). Conservation interventions designed to mitigate climate change impacts on species can also be used to facilitate the expansion of species, or to preserve habitat likely to be suitable for those species in the future (Heller and Zavaleta, 2009; Gillson et al., 2013). Interventions of this kind include facilitated range expansions, translocations and incorporating climate risk when planning protected areas (Lunt et al., 2013; Gillson et al., 2013). Predicting how, where, and which species will be impacted by climate change is key to informing where to implement interventions, which species to target, and what interventions should be carried out. These predictions are therefore essential for implementing successful conservation measures under climate change.

1.1.1. Which species are impacted by climate change?

Many studies have sought to identify which species are most at risk from climate change (Midgley et al., 2002; Foden et al., 2013; Pearson et al., 2014; Pacifici et al., 2015), often with the aims of identifying where resources should be focused as global temperatures rise (Pacifici et al., 2015). Species risk from climate change is generally identified using trait-based climate change vulnerability assessments, which use analysis of the traits of a species to determine the level of threat posed by changes to climatic variables (Pacifici et al., 2015). Because of the fact they can assess large number of species with a relatively small amount of data, climate change vulnerability assessments are increasingly being taken up by conservation practitioners and policymakers as a straightforward and low cost way of directing conservation efforts towards species deemed most at risk (Willis et al., 2015).

Climate change vulnerability assessments primarily assess three components of climate change vulnerability: exposure, sensitivity, and adaptability (Bellard et al., 2012; Foden et al., 2013; Foden et al., 2019). Exposure is the extent to which climate change is occurring, or predicted to occur, in the species' current range; species that live in the areas predicted to undergo the greatest changes in temperature and rainfall would have the highest exposure. Sensitivity refers to the ability of a species to tolerate climatic variation; species considered most at risk are those with clear thermal links in their phenology - whereby they rely on certain temperature or rainfall properties for key parts of their lifecycle, and species with low thermal tolerances leading to deaths through heat stress at high temperatures. Adaptability is the ability of the species to change its behaviour or physiology to mitigate climate change impacts; this could be those changes already observed to result from anthropogenic climate change – shifts in range or phenology - or changes in behaviour such as utilising microhabitats that buffer the effects of rising temperatures (Moritz, Craig and Agudo, 2013; Foden et al., 2013). Equally a species could change its size or colour to buffer against climate impacts. Species with the lowest adaptive capacity are likely to be those that are highly specialised to a particular food or habitat, with low mobility and long generation times (Pacifici et al., 2015).

Climate vulnerability assessments have increasingly been used to advise future conservation strategies, and have proved popular with conservation practitioners due to the ease of assessing a large number of species using only the available literature and climate data available online (Tuberville et al., 2015). Numerous tools and methodologies have been made available to conservation practitioners, with growing emphasis on developing easy-to-use open-access climate vulnerability assessment tools such as NatureServe (Young et al., 2010; Tuberville et al., 2015). Particularly in the United States of America, these assessments have increasingly been taken up by the government and state agencies and used to inform future conservation action plans (Hannah, Midgley, and Millar, 2002; Glick, Stein, and Edelson, 2011; Watson, Iwamura, and Butt, 2013). Shortcomings of this approach are increasingly being recognised, however, with studies finding limitations in their ability to assess vulnerability of herpetofauna (Tuberville et al., 2015), as well as migratory species where the climate vulnerability assessment may only capture threat in one section of their range (Small-Lorenz, Culp, Ryder, Will, and Marra, 2013). There is growing concern that these methodologies can be overly simplistic, and have the potential to miss key traits in data deficient species, underestimating their vulnerability (Tuberville et al., 2015; Pacifici et al., 2015).

The threat level of species is most commonly determined using the IUCN Red List, which categorises species based on their population numbers, trends and the areas of range they inhabit. The Red List uses a combination of data and expert opinion to determine the likelihood that a species will go extinct in the near future, with the aim of focusing conservation efforts on those species most in need (Rodrigues et al., 2006). Numerous concerns have been raised, however, about the ability of the Red List to identify risks resulting from climate change, as a result of the assessment criteria involving declines over time-scales as short as 10 years, much faster than many predicted climate change impacts, and a much shorter time period than it would take to reverse climate change (Akçakaya et al., 2006; Keith et al., 2008). Previous studies have found that the Red List does provide ample warning of climate change threats, but that interventions must happen early, once the species is listed as vulnerable (Keith et al., 2008; Stanton et al., 2015). For species that are already listed as endangered on the IUCN Red List, evidence of any climate change impacts will have implications for species persistence. Because of the Red List’s near-ubiquitous use in informing species conservation strategy, aligning climate change threats with the Red List criteria is likely to be critical in informing future conservation actions.

1.1.2. Where are species impacted by climate change?

Predicting where species are anticipated to experience the greatest climate change impacts is key in both directing where conservation efforts should occur and also identifying the places to which species may move as the climate warms. The most commonly used method of predicting where species are likely to persist under future changes in temperature and rainfall are correlative species distribution models (SDMs). These models are based on the niche concept, which describes how environmental conditions determine whether a population persists (Hutchinson, 1978). These models identify the climatic conditions within the areas that the species currently inhabits, and identify the areas that are predicted to be within that species' climatic niche under future climatic conditions (Kearney and Porter, 2009).

Correlative models of this kind are increasingly important in both ecology and evolutionary biology, and can be used to direct conservation efforts, identify potential suitable habitat for rare species, as well as predict species' historical ranges (Kearney and Porter, 2009; Store and Jokimäki, 2003). This technique has been applied to a wide variety of species, both plants (Bakkenes et al., 2002; Thuiller, 2004; Thuiller et al., 2005; Hamann and Wang, 2006) and animals (Peterson et al., 2002; Erasmus et al., 2002; Thomas et al., 2004), across numerous continents and habitats, to predict future range shifts in species. Species typically move toward cooler areas, towards the poles or to higher altitudes, as temperatures rise, although this is not consistent across all species (Thuiller, 2004; Parmesan, 2006).

These models can provide a good first approximation of climate change impacts (Green et al., 2008), and can be used on relatively sparse species occurrence data (Pearson et al., 2006). However, many species' ranges today are not limited by climate, but are instead limited by habitat loss. This can be more difficult to model, as modelling future human impacts on existing habitat is challenging. Similarly, for species that have already lost much of their range to human activities, predicting areas that will be climatically suitable in the future may not be particularly useful, as many of these may no longer contain suitable habitat. SDMs do not establish a causal link behind the correlations observed in the model between the species and local environmental variables (Kearney and Porter, 2009). It is impossible in most cases to differentiate between causal relationships, indirect effects, and direct responses from another variable which may not be present in the model (Nally, 2000). Because of the correlative nature of these models, it has been suggested that mechanistic data, linking functional traits of the study organism, such as ability to disperse (Leroux et al., 2013) or breed (Kearney et al., 2008), with local environmental data, such as temperature (Kearney et al., 2008) or vegetation cover (Porter et al., 2002), should be incorporated into SDMs for more accurate predictions of how species will respond to changes in climatic conditions (Kearney and Porter, 2009).

1.1.3. How are species impacted by climate change?

1.1.3.1. Species responses to climate change

As the climate warms it is predicted a wide range of species will be impacted across the globe. Species' responses to climate change have been split into three categories: changes in time, changes in space, and changes in self (Bellard et al., 2012). Change in time refers to species shifting the timing of key life history events, such as breeding seasons, in response to climatic changes. Change in space refers to shifts in the geographic range occupied by species. Change in self refers both to evolutionary adaptations to altered climatic conditions, and also to phenotypic plasticity, leading to changes in physical traits and behaviour of a species. These responses can help species to persist under changing climatic conditions, however they may also have harmful effect, for example loss of synchrony between the life-cycles of predators and prey (Miller-Rushing et al., 2010; Plard et al., 2014), moving into sub-optimal habitats (Laurance et al., 2011; Martin et al., 2015), or increased thermoregulatory behaviours leading to lower foraging success (du Plessis et al., 2012). Ultimately, the way in which species respond to changes in local temperature and rainfall will determine that species likelihood of persistence, and may have knock on effects at an ecosystem-wide level.

Changes in time, i.e., the shifting of major seasonal life history events – or phenology – such as seasonal reproduction are the most common area in which species adaptations to changing climatic conditions, are already being observed. These changes in phenology have been noted in the majority of taxonomic groups, including amphibians (Blaustein et al., 2001; Gibbs and Breisch, 2001; Ficetola and Maiorano, 2016), birds (Dunn and Winkler, 1999; Crick, 2004), mammals (Plard et al., 2014), insects (Roy and Sparks, 2000; Stefanescu et al., 2003), plankton (Edwards and Richardson, 2004) and plants (Menzel et al., 2006; Wolfe et al., 2005). In 2003 a global meta-analysis of 1700 species of birds, butterflies and alpine herbs found that 62% of species showed spring advancement over time, by an average of 2.3 days per decade, as a result of rising temperatures (Parmesan and Yohe, 2003). Meta-analyses across taxa in Europe and China have found similar results, with 78% of leafing dates across Europe showing advancement (Menzel et al., 2006), and 90.8% of plant and animal species examined showing advancement in spring and summer in China (Ge et al., 2015). These shifts, however, vary between taxa, which can cause mismatches between different trophic groups (Edwards and Richardson, 2004; Thackeray et al., 2010).

Changes in space have already begun to occur under current levels of climate change, with numerous taxa observed to be shifting their ranges in line with climatic shifts (Chen et al., 2011). Species typically move toward cooler areas, towards the poles or to higher altitudes, as temperatures rise, although this is not consistent across all species (Thuiller, 2004; Parmesan, 2006). Range shifts have been observed to be happening across a wide variety of taxonomic groups, across most of the globe (Chen, et al., 2011;Parmesan and Yohe, 2003; Parmesan, 1996). This also results in range contractions in a wide variety of species, particularly those found in the polar regions and at and high altitudes, due to the fact they inhabit the edge of the thermal range meaning there is nowhere cooler for them to move into (Lesica and McCune, 2004; Foden et al., 2007; Jones et al., 2010; Elmhagen et al., 2015). In order for a species to persist in a warming climate by shifting its range it must have a great enough dispersal ability to move at least as fast as the pace at which its habitat is warming. Many species, however, such as plants with long periods between one breeding event and the next, may lack such dispersal abilities (Dullinger et al., 2004; Pearson, 2006). When such constrained dispersal is combined with the threat of habitat loss, species can have few suitable areas to move into as the climate warms, and those that are available can be heavily fragmented, meaning that even species with the ability to disperse over long distances can have difficulty moving in line with changing climates (Travis, 2003; Thomas et al., 2004).

Climate change can also lead to habitat becoming less suitable for species through the movement of other organisms into that habitat, which can cause conservation problems such as novel predators, diseases or competitors move into areas where they were previously absent. One example is that rising temperatures have been attributed as contributing to amphibian extinctions as a result of the chytrid fungus, as warming meant the fungus was able to extend its range to higher altitudes (Pounds et al., 2006).

Changes in self describes shifts in both the genotype and phenotype of species in response to climate change. Whilst behavioural shifts resulting from climate change are not commonly studied, a large body of research has linked the impacts of temperature and rainfall on behaviour to climate change risks. Observed behavioural shifts at high temperatures include changes in habitat use (Hetem et al., 2012; Cunningham et al., 2015; Pigeon et al., 2016), increased thermoregulatory behaviour (du Plessis et al., 2012; Briscoe et al., 2014), changes in activity (Owen-Smith, 1998; Stokes et al., 2001; Woodroffe et al., 2017), and increased use of human infrastructure (Farmer and Brooks, 2012). Other changes to species phenotype are even less well studied, and disentangling plasticity from evolutionary shifts in response to climatic conditions is challenging (Hoffmann and Sgrò, 2011). Where climate driven plastic and evolutionary changes leading to phenotypic change in species have been disentangled, plasticity has been highlighted as the driver of the changes observed (Gienapp et al., 2008; Ozgul et al., 2010). Whilst there is experimental evidence for evolutionary change driven by changing environmental conditions (Hoffmann and Sgrò, 2011), so far evidence from the field remains sparse, and for longer-lived animals it is unlikely they have the ability to undergo genetic shifts that will keep pace with projected changes in climate (Hetem et al., 2014; Fuller et al., 2016).

There have increasingly been calls for the incorporation of how species respond to climate change into models predicting what impacts climate change will have on species (Kearney and Porter, 2009; Pacifici et al., 2015; Urban et al., 2016), as biotic mechanisms have been found to be key in determining how species respond to changing climatic conditions (Post, 2013). Incorporating how species respond to weather in models predicting climate change risks can identify where species will be most impacted, and which species will be most impacted, more accurately than models lacking this mechanism (Kearney and Porter, 2009), and can give evidence as to what conservation actions should be implemented (Urban et al., 2016). Mechanistic models incorporating physiology were some of the first to be developed. These models use the biophysical characteristics of an organism to identify its temperature niche, and use this to predict the future range of the species, through identifying fitness curves at different temperatures (Strasburg et al., 2007; Kearney and Porter, 2009; Kearney et al., 2010). Mechanistic models can incorporate many ways in which species respond to changing climatic variables, however, including phenotypic shifts, impacts on demography and shifts in dispersal dynamics.

1.1.3.2. Demographic impacts of climate change

Urban et al. (2016) identified six key factors for inclusion in mechanistic models of climate change impact on species: physiology, demography, evolutionary potential, species interactions, dispersal, and responses to environmental variation. Ultimately however, the way in which these mechanisms drive climate change impacts in always intrinsically linked to demography. Temperatures above physiological limits, alongside changes in behaviour such as habitat use or timing of activity, species interactions, and shifts in species range at high temperatures, impact population persistence through effects on survival and recruitment. This means that demographic impacts at high temperatures determine the likelihood of species persistence under future climate change. Demographic change is also particularly important to predict as population declines are often what is used to assign threat status to species (Keith et al., 2014).

Climate change can impact demography through impacting rates of survival, recruitment and the timing of life history events. Key demographic parameters that have been found to be impacted by climatic conditions include fecundity (Stoleson and Beissinger, 1999; Sillett et al., 2000; Møller et al., 2010), survival to adulthood (Griffin et al., 2011; Cunningham et al., 2015; Woodroffe et al., 2017; Jenouvrier et al., 2018), recruitment (where the cause, birth rate vs survival to adulthood, was not determined) (Koons et al., 2012; Bogstad et al., 2013), adult survival (Anctil et al., 2014; Meager and Limpus, 2014; Turbill and Prior, 2016; Jones et al., 2018), timing of breeding (McNutt et al., In Review.; Hill et al., 2000; Weiwei et al., 2012; Plard et al., 2014), and dispersal (Smith, 1974; Walls et al., 2005; Figuerola, 2007).

One of the most commonly observed impacts of climate on demographic traits is falls in recruitment, which has been observed in plants (Doak and Morris, 2010), birds (Bogstad et al., 2013), reptiles (Schwanz et al., 2010), amphibians (Blaustein et al., 2001) and mammals (Koons et al., 2012). Behavioural shifts can be the mechanism by which recruitment falls at high temperatures. For example, in the Southern fiscal, high temperatures lead to changes in foraging behaviour which lower foraging success (Cunningham et al., 2015). Lower foraging success in turn leads to lower chick provisioning which can impact not just the weight of chicks but their survival (du Plessis et al., 2012). Changes in phenology can also have an impact on recruitment, particularly when the timing of breeding in one species falls out of synchrony with the timing of breeding in its primary food species (Miller-Rushing et al., 2010). Another mechanism by which climate change may impact recruitment, particularly in species with temperature dependant sex determination, is by changing the sex ratio of populations, leading to a decrease in breeding individuals, which can lead to reductions in fecundity within the population (Janzen, 1994).

Adult mortality has also been found to be higher at high temperatures (D'Allaire et al., 1996; J.A. Welbergen et al., 2008; McKechnie et al., 2010) and rainfall (McDonough and Loughry, 1997; Dudley et al., 2001; Rittenhouse et al., 2009) in a variety of species. The impact of weather on adult mortality can be through deaths caused by extreme weather events (White et al., 2015), relationships between weather and biophysical limits (Kearney et al., 2008), or through behavioural changes leading to greater human-caused deaths, such as the increase in roadkill observed at higher temperatures (Farmer and Brooks, 2012). In addition to impacts of weather on adult survival, conditions early in life can have subsequent effects on adult phenotype and fitness, and therefore even when the impacts of weather on offspring are sub-lethal, they can still impact demographic traits as adults (Nord and Nilsson, 2016).

Whilst numerous studies have established correlations between weather and demographic variables, examining multiple demographic impacts is key to determining population level effects. A negative impact of weather on one aspect of demography is not enough to determine the impact of shifts in climate at a population level, however. This is because negative impacts on one aspect of demography can be countered by opposing impacts in other aspects, leading to neutral or even positive impacts of climatic shifts (Adahl et al., 2006; Doak and Morris, 2010; Dybala et al., 2013), for example Doak and Morris found that decreasing probabilities of propagules at the Southern edge of species' ranges was balanced out by increasing growth rates and increased fruit production in a number of tundra plant species (Doak and Morris, 2010). Despite this, the incorporation of multiple impacts of weather on demography into population scale models is uncommon (Mitchell et al., 2010; Diez et al., 2014; Merow et al., 2014; Buckley et al., 2015; McCauley et al., 2017), and cases where this has occurred have mostly focused on plants (Doak and Morris, 2010; Tye et al., 2018) and birds (Dybala et al., 2013; Precheur et al., 2016; Velarde and Ezcurra, 2018).

Quantifying the demographics impact of climate change, and the identifying the mechanisms driving such impacts, is particularly important for species that have little potential to shift their range in the face of rising temperatures (Stanton et al., 2015), or for evolutionary adaptation *in situ* as the climate warms (Parmesan, 2006). Many large mammals fall into both these categories, and projecting demographic impacts in time and space will be key in directing future conservation interventions, both in terms of where they are targeted and what actions are taken (Hetem et al., 2014; Fuller et al., 2016). Predicting demographic trends in these species will help to guide conservation planning aimed at ensuring these species persistence into the future.

1.2. Study species

1.2.1. The African Wild Dog

The African wild dog, *Lycaon pictus,* is a highly social, co-operatively breeding carnivore species that historically lived throughout most of sub-Saharan Africa (Creel and Creel, 2002). The majority of wild dog diet is made up of mammals, with impala (*Aepyceros melampus*) being an important food source across most study sites, and species ranging from hares (*Lepus spp*), to baboons (*Papio spp*), to wildebeest (*Connonchaetes taurinus*) found in their diet (Creel and Creel, 1996; Lawes et al., 1999; Creel and Creel, 2002). The composition of wild dog diets varies greatly by site; for example in Laikipia, Kenya wild dog diets consist of on average 80% dikdik (Woodroffe et al., 2007), whereas in Selous, Zimbabwe wildebeest have been found to be the predominant food source, and in Savé valley impala make up 74% of wild dogs' diets (Pole et al., 2004) . Hunting strategy also varies by location and prey type, with wild dogs in more open areas utilising long distance chases to catch and kill prey, while in areas of closed vegetation where wild dogs drive smaller prey from the undergrowth and engage in individual, short, chases (Hubel et al., 2016).

Wild dog packs typically consist of a breeding pair, the alpha male and female, and up to 28 subordinate individuals, alongside dependant offspring (Creel and Creel, 2002). Subordinate individuals usually do not breed themselves but are essential for pack survival, assisting in pup care, foraging and pack defence (Creel and Creel, 2002). When the alpha female breeds she is unable to hunt when heavily pregnant, and pack-mates are needed to kill for her, as well as to feed her when she is at the den for the first few weeks after the pups are born (Malcolm and Marten, 1982; Creel and Creel, 2002). Once the pups are three weeks old the other pack members also provision them with food while they are confined to the den for an average of three months (Malcolm and Marten, 1982). In these three months an individual is left at the den to defend the pups against predators each time the rest of the pack leaves the den to hunt (Malcolm and Marten, 1982). These helping behaviours are essential to pup survival (Creel and Creel, 1995; Courchamp and Macdonald, 2001; Courchamp et al., 2002), and therefore population persistence and growth. Breeding occurs seasonally every 12 months away from the equator, and aseasonally close the equator (McNutt et al., In Review), with dogs in Laikipia, Kenya, breeding on average every 11 months (Woodroffe et al., 2017)

Dispersal plays an important role in African wild dog demography and is essential for maintaining gene flow both within and between populations (Leigh et al., 2012). Pack persistence is closely linked to dispersal as packs only persist as long as their founding members survive, and dispersal is the mechanism through which new packs are formed (Woodroffe, et al., In Review a). Single sex dispersal groups are formed (McNutt, 1996) with an average size of three individuals (Woodroffe, et al., In Review). These groups can either leave a stable pack, or can be formed when an alpha in the pack dies (Woodroffe, et al., In Review). African wild dog packs range widely, with territories of 800km^2 or more, and dispersing individuals can cover thousands of kilometres searching for a dispersal group of the opposite sex (Woodroffe, et al., In Review b; Masenga et al., 2016).

The African wild dog has often previously been used to explore Allee effects, particularly with regards to decreased individual fitness at smaller pack sizes. Larger packs produce larger litters (Creel et al., 2004; Rasmussen et al., 2008; Woodroffe et al., 2017), and hunting success (Creel and Creel, 2002), prey size and energy intake per km travelled depend on pack size (Courchamp et al., 2002; Creel, 1997, Fanshawe and FitzGibbon, 1993) . Subordinate individuals are also essential in fending off kleptoparasites from stealing food once the kill has been made (Fanshawe and FitzGibbon, 1993; Courchamp and Macdonald, 2001). This results in larger packs fending off hyaenas from kills with greater levels of success than smaller packs, although in the largest groups these effects can be outweighed by having to share with more individuals (Carbone et al., 2005). A number of studies have found no decrease in mortality at higher pack sizes (Somers et al., 2008; Angulo et al., 2018). The apparent lower fitness at higher pack sizes has raised concerns of a group level alee effect, whereby small packs fail to persist and die out (Courchamp et al., 2000).

It was previously assumed that larger packs produced larger dispersal groups, which then went on to form new large packs (Courchamp et al., 2000). The converse, whereby small packs produced small dispersal groups, which went on to form small packs, was also assumed to be true (Courchamp et al., 2000). It was assumed that small pack sizes lead to unstable population dynamics where packs went extinct quickly, and there was a high turn-over in the population (Courchamp et al., 2000). Empirical studies however found no evidence of this pack level Allee effect (Somers et al., 2008; Woodroffe, 2011), however, and a more recent model of wild dog population dynamics predicts that dispersal behaviour should decouple pack and population sizes, preventing a group level Allee effect (Lerch et al., 2018). More recently, a study of wild dogs in Laikipia, Kenya, found that large packs produce more groups, as opposed to larger ones, and that the size of the new packs formed by the dispersal groups was not correlated with the size of the original pack from which the founding members of the new pack dispersed (Woodroffe et al., In Review a). This likely explains the lack of group level Allee effects observed in the species.

Lions and hyaenas are the main competitors of African wild dogs, and the literature suggests both can exert a supressing force on wild dog populations. Lions kill wild dogs, although they rarely eat them, and also steal their kills (Creel and Creel, 1996). In some areas of wild dog range, lions are the greatest cause of death in wild dogs, causing up to 47% of adult deaths (Webster et al., 2012). Wild dogs nearly always move away from simulated lion calls, and have rarely been observed to stand their ground against lions attempting to steal a kill, potentially as a result of the threat posed by lions (Creel and Creel, 1996; Mills and Gorman, 1997; Webster et al., 2012; Jackson et al., 2014). Wild dog populations in some areas have been observed to negatively correlated with lion numbers, most likely as a result of direct killing by lions, as well as, to a lesser extent, kleptoparasitism (Webster et al., 2012). Wild dogs den in more rugged areas when lions are present, likely to avoid lion predation on their offspring (Jackson et al., 2014).

Although spotted hyaenas only account for around 4% of adult wild dog deaths, and around 7% of juvenile deaths (Woodroffe and Ginsberg, 1999; Woodroffe, et al., 2007), they are the most common kleptoparasites of the species, and have even been recorded following wild dogs before the wild dogs have made a kill. Wild dogs can lose up to 50% of kills made out in the open to kleptoparasitism, and observed presence of hyaenas at wild dog kills can be as high as 86% (Fanshawe and FitzGibbon, 1993). This can have a large impact on wild dog behaviour, meaning they have to hunt in areas with lower risk of kleptoparasitism, as well as for an extended period of time if their kills are stolen (Carbone et al., 1997). Such kleptoparasitism may have an impact on populations, as a result of the high energetic costs. When kleptoparasitism impacts on wild dogs was modelled, it was suggested that a loss of 25% of kills could require spending 12 hours a day spent hunting as opposed to the observed 3.5 hours (Gorman et al., 1998).

The African wild dog is classified as endangered by the IUCN Red List, today inhabiting just 7% of its historic range, with fewer than 700 packs (equivalent to 700 breeding pairs) left in the wild (Woodroffe and Sillero-Zubiri, 2012). The species is threatened by habitat loss, disease and human-wildlife conflict. Any impacts of climate change are only likely to intensify already existing threats to the species. In order to preserve wild dogs it is essential that areas are identified for conservation priority which account for the shifting climate throughout the species range.

African wild dogs have been found to play a role in driving impala distribution, which has subsequent impacts on vegetation cover (Ford et al., 2014). Other predator species have been found to have similar ecological impacts across a wide variety of ecosystems and therefore are important candidates for climate change impact studies, as their persistence and distribution can drive ecosystem-wide processes, and directly affect prey distribution and dynamics (Peers et al., 2018; Gaynor et al., 2019; Jorgensen et al., 2019). Through studying the impacts of climate change on African wild dog we can examine how temperature can impact the interaction between group and population level effects of temperature, particularly as this species has often been the focus of studies looking at group dynamics in social species (Courchamp et al., 2000; Lunt et al., 2013; Angulo et al., 2018). Many large mammal species such as the African wild dog are both culturally important and comparatively well studied (Hetem et al., 2014), meaning they are ideal candidates for mechanistic models examining the impact of rising temperatures on their persistence and distribution.

1.2.2. Study Methods for the African Wild Dog

Wild dog movement and demography are commonly studied using either VHF - very high frequency - or GPS - geographic positioning system - collars. These collars are used to locate groups of wild dogs, allowing numbers of individuals, behaviour and breeding to be monitored. Radiocollared wild dogs are studied using radio-telemetry, where the animals are located on the ground or by aircraft. When tracked by aircraft the wild dogs can then be found and observed from a vehicle on the ground, and behaviour and number of dogs in the packs are noted. GPS collars record location data at predetermined intervals, along with, in some cases, a measurement of activity and temperature. GPS fixes from collars have been found to be relatively accurate over a large number of studies (van Beest et al., 2012), including on wild dogs (Woodroffe, 2011a), and good collars report 'dilution of precision' - a measure of the precision of the location- allowing the user to reject fixes with a lower level of precision. The locations can be used to establish home range size as well as movements, general ranging behaviour, and day range length, which is the sum of the distances travelled between each location. By locating and following the dogs at intervals during denning, pack size, as well as breeding behaviour, can be monitored, and GPS collars can be used to determine the start and end dates of the denning period through the movement patterns of the dogs as the consistently return to the den site (Woodroffe, 2011a).

In order to collar the animals they need to be anaesthetised, which could potentially entail a number of risks. General anaesthetic has the potential to cause health problems and even death, and in some species handling of animals has been known to cause rejection from social groups (Arnemo et al., 2006). This is particularly important to consider when a species is endangered, as a small fall in population numbers can have a large impact. Although in the past a number of concerns have been raised about survivorship of individuals after handling in wild dogs, evidence shows that this has no effect on mortality (Ginsberg et al., 1995; Woodroffe, 2001). Other studies have indicated that not only does radiocollaring not result in higher mortality, it does not cause chronic stress or heightened aggression (Creel et al., 1997). Monitoring by a number of researchers has shown that whilst immobilisation takes place the pack usually remain nearby, and once the animal is released back into the group no aggression has been recorded towards that individual, which has been found with the pack for a number of weeks after the collar has been fitted (Woodroffe 2011a).

Collaring wild dogs has enabled the collection of a wide array of data on behaviour, population dynamics, movements and territory use. Many GPS collars used today also have inbuilt temperature sensors, allowing relationships to be drawn between the behaviour of the dogs and the temperature of their surroundings. These have the advantage of providing a better resolution than using weather station data to establish temperatures, as well as recording the temperature of the animals’ immediate surroundings. On the other hand temperature readings can be affected by both ambient temperature, sunlight levels, and the body heat of the animal (Markham and Altmann, 2008). Collar data have been found to be more closely correlated with ambient temperature than body temperature in other species, such as moose (van Beest et al., 2012). Many collars have a mortality sensor, which allows researchers to accurately determine when an animal has died much more accurately than through monitoring without GPS collars.

2.2.3. Impacts of weather on the African wild dog

2.2.3.1. Behaviour

The behaviour of wild dogs has been found to be closely linked to temperature in a wide variety of locations throughout their current range. Daytime temperatures force wild dogs to remain inactive for most of the day, only hunting for four hours a day on average, around dawn and dusk (Hayward and Slotow, 2009; Woodroffe, 2011a) (Fig. 1.1). Studies have shown that up to 71% of wild dog activity occurs diurnally, with over 50% occurring between the hours of 06:00 until 08:00 and 18:00 to 20:00, with a period of almost complete inactivity between the hours of 12:00 and 14:00, when temperatures are highest (Hayward and Slotow, 2009).

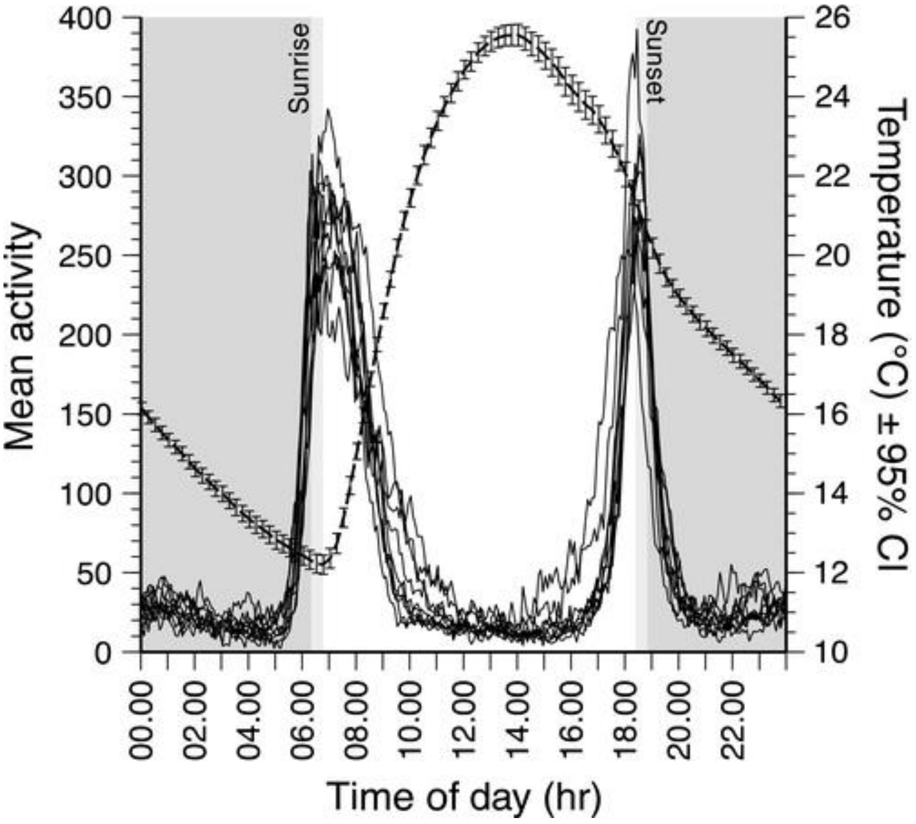


Figure 1.1 Daily activity patterns of African wild dogs in Laikipia, Kenya. Solid lines show mean activity for each 5-min time interval, for 10 GPS-collared wild dogs tracked in 2011–2015; the dashed line shows mean temperature measured every 15 min at a weather station in the study area over 329 days in 2012. Activity can vary between 0 and 510. Shading denotes night-time; lighter shading indicates the annual range in sunrise and sunset times (Woodroffe et al 2017).

Through long term study of wild dogs at an equatorial study site in Laikipia, Kenya, a link between the distance that pack members range and the daily maximum temperature has been established (Woodroffe, 2011a). At higher temperatures African wild dogs are less active in a 24 hour period, suggesting that high temperatures restrict the period which is a suitable temperature for wild dogs to engage in hunting behaviour (Woodroffe et al., 2017). It has been suggested, however, that African wild dogs may benefit from higher temperatures as their larger-bodied prey will be more negatively affected by the heat, leading to shorter chase times and less energy expenditure for hunting wild dogs (Creel et al,. 2016). Establishing whether African wild dogs becomes more active at night following hot days in an attempt to compensate for a loss in energy intake would shed light on the mechanism behind lower activity levels and distances travelled.

2.2.3.2. Recruitment

Temperature-related changes in wild dog hunting behaviour are likely to have an impact on pup survival. During denning periods, pack members have to travel away from the den to find food, and being forced to return to the den early due to higher temperatures may mean that the pups are provisioned with less food at the den. It has been discovered through examining datasets from Kenya, along with two others in Botswana and Zimbabwe, that wild dogs' reproductive success is linked to daily maximum temperatures (Woodroffe et al., 2017).

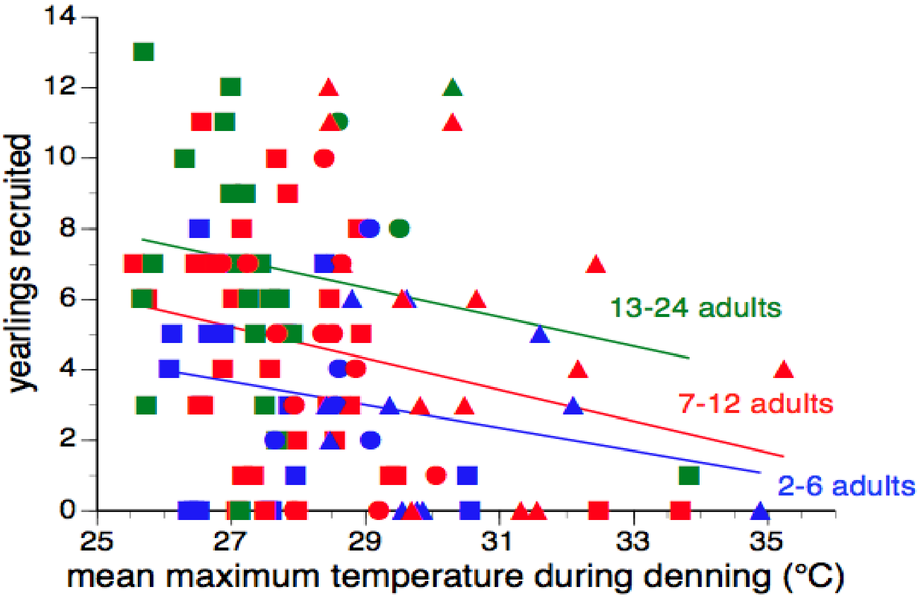


Figure 1.2 Number of yearlings recruited in Botswana, Zimbabwe and Kenya sites against mean maximum temperature during denning (data from Woodroffe, et al 2017). Colours represent different pack sizes.

Away from the equator, in Zimbabwe and Botswana, temperatures vary more substantially with the seasons, and wild dogs raise pups during the coolest part of the year (McNutt et al., In Review). In Kenya, where breeding is aseasonal, higher temperatures during the denning period cause a longer period between one litter and the next within a pack (McNutt et al., In Review). In all three study sites, higher temperatures during the denning period resulted yearlings being produced (Fig. 1.2). These findings provide a clear link between wild dog reproductive success and high maximum temperatures (Woodroffe et al., 2017). Establishing the mechanism behind these correlations is essential in order to gain an in depth understanding of temperature impacts, which is likely to enable improved predictions of the effects of climate change on the species. Alongside this, projecting the impacts of this fall in recruitment under climate change can help shed light on the species' persistence in the future, and indicate which areas may be more suitable for the species' under future climatic regimes.

A previous study of wild dog populations in South Africa, using similar methodology, found that higher levels of rainfall were associated with lower juvenile survival (Buettner et al., 2007). Due to the fact their hunting strategy has a high energetic cost, wild dogs often preferentially take prey that is in poor condition (Pole et al., 2004). Studies have shown mixed effects of rainfall on wild dog recruitment across sites, with some study sites showing increased pup survival when rainfall levels are higher, and others showing the reverse relationship (Buettner et al., 2007; Woodroffe et al., 2017). Further analysis is needed to establish rainfall effects throughout the wild dogs' geographic range, as this would be a factor in where wild dogs can persist under climate change, especially in light of the expected rainfall shifts across the continent in the future.

2.2.3.2. Adaptation

Changes in climate often result in species shifting their geographic range in response to changes in temperature and rainfall (Walther et al., 2002). In the case of wild dogs their range is limited by the Sahara Desert to the North, where there is little water or prey. South of their current range, former habitat within South Africa is increasingly fragmented by clearance for agricultural use, with very few areas of suitable habitat remaining. Both areas of the Sahara and much of Southern Africa, although part of their historic range, became unsuitable for the species over 80 years ago (Woodroffe and Sillero-Zubiri, 2012).

It is likely that any range shift would result in increased contact with humans, putting the species at further risk of deliberate and accidental killing and disease, to which wild dogs are already vulnerable (Woodroffe et al., 2007). There may be scope for human-assisted range shifts, however many of the areas of suitable habitat where the species is absent are heavily fenced, which would impinge on the species' dispersal dynamics, and re-introductions of the species have had mixed results (Gusset et al., 2007; Gusset et al., 2010). On top of this, the generation time of African wild dogs (5 years) means that any evolutionary change is unlikely to be able to keep pace with future temperature rises (Hoffmann and Sgrò, 2011).

Behavioural adaptation, through shifting to nocturnal hunting, is a key mechanism by which wild dogs could potentially avoid the heat, and therefore mitigate the impact of high temperatures. African wild dogs are less nocturnal than many other African predators, following a highly crepuscular activity pattern (Hayward and Slotow, 2009). African wild dogs have been found to increase their nocturnal activity, however, in response to human pressures (Rasmussen and Macdonald, 2012) and when there are high levels of moonlight (Cozzi et al., 2012). To date, there has been no published work on the effects of daytime temperature on wild dog activity at night. As high daytime temperatures appear to limit time spent active by individuals during daylight hours (Woodroffe et al 2017), and therefore potentially hunting, however, high daytime temperatures could potentially prompt higher levels of nocturnal activity. Impacts of temperature on night-time activity and ranging behaviour are something that is in need of further investigation, particularly as existing data are already available.

Wild dogs' lower nocturnal activity in comparison with other African carnivores in wild dogs may be a result of two factors. Sight is thought to be the most important sense for wild dogs when hunting (Estes and Goddard, 1967), which, if correct, would suggest that hunting at night is limited by their visual capabilities. This may explain why wild dogs are more active at higher moonlight levels (Cozzi et al., 2012). Equally, the main competitor species of wild dogs, lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), are nocturnal, and therefore crepuscular activity may be an adaptation to avoid overlap in time spent hunting between wild dogs and other more nocturnal species such as lions and hyaenas, which both kill wild dogs and steal their kills (Hayward and Slotow, 2009). Climate change is predicted to result in increased temperatures (Barros et al., 2014), further limiting the proportion of daylight hours when it is cool enough for wild dogs to hunt. It is unclear at present whether wild dogs can hunt successfully enough at night to meet their energetic requirements, and therefore whether they could shift to nocturnal hunting in response to rising temperatures. As there is little potential for wild dogs to adapt to climate change through shifts in phenology, range or evolution, behavioural shifts such as increased nocturnality are likely to be key in determining whether they persist under rising temperatures.

1.3. Research questions

Using data from African wild dogs, in this thesis I investigate a number of key research questions. Chapter 2 of this thesis explores the extent to which African wild dogs can adapt to rising temperatures through switching their activity to nocturnal periods, as well as examining the relationship between other environmental and demographic variables, such as rainfall, moonlight and pack status, on timing of activity and distances travelled. I hypothesise that wild dogs will be less active and travel shorter distances in the day when temperatures are higher, and more active and travel longer distances on nights following hot days.

Chapter 3 of this thesis investigates whether temperature and rainfall are associated with adult mortality in the African wild dog and examines the relationship between high temperatures and cause of death in the species. I also examine relationships between a number of demographic and environmental variables, including pack size, pack status, age and rainfall, on survival in the species. I hypothesise that wild dogs will have lower survival rates following periods of high temperature.

Chapter 4 combines the impact of high temperature on recruitment and survival in the African wild dog population Laikipia, Kenya, into an individual based model. This model allows me to observe how the population responds to high temperatures, and allows me to project population impacts of future climate scenarios for the area. I hypothesise that the wild dog population will decrease in size, and be less likely to persist under higher temperatures and more extreme climate scenarios.

In Chapter 5, I modify the individual based model from Chapter 4 into three demographic scenarios for the African wild dog, and use it to project how future climate change scenarios are likely to impact African wild dog populations across their range. I then use this to identify where in the species current, possible and recoverable range is mostly likely to be suitable for the species in the future, and use projected population and range declines to predict future IUCN Red List status for the species. I hypothesise that predicted population declines will be worse under more extreme climate change scenarios, and that the area that is climatically suitable for the African wild dog will be predicted to shrink under future climate change scenarios.

Chapter 2 of this thesis has been published in the journal *Oecologia* (Rabaiotti and Woodroffe, 2019).

Plate 2: Male African wild dog with GPS collar, Laikipia, Kenya

Chapter 2 Coping with climate change: limited behavioural responses to hot weather in a tropical carnivore

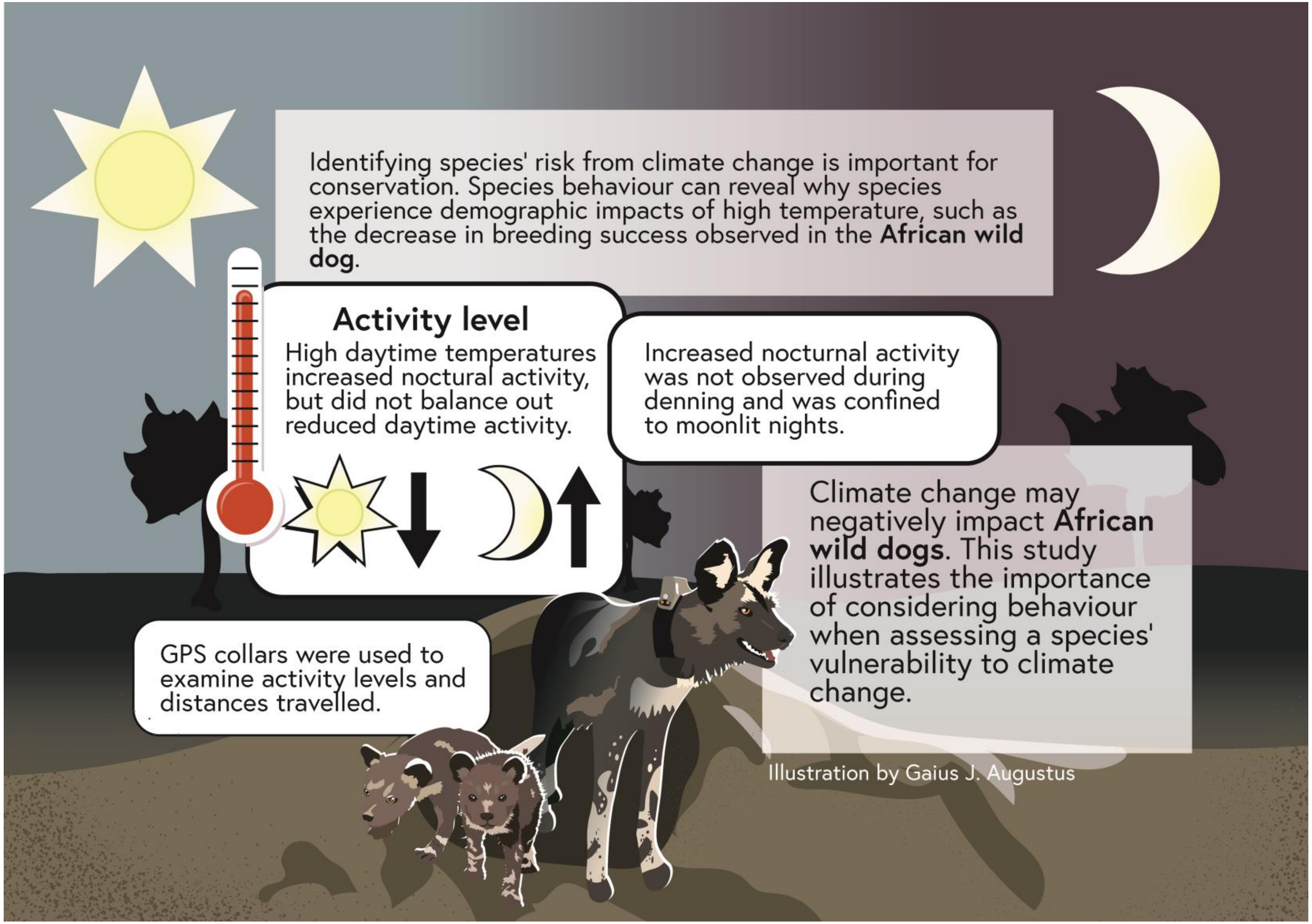
2.1. Abstract

Climate change is widely accepted to be one of the greatest threats to species globally. Identifying the species most at risk is therefore a conservation priority. Some species have the capacity to adapt to rising temperatures through changing their phenology, behaviour, distribution, or physiology, and, therefore, may be more likely to persist under rising temperatures.

Recent findings suggest that the African wild dog *Lycaon pictus* may be impacted by climate change, since reproductive success is consistently lower when pup-rearing coincides with periods of high ambient temperature. We used GPS collars, combined with generalised linear mixed effects models, to assess wild dogs' potential to adapt to high ambient temperatures through flexible timing of hunting behaviour. On days with higher maximum temperatures, wild dogs showed lower daytime activity and greater nocturnal activity, although nocturnal activity did not fully balance the decrease in daytime activity, particularly during the denning period. Increases in nocturnal activity were confined mainly to moonlit nights, and were seldom observed when packs were raising pups.

Our findings suggest that nocturnal activity helps this cursorial hunter to cope with high daytime temperatures. However, wild dogs appear not to use this coping strategy when they are raising pups, suggesting that their resource needs may not be fulfilled during the pup-rearing period. Given that moonlight availability – which will not change as the climate changes – constrains wild dogs' nocturnal activity, the species may have insufficient behavioural plasticity to mitigate increasing diurnal temperatures. These findings raise concerns about climate change impacts on this endangered species, and highlight the need for behaviour to be considered when assessing species' vulnerability to climate change.

Graphical abstract



Identifying species' risk from climate change is important for conservation. Species behaviour can reveal why species experience demographic impacts of high temperature, such as the decrease in breeding success observed in the **African wild dog**.

Activity level

High daytime temperatures increased noctural activity, but did not balance out reduced daytime activity.

Increased nocturnal activity was not observed during denning and was confined to moonlit nights.

GPS collars were used to examine activity levels and distances travelled.

Climate change may negatively impact **African wild dogs**. This study illustrates the importance of considering behaviour when assessing a species' vulnerability to climate change.

Illustration by Gaius J. Augustus

2.2. Introduction

As the climate warms, declines in wildlife population sizes and species richness, coupled with shifts in species distribution, are predicted to occur worldwide, across a wide variety of flora and fauna (Walther et al., 2002; Bellard et al., 2012). A number of studies have shown that climate change is already having an impact across a range of species, including phenological shifts (Parmesan and Yohe, 2003), geographic range shifts and contractions (Parmesan, 2006; Tingley et al. 2012), and population and species extinctions (Parmesan, 1996; Beever, Brussard, and Berger, 2003; Pounds et al., 2006, Sinervo et al. 2010).

Behavioural plasticity has the potential to buffer climate change impacts on wildlife. Species as diverse as the koala *Phascolarctos cinereus* (Briscoe et al. 2014), Arabian oryx *Oryx leucoryx* (Hetem et al. 2012), and Southern fiscal *Lanius collaris* (Cunningham et al. 2015) respond to high ambient temperatures by changing their behaviours. Such plasticity has the potential to mitigate climate change impacts (Martin et al. 2015). However, these thermoregulatory behaviours often come with a fitness cost, such as a decrease in foraging time, or reduced vigilance, which may impact survival and reproduction as the climate warms (Sinervo, B., et al. 2010; du Plessis et al. 2012; Cunningham et al. 2013, 2015; Turbill and Prior 2016). Species' behavioural responses are therefore likely to be key in determining the extent to which a species is impacted by rising temperatures.

Species can adapt to climate change in three ways: adaptation in time, whereby they shift their phenology, moving the timing of critical life events, such as breeding, in response to changing seasonality; adaptation in space, where species' ranges shift to remain within appropriate climatic conditions; and adaptation in self, whereby individuals of a species alter their behaviour or physiology in response to changing temperatures (Foden et al. 2013, Pacifici et al., 2015). Such adaptation to climate change can either occur through evolutionary change, whereby traits are inherited through generations, or through phenotypic plasticity, whereby species' traits are altered without altering their genes, often within the lifetime of an individual, in ways which mitigate climate change impacts. These traits can include species' physical characteristics, geographic range, physiology or behaviours, as well as changes to species phenology. However, most studies and models of climate change vulnerability either look solely at the correlation between species occurrence and climatic variables, ignoring the underlying mechanisms of climate change impacts (Kearney, Wintle and Porter, 2010; Pacifici et al., 2015), or else focus on physiological rather than behavioural traits (Bellard et al., 2012). Where models have incorporated behavioural thermoregulation, they have generally been focused on ectotherms (Kearney et al., 2009; Huey et al., 2012).

Ambient temperatures are predicted to rise significantly over the next 50 years, and Africa is projected to experience greater warming than the global average (IPCC, 2014). African species may therefore face particularly high extinction risks under climate change. We therefore explored the role of behavioural plasticity in a species vulnerable to climate change, the African wild dog *Lycaon pictus*.

The African wild dog is a highly social carnivore, with pack members cooperating to hunt, raise young, and defend resources (Creel and Creel, 2002). The species is globally endangered; the wild population numbers fewer than 700 packs, confined to just 7% of the species' former range within sub-Saharan Africa (Woodroffe and Sillero-Zubiri, 2012). Being highly mobile, with a relatively flexible diet, the species has few of the traits typically associated with climate change vulnerability (Bellard et al., 2012; Pacifici et al., 2015). Indeed, it has been suggested that wild dogs may benefit from rising temperatures that may reduce the ability of large-bodied prey, for example wildebeest (*Connochaetes taurinusto*), to outrun smaller-bodied predators such as African wild dogs (Creel, et al., 2016). However, demographic evidence indicates consistently harmful effects of hot weather on wild dogs, with high ambient temperatures associated with lower recruitment across multiple populations (Woodroffe, Groom, and McNutt, 2017) . Wild dogs hunt less on hot days, and these demographic impacts may reflect consequently lower food intake (Woodroffe, Groom, and McNutt, 2017).

A primary opportunity for African wild dogs to adapt to rising temperatures is through a change in self. Shifting activity to night-time, which is cooler than daytime, has been suggested as one of the primary ways large mammals may mitigate the impacts of rising temperatures (Fuller et al., 2016). Wild dogs are crepuscular, hunting for one to two hours at dawn and dusk (Creel and Creel, 2002, Cozzi et al., 2012, Woodroffe, Groom and McNutt, 2017). However, nocturnal hunts also occur (Cozzi et al., 2012), especially on moonlit nights, and increasing the frequency of nocturnal hunting might allow wild dogs to exploit lower night-time temperatures, potentially offsetting climate change impacts. Such a coping strategy might be especially important during the three-month period each year when pups are confined to a den and adults' energy demands are highest (Woodroffe, Groom and McNutt 2017).

We explored the potential for African wild dogs to cope with high daytime temperatures by increasing nocturnality. We predicted that wild dogs' night-time activity and ranging distance would be greater (i) following hot days, (ii) on moonlit nights, and (iii) during the pup rearing (denning) period.

2.3 Materials and Methods

2.3.1. Study Area

The study area covers Laikipia county in Northern Kenya (37°2'E, 0°6'N), and parts of neighbouring Samburu, Isiolo and Baringo counties. The habitat mainly comprises semi-arid bushland and savannah, with livestock farming and tourism as the primary land uses. Despite not being formally protected, as the majority of land is under private or community ownership, many landowners promote wildlife and tourism alongside pastoralism and ranching activities, leading to high levels of wildlife abundance and diversity. Mean annual rainfall is 590mm varying from around 400mm per year in the North East to over 900mm per year in the South West, with highly variable seasonality. Daily maximum temperatures range from 25-36°C with minimum temperatures falling between 12° and 17°C (Caylor K.K., Gitonga, J., Martins 2016). Wild dogs in this population feed primarily on dikdiks (*Madoqua spp.*) and impala (*Aepyceros melampus*; Woodroffe et al. 2007).

2.3.2. Field Data Collection

Data were collected between 2011 and 2016. We fitted GPS-collars (GPS-plus, Vectronic Aerospace GmbH, Berlin, Germany) to 15 wild dogs in 8 different packs; there was only one active GPS collar on each pack at any one time. Wild dogs were darted from a vehicle from a distance of 10-15 metres - further details of collar deployment methods are provided in Woodroffe (2011a). Individual wild dogs were GPS-collared for an average of 207 days (sd = 126); details of the monitoring dates and packs of individual study animals are shown in Online Resource 1. The collars contained accelerometers that recorded average acceleration in two (unspecified) dimensions every 5 minutes on a scale of 0 to 255. GPS collars were programmed to record locations at specific times throughout the day and night. The programmed number of GPS locations per 24 hour (24h) period varied between individuals from 6 to 13 (Online Resource 2). The GPS collars incorporated VHF beacons, and additional pack-members were also fitted with VHF collars to help locate the pack in case of GPS collar failure. We downloaded the data from GPS collars over a remote VHF link. We also made visual observations of wild dog behaviour throughout the study which corroborated the timing of periods of activity recorded by the collars. We identified denning dates, and dates when packs moved den sites, using GPS collar data, based on the distinctive movement pattern of repeatedly returning to the same location (Woodroffe, 2010). African wild dog packs switch den sites multiple times throughout a denning period – with an average of 5 den moves (s.d. 2.85) from birth until the last den is abandoned when pups are approximately 3 months old (Woodroffe, Groom and McNutt, 2017). Because den site changes repeatedly during the denning period, the number of days spent at each den site is not strongly correlated with pup age (Online Resource 3).

2.3.3. Variables analysed

We analysed two types of dependent variable: activity, and distance travelled. We calculated activity by summing accelerometer data for each 5min period from the two planes and then converting to percentages of the maximum value (510) to give a measure of activity from 0 to 100. Mean daytime activity was then calculated for the period between sunrise and sunset at the study site, and mean night-time activity was calculated for the period between sunset and sunrise (obtained from the US Naval Observatory (http://www.usno.navy.mil/). Mean activity across each 24h period between successive sunrises was also calculated.

We calculated distance travelled using GPS-collar locations. To avoid the influence of differing numbers of GPS points (i.e. spatiotemporal resolution) on the measures of distance travelled, the same six time points were used across all individuals: 06:30, 08:00,13:00, 18:00, 19:30, and 01:00 (see Online Resource 2). We estimated distance travelled by calculating the distance between consecutive GPS locations, then summing the distances 06:30-08:00-13:00-18:00 to give daytime distance travelled, 18:00-19:30-01:00-06:30 to give night-time distance travelled, and 06:30-08:00-13:00-18:00-19:30-01:00-06:30 to give 24h distance travelled (Online Resource 2). Periods when a GPS collar failed to record a location at one or more of the selected time points were discarded; the probability of at least one missing location was greater for longer periods, hence more 24h periods were discarded than daytime or nightime periods, leading to a lower sample size of 24h periods (Online Resource 3).

Typically, one pack member stays at the den guarding the pups while the rest of the pack hunts (Malcolm and Marten, 1982; Creel and Creel, 2002). To better represent the hunting behaviour of the pack during denning periods we excluded days when collared animals remained <200m from the den at times when the pack would normally hunt (06:30-08:00 or 18:00-19:00). Online Resource 3 shows the numbers of observations of activity and distance travelled analysed for each individual.

We tested the hypothesis that wild dogs nocturnal activity and ranging distance was greater following hot days by comparing activiy and distances travelled with dry bulb daily maximum air temperature (the highest temperature (in °C) within a 24h period). In models of nocturnal activity and distance travelled, maximum daily temperature referred to the preceding period of daylight. As heat stress is also effected by capacity for evaporative cooling, we also included total daily rainfall (mm) as an independent variable. Temperature and rainfall were measured at Mpala Research Centre (37° 2' E, 0° 6' N), within the study area (Caylor K.K., Gitonga, J., Martins 2016). We tested the hypothesis that wild dogs were more active and travelled further on moonlit nights by comparing activity and distances travelled with levels of moonlight, which were estimated (from data at http://www.usno.navy.mil/) as the number of hours the moon was in the sky between sunset and sunrise (0-12h), multiplied by the proportion of the full moon that was illuminated (0-1) to give a combined moonlight variable measured in full-moon-hours (0-12; Online Resource 5). For example, a moonlight value of 12 would indicate a full moon for 12 hours between sunset and sunrise. The moonlight variable did not account for cloud cover as these data were not available, however we would expect cloud cover to be correlated with rainfall. We tested the hypothesis that wild dogs were more active and travelled further during the denning period by comparing activity and distances travelled with reproductive status, was represented as denning/not denning. As behaviour during he denning period is impacted by days since occupying a particular den site and pup age (in days) (Woodroffe, Groom and McNutt 2017), these were included as independent variables in models of the denning period (Online Resource 4).

2.3.4. Statistical Analyses

We used generalised linear mixed effects models to investigate the associations between independent variables (maximum daily temperature, daily rainfall, moonlight, pack reproductive status, days spent at a den site, and pup age) and dependent variables (activity, distance travelled). In addition to these fixed effects we also included individual identity as a random effect. One set of models considered both denning and not denning periods, and included daily rainfall, maximum daily temperature, moonlight, and denning (yes/no) as independent variables. A second set of models considered data only from the denning periods. These denning-specific models included daily rainfall, maximum daily temperature, moonlight, pup age, and the number of days since occupying the den site (Online Resource 4). We also examined two-way interactions where they were considered to be potentially ecologically relevant (Online Resource 4).

Due to the distribution of the model residuals (Online Resource 6) gamma generalised linear mixed effects models were fitted to all datasets. Residuals were checked for normality and heterogeneity by eye using Q-Q plots (Online Resource 7). An information theoretic approach was used to select the top model set, comparing the corrected AIC (AICc) between models. As this approach yields several acceptable models, a model averaging approach was used to determine final estimates (Burnham and Anderson, 2002). The relative importance of fixed effects was evaluated by averaging the top models using Akaike weights (ΔAIC ≤ 5). As some literature suggests that ΔAIC ≤ 2 (Harrison et al., 2018) should be used as a cut off we also report the number of models in the ΔAIC ≤ 2 set that each fixed effect was included in. Tables of the top models are presented in Online Resource 8. All independent variables were tested for intercorrelation and all Pearson's correlations were found to be below $r=0.25$ (Online Resource 9). We carried out all analyses in R version 3.3.2 (R Core Team 2018) and used the *lme4* (Bates et al., 2015) package to fit models and model averaging was carried out using the package *MuMIn* (Barton, 2018) .

2.3.5. Projections

In order to examine how wild dog activity and distance travelled might change in the future under climate change we projected the models into the year 2070 under a variety of climate scenarios. We first defined the study area by drawing minimum convex polygons around the GPS locations used to calculate the distance travelled data for each wild dog, and these minimum convex polygons were then merged to give a single (non-convex) polygon. Current estimates (representative of the years 1960-1990) and future projections (for the year 2070) of mean monthly maximum temperature (the monthly mean of daily maximum temperature) and total monthly rainfall for the study site, at a spatial resolution of 30 arc seconds, were taken from WorldClim 1.4 (Hijmans et al., 2005). For future projections the dataset from the HADGEM2 climate model was used for both the best case scenario (Representative Concentration Pathway 2.6) and worst case scenario (Representative Concentration Pathway 8.5) (IPCC, 2014) predictions. For both WorldClim estimates (the current estimates and the future projections), we calculated mean daily maximum temperature and mean daily rainfall by averaging the estimates for all 12 months of the year for each pixel and dividing total monthly rainfall by 30 to give a daily average. A diagram illustrating these calculations can be found in Online Resource 10.

Estimated current mean daily maximum temperature for the study site from WorldClim estimates was significantly lower (mean 2.7°C lower) than the average daily maximum temperature taken from the weather station throughout the duration of this study (2011-2016), and estimated mean daily rainfall was higher (mean 0.4mm) than the average value from the weather station throughout the duration of this study (2011-2016). These differences are likely due to the interpolation method used by WorldClim, based on poor weather station coverage across Africa (UNECA, 2011), as well as the fact that WorldClim estimates were calculated for the whole study site rather than the location of the weather station alone. As the WorldClim current estimates differed consistently from the measurements from the weather station in the study site, which were used to build our models, two predicted change variables were created by subtracting the WorldClim estimate of current temperature across the study site, at a resolution of 30°, from the projected future temperature across the study site, at a resolution of 30°. This procedure was then repeated for current and future rainfall. The average projected changes in temperature and precipitation were calculated by taking the mean across all pixels across the study site in the predicted change rasters. We then calculated the average activity and distances travelled under current temperature conditions using the mean values from the weather station on site, and calculated the values predicted by the model of denning and non-denning periods combined, and for the denning period only. To get future predictions of activity and distances travelled we added the predicted change in temperature and precipitation, derived from the WorldClim estimates, to average temperature and precipitation from the weather station data, and used these values to calculate activity and distances travelled predicted by the models of denning and non-denning periods combined, and the non-denning period only, under the expected changes in temperature and precipitation. Current mean activity and distances travelled was then subtracted from future activity and distances travelled to get the predicted future change in the dependant variables between now and 2070. Analyses were carried out using the *rgdal* (Bivand et al., 2017), *raster* (Hijmans, 2017), *sf* (Pebesma, 2018), *maptools* (Bivand and Lewin-Koh, 2017) and *rgeos* (Bivand and Rundel, 2017) packages.

2.4. Results

Our analyses suggested that temperature, rainfall and denning status were all important predictors of African wild dog activity and distance travelled by day. During daylight hours, wild dogs were less active and travelled shorter distances on days when maximum daily temperatures were higher throughout both the denning and non-denning periods (Table 2.1, Fig. 2.1). Wild dogs also travelled less far when daily rainfall was higher during both denning and non-denning periods, but rainfall had a smaller effect, and was of lower importance, in the models of the denning period alone. An interaction between the effects of maximum temperature and rainfall was included in all top model sets, however the effect size was small, with the 95% confidence interval crossing zero in all cases other than the models for activity in the denning and non-denning periods combined. Rainfall appears to slightly lessen the impact of high temperatures on daytime activity and distances travelled, however this effect is less pronounced, or even reversed in the case of distance travelled, during the denning period (Table 2.1).

Table 2.1: Variables associated with wild dog activity and distance travelled during **daylight hours**.
Averaged estimated effects of predictor variables on the daily distance travelled, and average activity, of wild dogs during dawn and dusk, for the whole dataset and whilst wild dogs were denning, estimated using generalised linear mixed effects models. As the residuals were gamma distributed an exponent of the values should be taken to obtain true estimates. Relative importance of each parameter is shown along with the number of models in the Δ<2 and Δ<5 model sets that contain each variable (n,n). Maximum temperature = maximum daily temperature (°C) during the 24hr period (dawn-dawn) and Daily rainfall = rainfall over 24 hour period (mm). Variables where no estimate is shown were dropped from the final model as likelihood ratio tests showed models including those variables did not differ significantly from the null model. Individual identity was included as a random variable.

		Activity			**Distance travelled (km)**		
Period	**Variable**	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***
All	Intercept	3.58	3.4 – 3.8	(1,3)	1.88	1.6 – 2.1	(4,5)
	Maximum temperature (°C)	-0.035	-0.04 – -0.03	1.00 (1,3)	-0.028	-0.04 – -0.02	1.00 (4,5)
	Daily rainfall (mm)	-0.045	-0.06 – -0.03	1.00 (1,3)	-0.012	-0.05 – 0.02	0.95 (4,4)
	Denning (Yes)	0.13	0.1 – 0.2	1.00 (1,3)	0.54	-0.1 – 1.01	1.00 (4,5)
	Maximum temperature * Daily rainfall	0.0022	0.001 – 0.003	0.97 (1,2)	0.001	-0.0002 – 0.004	0.38 (2,2)
	Maximum temperature * Denning (Yes)	0.000044	-0.01-0.1	0.27 (0,1)	-0.028	-0.5 - -0.002	0.37 (2,2)
Denning	Intercept	3.62	3.2 – 3.9	(3,6)	2.47	1.7 – 3.3	(4,10)
	Maximum temperature (°C)	-0.034	-0.05– -0.02	0.98 (3,6)	-0.049	-0.08 – -0.02	0.8 (3,7)
	Daily rainfall (mm)	-0.044	-0.1 – 0.01	0.85 (3,5)	-0.012	-0.05 – 0.02	0.38 (1,6)
	Days at den	0.0016	-0.001 – 0.002	0.95 (3,6)	0.0059	-0.001– 0.01	1.00 (4,10)
	Pup Age	0.00051	-0.00009-0.001	0.78 (2,4)	-0.0025	-0.003 - -0.001	0.60 (2,7)
	Maximum temperature *Days at den	0.0034	0.002 – 0.005	0.22 (1,2)	0.00075	0.0002 – 0.001	0.07 (0,2)
	Maximum temperature *Rainfall	0.00015	-0.00001 – 0.0003	0.48 (2,2)	-0.0056	-0.01 – 0.001	0.10 (0,2)

In line with hypothesis iii) wild dogs were more active and travelled further during the denning period (Table 2.1, Fig. 2.1). During the denning period, wild dogs were also more active and travelled longer distances when the pack had spent more days using a specific den site (Table 2.1). The interaction between days using a den site and maximum temperature was of low importance, included in 2 out of 6 of the top model sets, with a small positive interaction between maximum temperature and days spent at the den site. Pup age was included in the top model sets of activity and distance travelled during the denning period, and had a small negative effect on both.

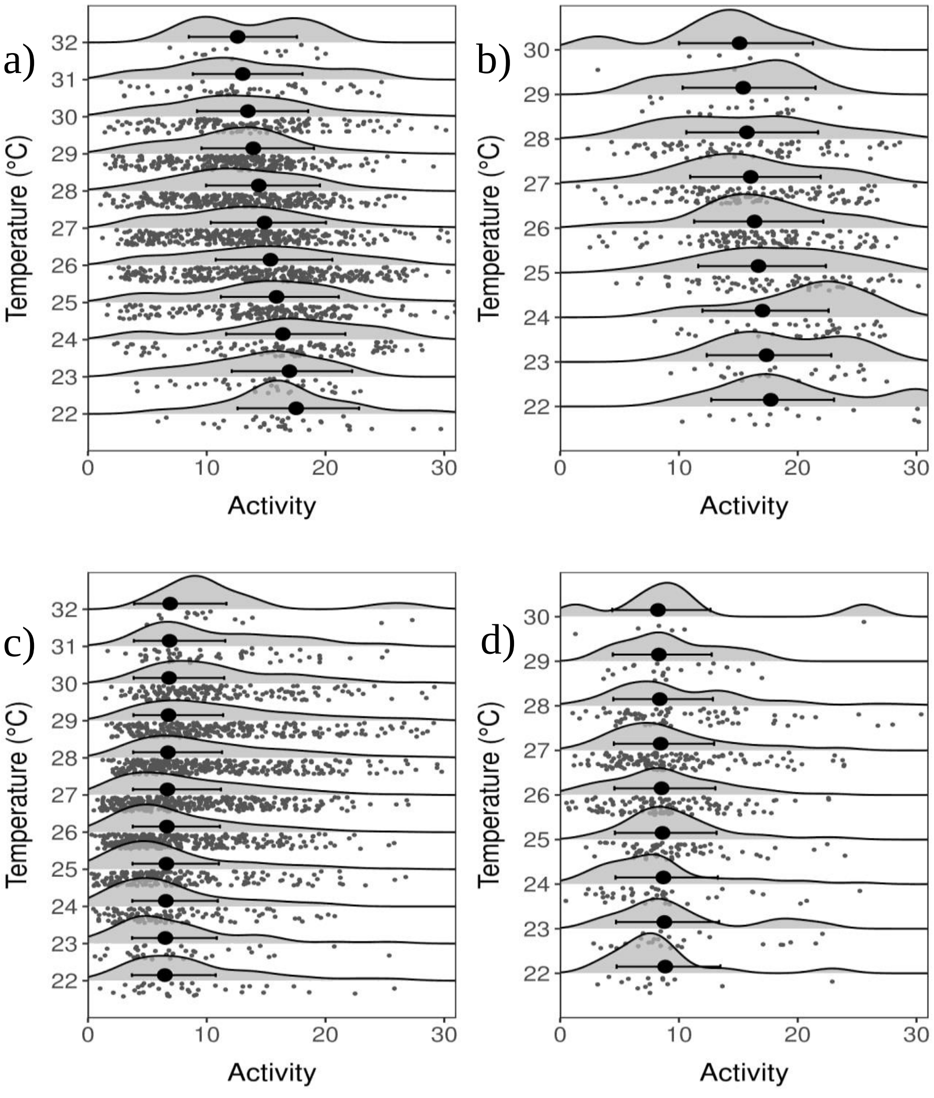


Figure 2.1 Relationships between African wild dog activity and maximum daytime temperature during (a) daylight hours outside the denning period (b) daylight hours inside the denning period (c) night-time hours outside the denning period and (d) night-time hours inside the denning period. Grey points represent the raw data, with the shaded curves representing the kernel density of the data in that 1°C temperature band. Black circles represent model estimates, with black horizontal lines indicating standard errors. The model outputs were calculated using mean vales for rainfall and moonlight.

2.4.2. Night-time activity and distance travelled

Moonlight, temperature, rainfall and denning status were important predictors of wild dog activity and distances travelled by night. In line with hypothesis i) packs increased night-time activity and distance travelled following hot days outside the denning period, (Denning (No) in Table 2.2). Contrary to our predictions, however, wild dogs did not significantly increase their nocturnal activity and distances travelled following hot days when denning (Table 2.2). The lack of increase in activity and distances travelled following hot days is indicated by negative interactions between the effects of temperature and denning on both distance travelled and activity levels in the models of denning and non-denning periods combined. This pattern is also shown by the 95% confidence intervals in the models of activity during the denning period crossing zero, and the negative relationship between temperature and distances travelled during the denning period (Table 2.2). Rainfall was of high importance for the denning and non-denning periods combined, being included in all top models for activity, and 3 out of 4 top models for distance travelled. Rainfall was included in a much lower proportion of the top models in the denning period, and the effect sizes were smaller. African wild dogs were more active at night when rainfall was higher.

As predicted in hypothesis ii) wild dogs were more active and travelled further when levels of moonlight were higher for denning and non-denning periods (Fig. 2.2, Table 2.2).

In line with hypothesis iii) wild dogs were more active and travelled further during the denning period than outside it. Days at den and pup age were of relatively low importance as predictors of wild dog activity and distances travelled during denning, and the 95% confidence intervals associated with the effect sizes crossed zero in all cases. Within the models for activity in the denning period only, there was an interaction between the effects of maximum temperature and days spent at a particular den site included in the top model set, however this variable was included in just 1 of the top 8 models and the effect size was small (Table 2.2).

Table 2.2: Variables associated with wild dog activity and distance travelled during **night-time**.
Average estimated effects of predictor variables on the distance travelled and average activity of wild dogs from dusk to dawn, for the data as a whole and whilst the dogs were denning, estimated using generalised linear mixed effects models. As residuals were gamma distributed the exponent of the values should be taken to obtain true estimates. Relative importance of each parameter is shown along with the number of models in the Δ<2 and Δ<5 model sets that contain each variable (n,n). Shaded cells indicate variables that were not in any of the models with delta <5. Maximum temperature = maximum daily temperature (°C) during the 24hr period (dawn-dawn) and Daily rainfall = rainfall over 24 hour period (mm). Variables where no estimate is shown were dropped from the final model as likelihood ratio tests showed models including those variables did not differ significantly from the null model. Individual identity was included as a random variable.

		Activity			**Distance travelled (km)**		
Period	**Variable**	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***
All	Intercept	0.71	0.5 – 0.9	(2,3)	0.71	0.3 – 1.0	(3,5)
	Moonlight	0.039	0.03 – 0.05	1.00 (2,3)	0.019	0.02 – 0.04	1.00 (3,5)
	Maximum temperature (°C)	0.050	0.04 – 0.06	1.00 (2,3)	0.033	0.02 – 0.04	0.97 (3,5)
	Daily rainfall (mm)	0.051	0.01 - 0.08	1.00 (2,3)	0.016	-0.03 – 0.06	0.71 (2,4)
	Denning (Yes)	0.72	0.2 – 1.2	1.00 (2,3)	0.54	-0.4 – 1.6	1.00 (3,5)
	Denning (Yes)*Maximum temperature	-0.031	-0.05 - -0.02	0.73 (1,2)	-0.063	-0.09 - -0.03	0.53 (2,2)
	Rainfall * Maximum temperature	-0.0026	-0.004 - -0.001	0.85 (2,2)	-0.0018	-0.004 – 0.0005	0.26 (1,2)
Denning	Intercept	1.82	1.4-2.3	(2,8)	1.40	1.8 – 3.9	(6,10)
	Moonlight	0.039	0.03 – 0.05	1.00 (2,8)	0.0019	-0.01 - 0.01	0.31 (1,4)
	Maximum temperature (°C)	0.016	-0.3 - 0.004	0.57 (1,6)	-0.013	-0.05 - -0.02	0.34 (2,5)
	Daily rainfall (mm)	0.0025	-0.023 – 0.028	0.29 (0,4)	0.00058	-0.04 – 0.04	0.20 (1,3)
	Days at den	-0. 0094	-0.03 - 0.007	0.31 (0,4)	0.0015	-0.01 - 0.01	0.38 (2,3)
	Pup Age	0.00008	-0.0002 – 0.002	0.19 (0,2)	-0.000015	-0.002 – 0.002	0.15 (1,1)
	Maximum temperature *Days at den	0.0014	0.0009 – 0.002	0.08 (0,1)	0.0028	0.001 – 0.004	0.01 (0)
	Maximum temperature *Rainfall	-0.00095	-0.004 – 0.002	0.02 (0,0)	-0.0023	-0.01 – 0.0018	<0.01 (0)

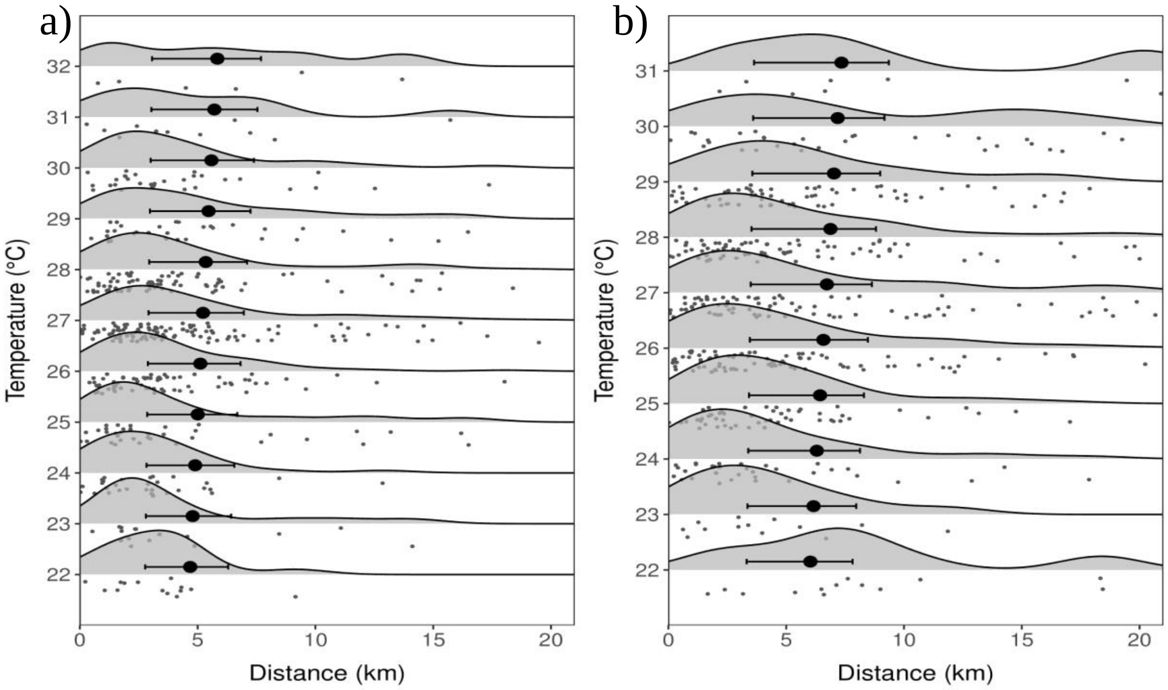


Figure 2.2 Relationship between daytime maximum temperature and subsequent night-time distances travelled by African wild dogs outside the denning period on nights with a low (0 h full moon equivalents) and b high (12-h full moon equivalents) levels of moonlight. Grey points represent the raw data, with the shaded curves representing the kernel density of the data in that 1 °C temperature band. Black circles represent model estimates, with black horizontal lines indicating the standard errors. The model outputs were calculated using mean daily rainfall

2.4.3. Activity and distance travelled over 24 hour periods

Denning, rainfall, temperature and moonlight were key predictors of activity and distances travelled across the 24h period from dawn to dawn, for denning and non-denning periods combined. Contrasting with hypothesis i) African wild dogs travelled less far and were less active on hot days both inside and outside the denning period. This negative effect of temperature, however, was greater inside the denning period than outside it, as indicated by the inclusion of a negative interaction between the effects of temperature and denning in the top models for both activity and distances travelled, and the importance of maximum temperature as a predictor of activity and distances travelled in the denning period (Table 2.3, Fig. 2.3). Despite being included in the top models, rainfall, days at the den site and pup age had little impact on activity and distances travelled, with confidence intervals for all estimates crossing zero.

Table 2.3: Variables associated with wild dog activity and distance travelled across a **24 hour period**.
Average estimated effects of predictor variables on the distance travelled and average activity of wild dogs across a 24 hour period (sunrise-sunrise) estimated using generalised linear mixed effects models. The residuals of the models were gamma distributed and therefore the exponent of the values should be taken to obtain true estimates. Relative importance of each parameter is shown along with the number of models in the Δ<2 and Δ<5 model sets that contain each variable (n,n). Shaded cells indicate variables that were not in any of the models with delta <5. Maximum temperature = maximum daily temperature (°C) during the 24hr period (dawn-dawn) and Daily rainfall = rainfall over 24 hour period (mm). Variables where no estimate is shown were dropped from the final model as likelihood ratio tests showed models including those variables did not differ significantly from the null model. Individual identity was included as a random variable.

		Activity			**Distance travelled (km)**		
Period	**Variable**	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***	***Estimate***	***95% CI***	***Importance (Δ<2, Δ<5)***
All	Intercept	2.66	2.5 – 2.8	(3,5)	2.16	2.0 - 2.4	(4,12)
	Maximum temperature (°C)	-0.0052	-0.009 - -0.002	0.95 (3,4)	-0.0035	-0.008 - 0.007	0.69 (2,6)
	Daily rainfall (mm)	0.0059	-0.02 – 0.007	0.99 (3,5)	0.0061	-0.01 – 0.03	0.53 (2,6)
	Moonlight	0.0043	0.003 - 0.006	1.00 (3,5)	0.0072	0.003-0.01	0.87 (4,9)
	Denning (Yes)	0.37	0.1 – 0.6	1.00 (3,5)	0.63	-0.3 – 1.5	0.77 (3,8)
	Denning (Yes)* Maximum temperature	-0.015	-0.02 - -0.009	0.66 (2,3)	-0.061	-0.09 - -0.04	0.33 (2,2)
	Maximum temperature *Rainfall	0.00074	0.0003 – 0.001	0.43 (1,2)	-0.00073	-0.002 – 0.0007	0.11 (1,1)
Denning	Intercept	2.90	2.6 – 3.2	(6,12)	2.71	2.0 – 3.4	(4,16)
	Moonlight	0.006	0.003 – 0.009	0.85 (6,9)	0.0042	0.007 – 0.01	0.25 (0,7)
	Maximum temperature (°C)	-0.018	-0.03 - -0.007	0.78 (4,10)	-0.038	-0.06 – -0.01	0.61 (2,10)
	Daily rainfall (mm)	-0.00079	-0.02 – 0.01	0.92 (6,10)	0.0061	-0.03 – 0.04	0.13 (0,8)
	Days at den	-0.0035	-0.01 – 0.005	0.96 (6,11)	0.0030	-0.005 - 0.01	0.62 (3,9)
	Pup Age	0.0036	-0.0002 – 0.0009	0.57 (4,7)	-0.00021	-0.003 – 0.0003	0.33 (1,5)
	Maximum temperature* Days at den	0.00064	0.0005-0.0007	0.29 (2,2)	0.0017	0.0009 – 0.003	0.02 (0,0)
	Maximum temperature *Rainfall	0.0001	0.0003 – 0.002	0.14 (1,2)	-0.0038	-0.01 – 0.002	0.01 (0,0)

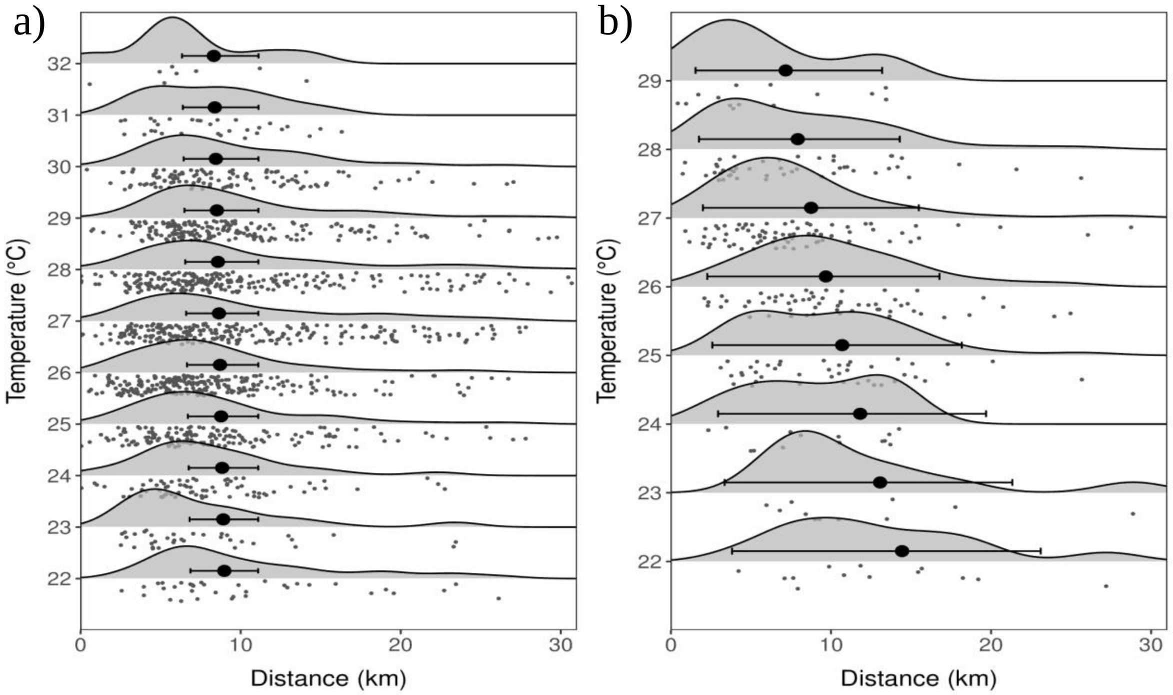


Figure 2.3 Relationship between total distance travelled across a 24 hour period from dawn to dawn and temperature a) outside and b) inside the denning period. Grey points represent the raw data, with the shaded curves representing the kernel density of the data in that 1°C temperature band. Black circles represent model estimates, with black horizontal lines indicating the standard errors. The model outputs were calculated for mean daily rainfall and moonlight.

Across the denning and non-denning periods African wild dogs were more active, and travelled further, across a 24h period when moonlight levels were higher, in line with hypothesis ii). As predicted by hypothesis iii) African wild dogs were more active and travelled further during the denning period compared to outside the denning period across a 24h period (Table 2.3, Fig. 2.3). Top models for activity during the denning period included interactions between temperature and days spent at the den site, and temperature and rainfall. These were only included in 2 out of 12 top models, however, and had small positive effects.

2.4.4. Projected changes in activity and distance travelled

Climate change projections suggested that the study site was expected to warm by between 1.6 and 3.9 degrees, and to experience lower rainfall levels by 2070 (Online Resource 11, Online Resource 12). In the best case climate scenario, wild dogs were predicted to reduce 24h activity and distance travelled outside the denning period by 1%, reducing daytime activity by 5% but increasing nocturnal activity by 7%, and reducing daytime distance travelled by 4%, while increasing distance travelled at night by 6% (Table 2.4). During the denning period, however, the models predicted greater reductions in 24h activity and distance travelled. African wild dogs were predicted to decrease 24h activity and distances travelled by 4% and 8% respectively at average moonlight levels (Table 2.4).

Greater impacts were predicted in the worst case climate scenario, with wild dogs projected to reduce activity and distances travelled across a 24h period by 2% outside the denning period, with a decrease in activity of 12% in the day and an increase of 18% at night. A decrease in daytime distances travelled of 10% was predicted, alongside a subsequent increase of 15% in night time distance travelled. Inside the denning period, when wild dogs have first started using a den site, they were predicted to be 8% less active and travel distances 14% lower across a 24h period than under current temperatures (Table 2.4).

Table 2.4: Predicted differences in mean activity (0-100) and total distances travelled (km) during the day, by night, and across 24 hour from dawn to dawn between 2012-2016 and 2070 under the best and worst case climate scenarios. Percentage change is shown in brackets. Best case is IPCC representation concentration pathway 2.6 and worst case is representation concentration pathway 8.5.

Time Period		Best case		Worst case	
		Activity	Distance (km)	Activity	Distance (km)
Not Denning	Day	-0.71 (-5%)	-0.17 (-4%)	-1.00 (-12%)	-0.24 (-10%)
	Night	0.74 (7%)	0.31 (6%)	1.15 (18%)	0.50 (15%)
	24 hours	-0.12 (-1%)	-0.04 (-1%)	-0.18 (-2%)	-0.05 (-1%)
Denning 0 days at den site	Day	-0.84 (-5%)	-0.27 (-8%)	-1.18 (-13%)	-0.35 (-19%)
	Night	0.29 (3%)	-0.05 (-2%)	0.43 (5%)	-0.06 (-5%)
	24 hours	-0.37 (-3%)	-0.31 (-6%)	-0.53 (-8%)	-0.42 (-14%)
Denning 23 (Mean) days at den site	Day	-0.86 (-5%)	-0.35 (-7%)	-1.23 (-12%)	-0.47 (-13%)
	Night	0.30 (3%)	0.02 (1%)	0.46 (8%)	0.04 (2%)
	24 hours	-0.35 (-3%)	-0.34 (-6%)	-0.51 (-7%)	-0.46 (-14%)

2.5. Discussion

We found that African wild dog activity and distance travelled were strongly associated with ambient temperature, moonlight, and pack reproductive state. As predicted, our results showed that on days with high maximum ambient temperatures, wild dogs showed lower daytime activity and moved shorter distances than they did on cooler days. In line with our hypotheses, high daytime temperatures were also associated with increased nocturnality. Outside the denning period, this increase in activity at night was nearly sufficient to balance lowered daytime activity, resulting in only slight reduction in activity and distance travelled at higher temperatures over a 24h period. During the denning period, however, much more limited nocturnality meant that packs did not compensate for lost hunting activity during the day, with 24h activity and distances travelled falling significantly when wild dogs had pups in the den.

Our finding that nocturnal activity was lower during the denning period contrasted with our prediction, which was based on an expectation that a means of coping with high daytime temperatures would be especially important when energetic demands are highest. This difference between prediction and observation may reflect packs' need to guard their pups at night, when predators, such as lions (*Panthera leo),* leopards (*Panthera pardus*), and hyaenas (*Crocuta crocuta*), are more active. Lower activity and distances travelled are likely to indicate that wild dogs are hunting less, which might in turn indicate lower food intake. Hence, a failure to compensate for lost hunting opportunities on hot days during the denning period may lead to decreased food intake for adults and pups alike, at a time when wild dogs face elevated energetic demands. This reduced food intake might therefore contribute to low pup survival at high ambient temperatures during the denning period. Similarly lower food intake in early life is likely to affect both the growth of the pups and their immune function(Moore et al., 2006), which may lead to higher mortality once they have left the den. Our findings therefore help to explain the lower survival of wild dogs pups raised at higher ambient temperatures (Woodroffe, Groom and McNutt, 2017).

In contrast with our conclusions, Creel et al. (2016) suggested that high ambient temperatures might benefit wild dogs. They reported that wild dog hunts entailed shorter chases at higher temperatures, attributing this pattern to large-bodied prey overheating before their smaller-bodied predators. Chases, however, have been found to make up only around 8% of the distance covered by wild dogs in Northern Botswana (Hubel, Myatt, Jordan, Dewhirst, Tung, et al., 2016), a site where chase distances were significantly longer than those estimated for our study site (Woodroffe et al. 2007). The fact chases make up such a low percentage of distances covered by wild dogs would suggest that chases make up only a relatively small proportion of energy expenditure compared to searching for prey, similar to findings of studies into cheetah (*Acinonyx jubatus*) energetics (Scantlebury et al., 2014). If daytime hunting were more efficient on hotter days, as suggested by Creel et al (2016), there would be no need for the subsequently increased activity at night described here, and no reduction in reproductive success at high ambient temperatures, as described by Woodroffe et al. The difference between this study and that of Creel et al (2016) may also reflect differences in the size of prey species (10kg (main prey species dikdik and impala), Woodroffe et al. 2007, vs

88kg mean mass (main prey species wildebeest and impala), Creel et al. 2016) and the more open habitat found in Creel et al's (2016) study site that could potentially facilitate longer chases.

Wild dogs' nocturnal activity and ranging behaviour was restricted by levels of moonlight (also see Pole 2000; Cozzi et al. 2012; Rasmussen and Macdonald 2012). Rasmussen and Macdonald (2012) suggested that wild dogs increased their night time activity in response to human presence, suggesting that packs might likewise be able to increase their nocturnality in response to high ambient temperatures. However, Rasmussen and Macdonald (2012) also found that nocturnality was also found to be restricted by low levels of moonlight. As nearly half of nights have moonlight levels of less than 25% full moon-night-equivalents (Online Resource 13), moonlight appears to be a major constraint on nocturnal wild dog activity.

Wild dogs' tendency to avoid hunting on moonless nights might reflect limited visual acuity at low light levels (Jacobs, 1993). Poor nocturnal vision would make both hunting and avoidance of competitors challenging, as wild dogs may be less able to detect lions and hyaenas during nights with less light, resulting in greater levels of kleptoparasitism and mortality. However, wild dogs' nocturnality was also largely restricted to moonlit nights at a site with very low lion and hyaena numbers (Pole, 2000), suggesting that wild dogs' reliance on moonlight may be related to their own hunting ability at low light levels, rather than predator avoidance.

Wild dogs were less active and travelled less far in the day, and travelled further at night, when the weather was wetter, likely due to sheltering from the rain. Interaction terms indicate that rainfall reduces the impact of high temperatures a small amount. The decreased response to high temperatures observed at higher rainfall levels might reflect the lower ambient temperatures observed directly after rain (Woodroffe, Groom and McNutt, 2017), greater cloud cover, or access to standing water facilitating heat loss, meaning that wild dogs' activity is less restricted by high temperatures on days where it rains. This impact of rainfall on activity and distances travelled was far less marked in the denning period, which may reflect increased energetic demands on the dogs when they have pups to feed, forcing them to hunt even in sub-optimal weather.

Future projections suggest that wild dogs will be less active and travel less far under future climate change, particularly in the denning period. Recent climate assessments have suggested that the best case scenario is unlikely, and therefore future increases in temperature are likely to be higher than those used in our best case scenario predictions (Cox et al., 2018). This would mean that when wild dogs are denning average decreases in activity of greater than the 3% per 24h and decreases in distances travelled of greater than 6% per 24h, as predicted in the best case scenario, are likely by the year 2070. As demographic effects are already apparent at high temperatures under the current climate regime (Woodroffe et al. 2017), the impact of the consistently higher temperatures projected for 2070 on wild dog demography is likely to be marked. As African wild dogs' hunting strategy relies on covering large distances in order to consume enough prey to maintain their energy balance (Hubel, Myatt, Jordan, Dewhirst, Tung, et al., 2016), they potentially have greater energy expenditure than many other species (Gorman et al., 1998). Reduced activity and distances travelled at high temperatures are likely to have an impact on food intake, and hence may exacerbate the impacts of temperature on recruitment already observed in the field (Woodroffe, Groom and McNutt, 2017). Outside the denning period, while 24h activity and distance travelled might change little, the shift from day-time to night-time hunting, with around 5-10% of their activity shifting from day to night, might decrease wild dog hunting success as a result of a greater percentage of hunts occurring at low light levels, as well as putting wild dogs at greater risk of predation by lions and hyaenas.

Our projections may under-estimate the impact of climate change, since they assume there are no restrictions on wild dogs' ability to increase their nocturnal activity outside the denning period. However, wild dogs' nocturnality was heavily constrained by the availability of moonlight. Projections were modelled at average moonlight levels, however there can be periods of up to 18 consecutive days where moonlight levels are lower than this. At high temperatures during these periods of low moonlight, wild dogs' nocturnal activity will be even further limited, and this may impose further reductions in food intake for individuals across those periods. Although wild dogs might experience relatively high food intake during moonlit periods, they would be unable to maintain this intake through periods without moonlight, because they do not cache their food. Hence, low moonlight levels are likely to place them under more energetic stress in combination with hot weather, compared to periods of high levels of moonlight. This change could result in lowered food intake at higher temperatures when moonlight levels are low, which may have effects on adult condition, and even mortality.

Our findings highlight the constraints to climate change adaptation in African wild dogs. There is little opportunity for wild dogs to adapt to rising temperatures in space, since their distribution is already limited by habitat loss and human activity (Woodroffe and Sillero-Zubiri, 2012). For wild dog ranges to expand into new areas there would need to be an extensive programme of habitat restoration and translocations (Gusset et al., 2007). As they already breed at the coolest period of the year where this period is predictable (McNutt, Groom and Woodroffe, in review), there is no opportunity for shifts in the timing of breeding to compensate for rising temperatures. Previous studies have suggested that large mammals like the African wild dog are unlikely to be able to adapt to rising temperatures through evolutionary change, as their long generation times mean that climate change is likely to outpace the species' rate of evolution (Fuller et al., 2016). Since wild dogs have little potential for adaptation in time and space, and are limited in their rate of evolutionary change by long generation times, this leaves behavioural adaptation as one of the most plausible forms of climate change adaptation. However our findings suggest that a shift to increased nocturnal hunting would be severely constrained in the African wild dog, because both moonlight and the need to guard pups during the denning period will remain fixed as temperatures rise. Consequently, wild dogs may not be behaviourally flexible enough to enable them to compensate sufficiently as temperatures continue to rise, contrasting with the pattern reported from other species, which have been observed shifting activity to cooler times and microclimates in response to higher temperatures (Hetem et al., 2012; Cunningham et al., 2015). These findings have clear implications for the future conservation of African wild dogs, as it may be necessary to focus conservation efforts on areas predicted to experience less warming in the future, for example the southernmost parts of Africa or high altitude areas, in order to protect the species from extinction.

2.6. Wider Implications

Behavioural plasticity is likely to be a key determinant of the severity of climate change impacts across a wide variety of species. Mammals have some of the most complex behaviours of any taxa, and behavioural plasticity is likely to play an important part in their responses to climate change (McCain and King 2014). Such flexibility may be particularly significant for crepuscular species, since, as temperatures rise, each day will include fewer hours when low ambient temperatures coincide with high light levels. Behaviour changes at higher temperatures is likely to be key in determining species' climate change responses, and ultimately impacts of climate change on the species' viability in the future. It is vital that crepuscular species' ability to become active at night is investigated in future research.

The ability of species to shift their behaviour in response to high temperatures is likely to be an important determinant of the extent to which they can adapt to rising temperatures. However, thermoregulatory behaviours must be traded off against other behaviours, such as foraging (Cunningham et al. 2015), and have been found to impact reproduction in some species (Cunningham et al., 2013). In the African wild dog, the thermoregulatory behaviour of lower activity during the day on hot days, coupled with their constrained behavioural shift to nocturnality during the denning period, is likely to result in lower pup survival. It is important that such trade-offs are identified, and their effects on population dynamics and viability established, for other species. In order to identify these impacts, long-term, detailed, studies of species are essential. Behavioural shifts need to be incorporated into vulnerability assessments of species through including the behavioural plasticity of species into trait-based assessments where this information is available. For species with high conservation priority, mechanistic, species-specific assessments which incorporate detailed behavioural responses to climate change are likely to be most appropriate in informing future conservation actions.

Plate 3: Juvenile female African wild dog, Laikipia, Kenya.

Chapter 3 High temperatures and human pressures interact to influence mortality in an African carnivore

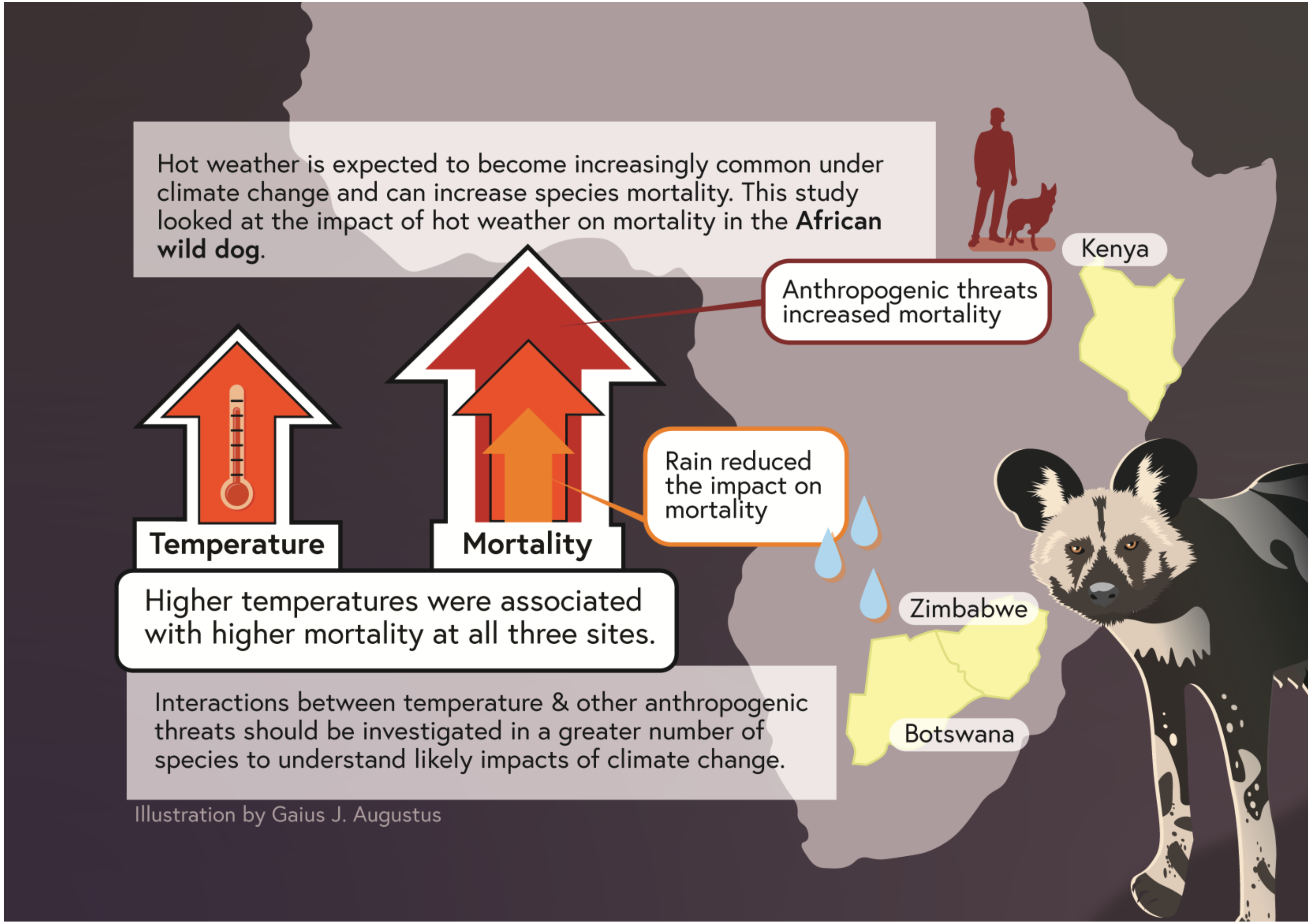
3.1. Abstract

The impacts of high ambient temperatures on mortality in humans and domestic animals are well understood. However much less is known about how hot weather affects mortality in wild animals. High ambient temperatures have been shown to impact African wild dogs', *Lycaon pictus*, hunting activity and reproductive success, but whether high temperatures might be linked to increased rates of mortality is unknown.

I analysed mortality patterns in wild dog populations under long term study in Kenya (0°N), Botswana (20°S) and Zimbabwe (20°S), to examine whether temperature impacted adult mortality. Causes of death varied markedly between sites, with most radio-collared wild dogs killed by predators or conspecifics (27%) or infectious disease (26%) in Kenya, snaring in Zimbabwe (40%) and unconfirmed causes in Botswana (60%). I found that high ambient temperatures were significantly associated with increased mortality at all three sites. Rainfall reduced the impact of high temperature at the highly seasonal sites in Botswana and Zimbabwe, but not at the less seasonal site in Kenya. At the Kenya study site, which had the highest human density, high ambient temperatures were associated with increased risks of wild dogs being killed by people, and by diseases linked to domestic dogs. In contrast, temperature was not associated with the risk of snare-related mortality at the Zimbabwe site, which had the second-highest human density.

These findings suggest that anthropogenic threats to this endangered species may be exacerbated by rising temperatures, with implications for species conservation. This evidence suggests that temperature-related mortality, including interactions between temperature and other anthropogenic threats, should be investigated in a greater number of species to understand and mitigate likely impacts of climate change.

Graphical abstract



Hot weather is expected to become increasingly common under climate change and can increase species mortality. This study looked at the impact of hot weather on mortality in the **African wild dog**.

Anthropogenic threats increased mortality

Rain reduced the impact on mortality

Higher temperatures were associated with higher mortality at all three sites.

Interactions between temperature & other anthropogenic threats should be investigated in a greater number of species to understand likely impacts of climate change.

Illustration by Gaius J. Augustus

3.2. Introduction

Weather conditions have well-documented impacts on mortality in both humans and domestic animals. Mortality rates in humans have been found to increase 1-3% / °C above site-specific temperature thresholds across many parts of the globe (Hajat and Kosatky, 2010). Much of this increased mortality at high temperatures is attributed to increased risk cardiovascular, respiratory and cerebrovascular disease. However, death rates due to many other diseases have also been found to increase at high temperatures (Basu and Samet, 2002). High temperatures are also a strong predictor of human deaths due to drowning (Fralick et al., 2013), an example of how changes in human thermoregulatory behaviour can increase mortality risk.

Increased mortality rates at higher temperatures have likewise been documented for domestic animals, including chickens (Warriss et al., 2005), cattle (Cox et al., 2016) and pigs (D'Allaire et al., 1996). As in humans, there is evidence that such increases in mortality for some species are caused by the interaction between heat stress and other forms of disease, as opposed to heat stress directly. Diseases such as cardiovascular diseases and obesity have been linked to high temperatures in livestock (D'Allaire et al. 1996), however a causal link has not been established for most species (Cox et al. 2016). It has been widely acknowledged that the negative impacts of high temperatures on both human and livestock, including mortality, are likely to be increased by the effects of climate change (Barros et al., 2014).

Whilst correlations between mortality rates and temperature are well documented in humans and domestic animals, and some of the mechanisms driving the increase in human mortality in hot weather well understood, much less is known about how wild animal mortality rates might be impacted by high ambient temperatures. Extreme weather events, such as heat waves, regularly cause mass die offs in wild mammals and birds (Gordon et al. 1988; Welbergen et al. 2008; Jones et al. 2018). Less well studied, however, are the impacts of generally increasing average daily temperatures on mortality rates of wild species outside of such extreme weather events. A wide variety of species have been documented changing their behaviour in response to warmer temperatures (Hetem et al., 2012; Briscoe et al., 2014; Martin et al., 2015), and such changes may entail trade-offs between behavioural thermoregulation and selection of favoured or optimal habitats (Farmer and Brooks, 2012; Pigeon et al., 2016) or foraging success (Cunningham et al., 2015). This shift away from optimal behaviours has been linked to lower recruitment in a number of species, including birds (Sillett et al., 2000; Cunningham et al., 2013; Nord and Nilsson, 2016), mammals (Koons et al., 2012; Woodroffe et al., 2017), fish (Bogstad et al., 2013) and reptiles (Schwanz et al., 2010). Changes in species behaviour in response to high temperatures have also been shown to impact adult mortality, particularly in cases where behavioural changes bring animals into closer contact with human threats, and experience higher mortality rates as a result (Shepard et al., 2008; Farmer and Brooks, 2012).

Awareness of behavioural responses to temperature and their demographic consequences is important for understanding the impacts of climate change on species, and for designing conservation interventions accordingly. As climate change is seldom the only threat to endangered species, it may be possible to offset its effects by increasing survival or recruitment in other ways. Alternatively, it may be possible to concentrate conservation efforts on areas where populations are less likely to experience demographic impacts, that is, reduced recruitment or increased mortality.

The African wild dog is a highly social species of canid that historically lived throughout much of sub-Saharan Africa, however today the species is restricted to just 7% of its historic range (Woodroffe and Sillero-Zubiri 2012). The main threats to the species include habitat loss, accidental snaring, direct killing by people, and disease, which is often transferred from domestic dogs (Woodroffe and Sillero-Zubiri 2012, Prager et al. 2012). These threats vary between sites (Woodroffe, Davies-Mostert, et al., 2007), but are all related to human expansion into wild dog habitat. Wild dogs' social behaviour can put them at greater risk of human killings, as if the one of the dominant pair dies the pack will often splinter, meaning that the death on one individual in the pack can lead to the break-up of a back, and therefore prevent future breeding by that group (Woodroffe, et al., In Review). Sociality is important for African wild dog hunting, reproduction and defence against inter- and intraspecific competitors, and larger packs have consistently greater reproductive success (Creel et al., 2004; Rasmussen et al., 2008; Woodroffe et al., 2017). Larger pack size has been linked to lower adult survival, from one study (Creel and Creel 2002), although concerns have been raised about the ability of this study to differentiate between death and dispersal (Woodroffe et al., In Review), and no such pack size effect on mortality has been found elsewhere (Angulo et al., 2013).

High ambient temperatures have been shown to influence both African wild dog behaviour and reproductive success. Wild dogs are crepuscular, hunting at dawn and dusk when the ambient temperature is low, and avoiding the heat of the day by resting in the shade (Woodroffe et al., 2017). On hot days African wild dogs are less active and travel less far, restricting their morning and evening hunts to shorter time periods (Pomilia et al., 2015; Woodroffe et al., 2017; Rabaiotti and Woodroffe, 2019). They also move their timing of hunting so that it overlaps more with nocturnal periods, which may bring them into greater risk of contact with predators (Rabaiotti and Woodroffe 2019). African wild dog timing of breeding is linked to ambient temperature, with packs in seasonal areas breeding at the coolest time of year (McNutt et al. In Review), and those in aseasonal areas taking longer between each breeding attempt when temperatures during the denning period have been higher (Woodroffe et al., 2017). High temperatures during wild dog denning lead to lower pup survival (Woodroffe et al., 2017), and therefore a decrease in recruitment. This is likely a result of decreased food provisioning, and/or reduced pup guarding during periods of hot weather when adult food intake is low (Woodroffe et al., 2017).

As high ambient temperatures affect the hunting behaviour of adult wild dogs, and the survival of their pups, and because high temperatures have been directly linked to increased mortality in humans and domestic animals, I predicted that high ambient temperatures would also be associated with reduced adult survival. I tested this hypothesis by investigating variables associated with adult mortality in African wild dogs at three sites, representing a range of environmental conditions.

3.3. Methods

3.3.1. Study sites

In this study I analysed three long term datasets on African wild dog mortality from three different sites – Laikipia, Kenya; the Okavango Delta, Botswana; and Savé Valley, Zimbabwe. All three study areas are semi-arid, savanna ecosystems. However there are significant differences between sites in human activities and climatic conditions. In particular, the Kenya study site has variable rainfall year-round and low levels of within-year temperature variation, whereas the Botswana and Zimbabwe sites consistently experience a cool dry season and a warm wet season each year (Woodroffe et al., 2017).

3.3.1.1. Kenya study site

The Kenya study site (37° 2' E, 0° 6' N) covers Laikipia County, incorporating parts of neighbouring Samburu, Isiolo, and Baringo Counties. The area is a mix of privately owned cattle ranches and community land. Primary land uses are subsistence pastoralism, livestock ranching, and wildlife-based tourism. Daily maximum ambient temperatures are comparatively low to the other sites, with maxima 25 - 36°C and minima 12° - 17°C. Mean annual rainfall is 590mm, varying from around 400mm in the North East to > 900mm in the South West, with short, irregular wet and dry seasons (Franz et al., 2010). Lion density at the site is estimated at 5/100km^2, and is considered depressed primarily due to conflict with livestock farmers (Woodroffe and Frank 2005). The mean human density across the study site is 42.6 people /km^2 (O'Neill et al., In Review)

3.3.1.2. Botswana study site

The Botswana study site (23° 38' E, 19° 30' S, 960m ASL) includes sections of the Moremi Game Reserve as well as adjacent Wildlife Management Areas on the eastern side of the Okavango Delta. The area comprises of savanna woodland and seasonal floodplains. Mean annual rainfall is 430mm and maximum daily temperatures range from 22 degrees in the cool season, to 38 degrees in the hot season (Harcourt et al., 2001). Lion density across the Okavango Delta varies dependant on habitat but averages 5.8/100km^2, with very low densities (<1/100km^2) rising to 23.1 /100km^2 in the floodplains where much of the study was done (Cozzi et al. 2013). Very few people live in Moremi and the surrounding areas, leading to average human densities of <1 person /km^2 (Harcourt et al., 2001).

3.3.1.3. Zimbabwe study area

The Zimbabwe study site (32° 00' E, 20° 05' S, 550m ASL) is the Savé Valley Conservancy in the South-Eastern lowveld. The area is primarily woodland savanna covering low hills, interspersed with rocky outcrops. The Conservancy is bordered by a cattle fence and has very low occupancy with human densities of approximately 1 person/km^2 (Mbizah et al., 2012), however it is surrounded by mostly community lands with human densities of between 11 and 82 people per km^2 (Lindsey et al., 2008).

3.3.2. Field Data Collection

Only wild dogs fitted with either radio or GPS collars were included in the analyses in order to eliminate biases in mortality due to differences in detectability between collared and uncollared wild dogs. This approach also allowed accurate distinction between individuals that died and those which dispersed.

At the Kenya study site 131 African wild dogs from 41 packs were monitored throughout their lifetimes between 2001 and 2016. Individuals were fitted with either Televilt GPS collars (GPS-Posrec, Televilt, Lindesberg, Sweden), Vectronics GPS collars (GPS Plus, Vectronic Aerospace GmbH, Berlin, Germany), or radio-collars (Telonics, Mesa AZ, USA). All three collar types included a mortality sensor programmed to emit a characteristic radio signal if completely stationary for ≥4h. At the Zimbabwe study site 58 wild dogs from 34 packs were monitored using radio collars (African Wildlife Tracking) between 2008 and 2017. Using radio-collars 34 wild dogs from 16 packs were monitored at the Botswana site between 1992 and 2004. At all three sites, packs were generally located regularly on a weekly to biweekly basis and the number of adults (defined as individuals older than 12 months) in the pack recorded. In addition to this, packs' breeding status – denning or non-denning was recorded at all three sites. The dominance status, ie whether they were alpha or subdominant, was monitored, and alpha status was identified from the individual's behaviour, namely: consistent close association with a specific individual of the opposite sex, co-ordinated scent marking and reproductive activity (Jordan et al., 2014).

Any collared animal found dead was carefully examined with the aim of establishing a cause of death. At the Botswana site cause of death was only recorded in cases where the death was directly observed, or during disease outbreaks, and therefore the majority of causes of death were unconfirmed, although the vast majority are likely to be from natural causes. A combination of the decomposition of the body and date of first detection of mortality signals from the collar were used to estimate the date of death when not observed directly, and where this was not possible an estimated date of mortality was made based on the date midway between the last sighting and the discovery of the body or collar was used. If a body or collar was discovered more than 30 days after the last sighting the animal was considered lost from the study due to the inaccuracy of the date of death. If any study animals were not observed in their resident pack for over one month, no mortality signal was detected, and no carcass was found, they were recorded as being lost from the study the day after the date of the last observation. Lost animals were included in the analysis but were censored from the date of the last sighting of that individual.

Environmental variables included in the analyses were temperature, rainfall, land use and moonlight. Data on daily dry-bulb maximum temperature and total daily rainfall were obtained from the nearest weather station at each site – within the study site in Kenya, 12km away for the Zimbabwe site and 30km away for the Botswana site (Woodroffe et al., 2017). At each site a rolling average of daily maximum temperature and a rolling total of daily rainfall were calculated. These rolling values were calculated over 90-day periods in Botswana and Zimbabwe, and over 30-day periods in Kenya, to account for the shorter and less variable seasons at this equatorial site. Since high ambient temperature is associated with low pup survival (Woodroffe et al., 2017) I hypothesised that it might also reduce adult survival. Rainfall has been shown to have a positive effect on pup survival at the Botswana study site and a negative effect on pup survival at the Zimbabwe and Kenya study site (Woodroffe et al., 2017) and therefore I predict impacts on adult survival in line with the impacts on pup survival at each site.

Data on moonlight levels were obtained from the R package suncalc (Benoit and Achraf, 2019). African wild dogs are more active on moonlit nights (Cozzi et al., 2012; Rabaiotti and Woodroffe, 2019) therefore higher rates of death due to predation may be expected on brighter nights as both lions and hyaenas are most active at night and therefore the periods in which all three species are active would have greater overlap.

Packs in the Botswana and Zimbabwe study sites resided primarily in wildlife areas, whereas packs in Kenya could be classified into those residing primarily on community land (≥90% of recorded locations, Woodroffe (2011a)), and those residing primarily on private ranches (≥70% of locations, Woodroffe (2011a)). I predict that individuals on community land may be more likely to die compared with those residing predominantly on commercial land as livestock and human densities are higher and conflict (resulting in direct persecution) more likely (Woodroffe, et al., 2007).

Individual characteristics included in the analyses were gender, age, dominance status, pack status (denning resident, non-denning resident, or dispersing), size of pack, and time since last litter. Wild dog age was known for many individuals at the Kenya and Zimbabwe sites, otherwise it was estimated from tooth wear when the dog was collared. Higher mortality has been observed in males (Owens, 2002) and older individuals (Loison, et al., 1999; MacNulty et al., 2009) in a wide variety of species, however this hasn't previously been noted in wild dogs. Dominant status has been linked to higher stress and parasite load in chimps and socially breeding mammals and birds, as well as higher levels of conflict (Creel, 2005; Muehlenbein et al., 2010). I therefore anticipated that dominant individuals would have higher mortality.

One study noted higher adult mortality at larger pack sizes (Creel et al 2002), however other studies found no effect (Angulo et al., 2013), and because of the social nature of the species it would be anticipated that survival would be greater at higher pack sizes.

At the Kenya and Zimbabwe sites wild dogs were defined as dispersing if they left their pack for multiple days and did not return, otherwise they were defined as resident. Dispersal status of individuals was not known for the Botswana site, so mortality rates between dispersers and resident individuals were not compared. Wild dogs have lower survival when they are dispersing as they are more likely to encounter human threats and disease (Woodroffe et al., In Review). For all three sites the dates each pack was raising pups at the den were recorded, and dogs in packs which had pups in the den were classified as resident denning. I hypothesised that be more likely to die when they are denning due to greater energetic pressure and the fact they stay near the den site, putting them at risk from humans and predators (Woodroffe et al. 2007). In the Botswana and Zimbabwe sites the denning period is seasonal – with most denning attempts starting between May and July (Woodroffe et al., 2017). In Kenya African wild dogs breed aseasonally, on average every 11 months, and therefore time since the last litter that the individual was involved in raising was recorded. I hypothesised that individuals may be more likely to die soon after raising a litter of pups due to energetic stress (Woodroffe et al 2011a).

3.3.3. Data analysis

Causes of death were separated into four primary categories: 1) disease - which included any death where animals were observed to be sick prior to death, or other pack members were observed to show disease symptoms 2) human causes - deliberate killing (e.g. shooting) or accidental killing (e.g. road-kill or snaring) 3) natural causes – this category included injuries sustained while hunting, death by other predators, prey or wild dogs and 4) unconfirmed – where the cause of death couldn’t be confidently established.

Primary analyses evaluated associations between the candidate explanatory variables and mortality due to all causes. I also conducted secondary analyses considering associations between explanatory variables and specific causes of death that resulted in the mortality of more than ten individual wild dogs at a single site; for these secondary analyses, deaths due to other causes were censored. Causes of death where there were fewer than 10 deaths were not included the secondary analyses. Effects of the factors on adult mortality on a daily scale were assessed in mixed effects Cox proportional hazards models using the ‘coxme’ function in the ‘coxme’ R package (Therneau and Grambsch, 2000). Pack identity was included in the models as a random variable.

For each analysis I dropped successive variables from the full model until only statistically significant effects remained. All independent variables were tested for autocorrelation and all were found to be correlated at values below 0.5. I carried out all analyses in R version 3.3.2 (R Core Team 2015).

3.4. Results

3.4.1. Causes of death

The primary causes of death varied between the sites (Table 3.1). In Kenya, the leading causes of death were disease (26%) (Woodroffe and Donnelly, n.d.; Woodroffe et al., 2012) - and natural causes (35%). Most human caused deaths (84% of human caused deaths) were deliberate killings by people. By contrast, in Zimbabwe, the leading cause of death was accidental human caused deaths – specifically snaring (40%). At the Botswana site the majority of deaths were due to unconfirmed causes (60%) (Table 3.1).

Table 3.1: Causes of African wild dog mortality at each study site. Percentages of total deaths are indicated in brackets

Site	Category	Number of deaths (percentage)	Cause of death	Number of deaths (percentage of total)
Kenya	Natural	27 (35)	Predator or conspecific	21 (27)
			Injury or other	6 (5)
	Human	18 (23)	Deliberate	16 (19)
			Accidental	3 (4)
	Disease	20 (26)	Disease	20 (26)
	Unconfirmed	13 (17)	Unconfirmed	13 (17)
			All deaths	78
			Number censored	52
Zimbabwe	Natural	8 (32)	Predator or conspecific	6 (24)
			Injury or other	2 (8)
	Human	10 (40)	Deliberate	0
			Accidental	10 (40)
	Disease	1(4)	Disease	1 (4)
	Unconfirmed	6 (24)	Unconfirmed	6 (24)
			All deaths	25
			Number censored	33
Botswana	Natural	3 (13)	Predator or conspecific	2 (9)
			Injury or other	1 (4)
	Human	0	Deliberate	0
			Accidental	0
	Disease	6 (26)	Disease	6 (26)
	Unconfirmed	14 (60)	Unconfirmed	14 (60)
			All deaths	23
			Number censored	11

3.4.2. Factors influencing probability of survival

High ambient temperature was associated with mortality to some extent at all three sites, however the impact varied across sites (Table 3.2).

At the Kenya study site, African wild dogs had higher mortality (due to all causes) at higher temperatures, when they were in smaller packs and when they were dispersing rather than resident (whether denning or non-denning), and on community owned land (Table 3.2). Wild dogs at the Kenya site showed higher mortality from human causes and disease at higher temperatures (Table 3.3). Mortality from human causes was also higher at lower pack sizes, as was mortality from natural causes (Table 3.3). There were higher death rates from unknown causes when wild dogs were dispersing.

At the Botswana site there was a significant interaction between the effects of rainfall and temperature, with rainfall mediating the impacts of high temperature on mortality (Table 3.2). At the Botswana site wild dogs in larger packs had lower mortality rates.

At the Zimbabwe site mortality due to all causes was not significantly associated with any of the variables investigated. There was no significant correlation between deaths by snaring and either rainfall or temperature, however there was a negative interaction between the impacts of higher maximum temperatures and at higher levels of rainfall on mortality from non-human causes (Table 3.2 and 3.3). No variable had a significant effect on rates of mortality from human causes.

Table 3.2: Results of survival analyses, considering all mortality causes. These models also include pack identity or dispersal group as a random variable. Hazard ratios of less than 1 indicate a reduction in the probability of death, and more than one indicate an increase in the probability of death occurring.

Study site	Variable	Hazard Ratio	SE	p
Kenya	Pack size	0.91	±0.03	0.003
	Mean daily maximum temperature (°C, 30 days)	1.24	±0.09	0.01
	Land use – community land vs private ranch	2.26	±0.31	0.01
	Status – denning vs resident-nondenning	0.71	±0.4	0.3
	dispersing vs resident-nondenning	7.02	±0.5	<0.001
Botswana	Pack size	0.86	±0.09	0.05
	Mean daily maximum temperature (°C, 90 days)	1.51	±0.19	0.03
	Mean daily total rainfall (mm, 90 days)	1.12	±0.06	0.05
	Temperature * Rainfall	0.99	±0.002	0.05
Zimbabwe	Denning	3.21	±0.5	0.02

Table 3.3: Results of survival analyses from Kenya and Zimbabwe broken down by cause of death.

Site:		Kenya			Zimbabwe		
Cause of death	Variable	Estimate	SE	p	Estimate	SE	p
Human	Mean daily maximum temperature (°C, 30 days)	1.54	±0.1	0.003	-	-	-
	Pack size	0.84	±0.08	0.02	-	-	-
Disease	Mean daily maximum temperature (°C, 30 days)	1.52	±0.2	0.03	-	-	-
Natural	Pack size	0.88	±0.05	0.02	-	-	-
Unconfirmed	Pack Status (vs resident not denning) Dispersing	103.75	±1.3	<0.001	-	-	-
	Denning	0.0000002	3813.18	1	-	-	-
Non snaring	Mean daily maximum temperature (°C, 90 days)	-	-	-	1.36	±0.001	0.19
	Mean daily total rainfall (mm, 90 days)	-	-	-	1.04	±0.004	0.04
	Temperature * Rainfall	-	-	-	0.99	0.000002	0.05

3.4.3. Mortality rates

Overall annual mortality rates differed across the three sites. The Botswana site had the lowest predicted mortality rate, with the second lowest mortality rate at the Kenya site, with the highest mortality rates observed at the Zimbabwe field site (Table 3.4).

Table 3.4: Estimated annual mortality rates by cause at average temperatures, rainfall levels and pack sizes, for an individual in a resident pack that is not denning.

Site	Cause	Mortality rate
Kenya	All	0.18
	Natural	0.09
	Disease	0.09
	Human	0.06
	Unconfirmed	0.02
Botswana	All	0.15
Zimbabwe	All	0.23
	Non-human	0.19
	Human	0.10

3.5. Discussion

Our findings indicate that climatic variables and human activity interact to influence survival in the African wild dog. High ambient temperatures were associated with increased African wild dog mortality across all three sites, indicating that African wild dogs were more likely to die after a period of hot weather. This impact of temperature varied between sites, however there was a consistent interaction between temperature and rainfall across both Southern African sites. At the Kenya study site higher mortality at higher temperatures was driven by direct human killings and disease, which contrasted with Zimbabwe and Botswana, where African wild dogs had increased mortality at high temperatures due to non-human causes.

Rainfall modified the impact of high temperatures at both the Zimbabwe and Botswana sites. The interaction between rainfall and temperature indicates that at seasonal sites high temperatures have the greatest impact when there has been lower levels of rainfall. The interaction does not appear to be driven by the fact denning occurs in the dry, cooler period as denning was not a significant factor impacting mortality.

The higher rates of mortality I observed at higher ambient temperatures do not appear to be driven by deaths caused directly by heat stroke, as most individuals did not die of these causes. Instead, as is found with human mortality at high temperatures, high temperatures appear to exacerbate the risk of mortality from other causes. Whereas the risk of mortality by natural causes remained the same in a month that was hotter on average at the Kenya site, overall monthly rates of mortality would rise by 4% per degree of temperature change as a result of increased risk from disease and direct killing by humans. At high temperatures African wild dogs are less active, and are assumed to hunt less (Rabaiotti and Woodroffe, 2019). This means that under prolonged periods of hot weather wild dogs are likely to be hungry, and under greater energetic stress. Malnourished animals have been found to have compromised immune systems (Losada-Barragán et al., 2017), and are more likely to contract disease (Harvell et al., 2002) , and to die once they are infected (Kim et al., 2018), as a result. African wild dog behaviour changes at high temperatures, and they are likely to be hunting less in hot weather, leader to greater energetic stress (Rabaiotti and Woodroffe, 2019). Wild dogs have been shown to move their activity in response to human presence (Hayward and Slotow, 2009). In hot weather wild dog activity is already greatly restricted, so high temperatures may restrict their ability to avoid humans. Weather has been shown to influence the number of predation incidents by both lions and leopards (*Panthera pardus*) (Patterson et al., 2004; Dar et al., 2009). Increased deaths at high temperatures may also reflect increased wild dog predation on livestock when it is hot. The greater energetic stress imposed by high temperatures, or the movement of prey species into less accessible areas may lead to a higher likelihood of targeting domestic animals as opposed to wild prey, leading to retaliatory killings.

Rainfall appears to mitigate some of the impacts of high temperatures on African wild dog mortality, decreasing the risk of mortality by an estimated 1% per mm of rainfall at the Botswana site. In Botswana 51mm of rainfall has to fall over the previous 90 days to compensate for 1°C increase in temperature, and 36mm of rainfall has to fall over the previous 90 days in Zimbabwe. Rainfall levels are higher over the previous 90 days than the 51mm needed to compensate for 1°C of temperature change on 50% of days in Botswana, and rainfall levels above those needed to compensate for temperatures 5°C higher than average on 13% of days. In Zimbabwe rainfall levels are higher over the previous 90 days than the 31mm needed to compensate for a 1°C rise in temperature 58% of the time, however the hottest months are 5°C above average temperatures, and there is only enough rainfall over the previous 90 days to compensate for this on 2% of days. Levels of rainfall that are sufficient to offset high temperatures more commonly occur in the wet, warmer, season at both sites, suggesting higher than average temperatures outside of these times pose a greater risk to African wild dog survival. This has implications for neighbouring areas with much lower rainfall levels, such as the Kalahari, where increased wild dog adult morality at high temperatures is unlikely to be buffered by rainfall.

Rainfall has been shown to impact wild dog behaviour on a daily basis (Rabaiotti and Woodroffe, 2019) – mitigating the impact of temperature through being associated with an increase in African wild dog activity and ranging on hot days, however the daily impact of rainfall did not appear to impact adult mortality across a monthly time-frame at the Kenya site. The lower impact of temperatures on mortality at high levels of rainfall may reflect the ability of wild dogs to cool off in standing water after periods of high rainfall, or the greater availability of shade for thermoregulation once there is more foliage on the vegetation. Temperatures at the Kenya site are never as high as in the wet, hot season at the Zimbabwe and Botswana sites, and therefore standing water may play less of an important role at the Kenya site.

In contrast to previous findings (Creel and Creel, 2002; Angulo et al., 2013) none of the three sites had positive associations between pack size and mortality, with significant negative effects at two of the sites. At the third, Zimbabwe, one wild dog was killed by a lion in a very large pack of 28 individuals, which may be masking any pack size effects present. In Kenya higher mortality at lower pack sizes was due to the impact on deaths by natural causes and by intentional deaths due to humans, which would suggest that larger packs are better at avoiding death due to lions and other wild dogs, as well as direct persecution by people.

A previous study from Tanzania found that greater pack size was detrimental to adult wild dog survival (Creel et al., 2004). Findings from the Botswana and Kenya study sites contrast with these previous findings, as adults had lower mortality in larger packs. The findings of the cause of death analyses for the Kenya study site indicated that larger pack sizes decreased mortality resulting from human impacts and natural causes. Larger packs are more likely to be able to defend against hyaenas and other packs of wild dogs, and may potentially make individual wild dogs a more difficult target for people looking to kill wild dogs in retaliation for livestock deaths. Large packs may also be better able to support any injured members of their group. Defence against lions, hyaenas and other wild dogs is likely also the mechanism behind higher survival at higher pack sizes in Botswana – where there are no deaths from human causes and the majority of deaths are through natural causes. As I used only data from radio-collared animals I was able to distinguish between dispersals and deaths, which are easy to conflate when including uncollared dogs in the analysis.

There was no significant effect of moonlight levels on mortality which suggests that wild dog deaths at higher temperatures may not be due to increased nocturnal activity as wild dogs are more active on nights with higher levels of moonlight (Cozzi et al., 2012; Rabaiotti and Woodroffe, 2019). Neither denning or time since denning had an impact on mortality rates which suggests that increased energetic pressures in the denning period don’t increase the chanced of adult mortality. Dominance status, gender and age had no significant impact on mortality rates.

Human activity had a clear impact on wild dog mortality. Rates of mortality varied in line with human density – the Zimbabwe and Kenya sites had higher human densities and higher rates of mortality due to human causes than the Botswana site. At the Kenya site, which was both outside protected areas and had the highest human density, wild dogs were more likely to die on community than commercial lands. Community land has higher grazing pressure, lower numbers of prey species, and higher domestic dog densities than commercial lands (Woodroffe et al., 2005), all of which are likely to have negative impact on African wild dogs living in the area. Human activity is also likely to contribute to the higher mortality of dispersing African wild dogs in the Kenya study site. This is because dispersing African wild dogs range outside of their home range, coming into contact with higher human densities (O’Neill et al In Review). Dispersing African wild dogs have previously been found to have higher rates of human caused deaths than resident wild dogs (Woodroffe et al, In Review b). I also found that African wild dogs were more likely to die from unconfirmed causes of death when dispersing – this is likely to reflect longer time taken to find dispersing wild dogs once they have died, making it more difficult to determine the cause of death.

This paper highlights the importance of temperature for African wild dog survival – revealing evidence for increased mortality after periods of hot weather across all three sites. As the climate becomes warmer and Southern Africa becomes dryer, lessening the moderating effect of rainfall, African wild dog adult mortality rates are likely to rise. This increase in adult mortality is in addition to predicted falls in recruitment as wild dog pup survival falls at higher temperatures (Woodroffe et al., 2017). Both combined impacts are likely to have population level effects, and it will be important that these are examined if scientists are to understand the likely impact of rising temperatures on the species.

It is clear that human activity and climatic variables interact to impact mortality in the African wild dog. While this is cause for concern, it also suggests that the relatively intractable threat from global climate change might be mitigated by addressing other threats. There is evidently potential for conservation measures to reduce deliberate killing of wild dogs, for example by reducing human wildlife conflict. There is evidently potential for conservation measures targeting human wildlife conflict to simultaneously mitigate the impacts of climate, particularly in sites where direct human killings are common causes of death such as in out Kenya study site (Woodroffe, et al., 2007; Gusset et al., 2008; Dickman, 2010). In areas where infectious disease is a major threat, vaccination programmes targeting either wild dogs or domestic dogs (Vial et al., 2006; Prager et al., 2011; Prager et al., 2012) may help reduce disease impacts, and, hence, climate impacts. On the other hand where deaths are mostly due to natural causes other solutions, such as water points, which can be used by wild dogs to assist in thermoregulation in hot weather, may be more appropriate. While African wild dogs have been found to show attraction to water points the driving mechanism, and relation to temperature, behind this is unclear (Ndaimani et al., 2016), and the use of standing water by wild dogs for thermoregulation needs investigating. It is clear that threats to African wild dogs vary greatly between sites, and therefore site-specific needs should be taken into consideration within conservation planning.

Hot weather can increase mortality rates in wild animals, however little focus has been given to the impact of high temperatures on wild animal mortality in the literature. Spells of hot weather and rainfall variability are predicted to increase under climate change, with serious implications for the survival of temperature sensitive species. Thermoregulatory behaviour comes with trade-offs, which can not only impact reproduction but also adult survival. It is important that the species which respond to high temperatures by changing their behaviour in a way that reduces their fitness are identified as these species are likely to be at greater risk from rising temperatures. Many species, particularly large vertebrates, have had their ranges greatly restricted as a result of habitat loss. For wide-ranging species, such as the African wild dog, that have little opportunity to shift with the climate due to extensive habitat loss, behavioural shifts will be key in how they respond to rising temperatures in the future. It is therefore important that conservationists understand the impact of these behavioural shifts in response to temperature on individual mortality. These mortality impacts are crucial in determining how populations will respond to climate change, and understanding these population responses is paramount if researchers are to accurately identifying climate impacts across species.

Existing human-driven threats and climatic threats are likely to interact for a wide variety of species. The most obvious interaction is that between climate change and habitat loss, which restricts the ability of species to move to more favourable habitats as the climate warms. This paper also highlights, however, that other human pressures can interact with climatic conditions to influence demographic outcomes in an endangered species. For many species it may be that by reducing other human impacts through increasing connectivity and reducing human-wildlife conflict conservationists can simultaneously buffer the impacts of climate change.

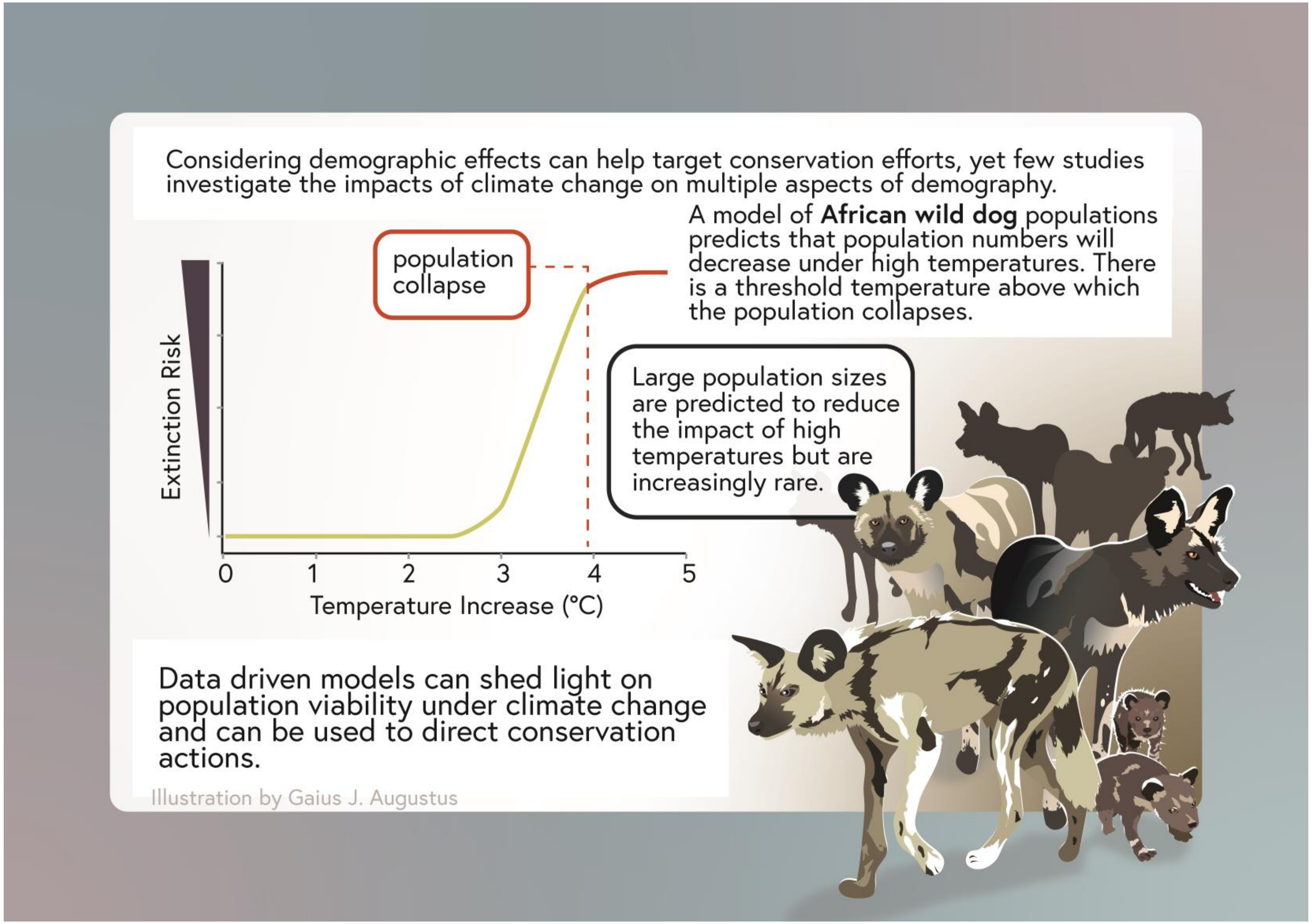
Plate 4: Adult African wild dog with GPS collar, Mpala Ranch

Chapter 4 Dog days are over? Modelling population dynamics of a tropical carnivore under climate change.

4.1. Abstract

Demographic impacts of climate change are already being observed across multiple species. Few studies, however, consider the impacts of climate change on multiple aspects of demography when predicting where and how species may be impacted by climate change. This is despite the fact that the inclusion of demographic effects in climate change risk assessments can help target conservation efforts aimed at mitigating climate change risk, such as reintroductions and targeted habitat restoration. Using an individual based model incorporating demographic responses to ambient temperature in an endangered species, the African wild dog *Lycaon pictus,* I show that there is a threshold temperature above which populations of the species collapse. This impact of high temperatures is reduced by a larger population size; however populations of this kind are increasingly rare across the species' range. The model highlights that detailed data-driven models can shed new light on population viability under climate change, and the importance of social dynamics in buffering climatic impacts in social species. Data-driven, individual-based, models incorporating climatic impacts can be used to direct interventions that may increase population viability in the future as climatic conditions become less favourable to species.

Graphical abstract



Considering demographic effects can help target conservation efforts, yet few studies investigate the impacts of climate change on multiple aspects of demography.

A model of **African wild dog** populations predicts that population numbers will decrease under high temperatures. There is a threshold temperature above which the population collapses.

Large population sizes are predicted to reduce the impact of high temperatures but are increasingly rare.

Data driven models can shed light on population viability under climate change and can be used to direct conservation actions.

Illustration by Gaius J. Augustus

4.2. Introduction

Climate change impacts on wildlife are increasingly being observed, however predicting how species are likely to be impacted still proves challenging despite the fact that climate change has been a causal factor in a number of contemporary extinctions of both populations (Cahill et al., 2012) and species (Waller et al., 2017). Shifts in temperature and rainfall as a result of climate change can lead to demographic impacts (McKechnie et al., 2010). One of the more conspicuous mechanisms by which climate change negatively impacts species mortality is through extreme weather conditions resulting in mass mortality events, where large numbers of a species die over a short time period. In recent years there are an increasing number of records of extreme climatic conditions leading to mass mortality through starvation (Jones et al., 2018), dehydration (Albright et al., 2017), and heatstroke (Welbergen et al., 2008; Hajat and Kosatky, 2010; McKechnie et al., 2010; White et al., 2015; O'Shea et al., 2016) in multiple species.

Temperature and rainfall shifts can also produce demographic effects through less direct routes, however. Changes in habitat use at high temperatures can impact food provisioning for both adults and offspring (Yasue et al., 2003; van Beest et al., 2012), and engaging in thermoregulatory behaviours to stay cool can put species at higher risk of predation (Yasue et al., 2003) or interactions with people (Farmer and Brooks, 2012), impacting survival rates. Temperature can also impact foraging time (Owen-Smith, 1998; Rabaiotti and Woodroffe, 2019), leading to lower food intake which can impact both survival and reproduction (Cunningham et al., 2013; Cunningham et al., 2015). Impacts on vegetation can have repercussions on herbivore numbers (Masters et al., 1998; Martin and Maron, 2012; Zhou et al., 2017), and lower prey species density as a result of changes to vegetation can subsequently impact predator recruitment and survival (Lawton et al., 1980; Soto et al., 2004; Møller et al., 2010). All these impacts of high temperature can lead to changes in both fecundity and mortality, which have implications for population growth rates and persistence.

Two of the approaches most commonly used to assess species vulnerability to climate change are trait based assessments and correlative species distribution models (Thuiller, 2004; Pacifici et al., 2015). Trait based assessments use species traits such as fecundity, geographic range size and mobility to predict which species are most likely to be threatened by climate change. Range restricted, long-lived, slow moving species with low fecundity are often highlighted as most at risk in trait based assessments (Foden et al., 2013). Correlative species distribution models, on the other hand, identify the climatic niche that a species inhabits, and identify areas predicted to have the same climatic properties under future emissions scenarios. Species distribution models also often highlight range restricted species with restricted movement capabilities as most under threat from climate change (Midgley et al., 2002; Pacifici et al., 2015).

Both trait based assessments and correlative species distribution models fail to take into account the mechanisms which generate climate change impacts and therefore there have been increasing calls to build data driven models, often referred to as mechanistic models, as they take into account the causal process by which species are prevented from, or facilitated in, persisting under certain climatic conditions (Guisan and Thuiller, 2005; Kearney and Porter, 2009; Austin and Van Niel, 2011; Urban et al., 2016). A number of studies have highlighted the need for the inclusion of demographic impacts in such models (Buckley and Kingsolver, 2012; Ehrlén and Morris, 2015; Urban et al., 2016).

Another approach to predicting climate change impacts are large scale, system-based, global models. These approaches to modelling climate change impact are often parameterised on experimental data from lab organisms, particularly insect systems. As most insects are ectotherms, predator attack rate rises at higher temperatures (Logan et al., 2006), meaning that predators in these models are generally predicted to have a higher capture rate under climatic warming scenarios, and will benefit as long as prey numbers remain high. The assumption that attack rate increases at high temperatures is incorporated into models such as the Madingley model, which increasingly used to predict the impact of a variety of impacts of global change, including climate change, on biodiversity. In contrast to this, a number of endothermic animals, however, including some mammals (Owen-Smith, 1998; Hetem et al., 2012; Rabaiotti and Woodroffe, 2019) and birds (du Plessis et al., 2012), activity levels have been shown to be lower at high temperatures, and behaviour often shifts in ways that can lead to lower predation rates on prey species (Rabaiotti et al., In Prep; Cunningham et al., 2015). These changes in predation rate can have demographic repercussions on both predators and prey (Cunningham et al., 2013; Woodroffe et al., 2017).

A large body of work has looked at the correlative relationship between climate and various demographic traits in wildlife, including recruitment (Griffin et al., 2011;

Koons et al., 2012; Bogstad et al., 2013; Cunningham et al., 2015; Nord and Nilsson, 2016), dispersal (Smith, 1974; Walls et al., 2005; Figuerola, 2007) and mortality (Anctil et al., 2014; Meager and Limpus, 2014; Turbill and Prior, 2016; Jones et al., 2018). Far fewer studies, however, have used these demographic impacts to model impacts on population trends and viability, despite the fact that climatic impacts on a single demographic variable can be counteracted by opposing changes in other demographic variables, leading to a neutral or even net positive impact of climatic changes (Adahl et al., 2006; Doak and Morris, 2010; Dybala et al., 2013). Where studies have used projected climatic impacts on demography to model population level effects (Mitchell et al., 2010; Diez et al., 2014; Merow et al., 2014; Buckley et al., 2015; McCauley et al., 2017) the incorporation of the impact of climate on more than one demographic parameter is uncommon, and studies which have examined population level effects have mostly focused on birds (Dybala et al., 2013; Precheur et al., 2016; Velarde and Ezcurra, 2018) or plants (Doak and Morris, 2010).

Effects of temperature on demography will be increasingly relevant to species conservation as temperatures rise, as population dynamics are often more important than physiological limits in determining the ability of species to persist under rising temperatures (Sillett et al., 2000; Thompson and Ollason, 2001; Fordham et al., 2013). Models which integrate the effects of temperature on demography are likely to provide more accurate predictions of climatic impacts than those that look at the climatic niche of a species alone. Despite the potential of demographic models to highlight species threatened under climate change, demography is not often taken into account when predicting climate change impacts on species (Urban et al., 2016), and where demographic impacts have been observed these are rarely built into models which look at population trends (Bogstad et al., 2013; Meager and Limpus, 2014; Nord and Nilsson, 2016). Studies also commonly focus on species where the impacts of temperature on demography are direct, for example reptile species in which offspring sex is determined by temperature (Hulin et al. 2009; Mitchell et al. 2010). Understanding these demographic effects is key in order to enact conservation actions which are aimed at reducing the impacts of climatic change on species (Correia et al., 2015).

Most previous approaches to modelling the impacts of climate change on population dynamics have used matrix-based models, likely in part due to their focus on organisms with simple social systems, combined with the fact that much of the data was collected at broad time-scales as opposed to resulting from continuous monitoring over time (Poloczanska et al., 2008; Doak and Morris, 2010; Merow et al., 2014; McCauley et al., 2017; Tye et al., 2018; Jenouvrier et al., 2018). Social behaviour has an important demographic impact in many species, however, and animals with complex social behaviours the incorporation of these group level dynamics is key in predicting population trends (Bateman et al., 2012; Bateman et al., 2013; Angulo et al., 2013). For animals with more complex social dynamics and behaviours, individual based models may be more appropriate as they are well suited to modelling climatic impacts due to their ability to capture the social dynamics of species (Deangelis and Grimm, 2014). Individual based models have been commonly used throughout the population modelling literature to model the impacts of environmental and social change in species (Grimm and Railsback, 2005), and are particularly useful when investigating demographic shifts that could potentially be mitigated by conservation or management interventions (Deangelis and Grimm, 2014). IBMs are especially suitable for modelling the demographics of wide ranging species under climatic shifts as the incorporation of spatial variables is relatively straightforward (Grimm and Railsback, 2005). Large mammals, which often have complex social dynamics and range over large distances, have been highlighted as a group of animals that may be under particular risk from climate change (Fuller et al., 2016). IBM’s are a good method of predicting future population trends on large mammals as there is sufficient data and complex social dynamics can be incorporated into future projections.

One large mammal that has shown multiple demographic impacts of high temperature is the African wild dog (*Lycaon pictus*), a highly social canid that lives in packs of between 2 and 26 adults. African wild dogs are obligate co-operative breeders, with an alpha pair typically monopolising reproduction within each pack. Other, sub-dominant, pack members assist in raising the pups through food provisioning and guarding the den, when other members of the pack are hunting. African wild dogs were historically found throughout most of sub-Saharan Africa, however today they are restricted to just 7% of their historic range, with the largest populations found in Sothern and Eastern Africa. African wild dog breed aseasonally near the equator and seasonally away from the equator, at the coolest time of year (McNutt, et al., In Review). Dispersal occurs in single sex groups, which leave their natal packs and search for groups of the opposite sex. If dispersers locate a group or single disperser of the opposite sex they then form a new pack and a new alpha pair is established (Woodroffe et al In Review b). When one of the alpha pair dies there are two possible outcomes: if another founder of the same sex is present, it will then replace the dead alpha within the alpha pair; if no pack founders of the same sex are present the pack will split into two single sex dispersal groups (Woodroffe et al In Review a).

Previous studies have shown that African wild dog reproduction and survival are all negatively impacted by high temperatures, with lower adult (Rabaiotti and Woodroffe 2019) and juvenile survival (Woodroffe et al., 2017) at high temperatures. A longer period of time between one breeding attempt and the next when temperatures are higher during the denning period (equivalent to the first three months of the litter's life) has also been observed at a site with aseasonal breeding (Woodroffe et al., 2017).

I used demographic data from the African wild dog to construct an IBM incorporating the relationship between temperature, survival, and reproduction in the species. I then used this model to explore the impact of high temperature on key demographic variables, in particular: pack size, pack longevity, survival rates, litter size and timing of breeding. By running the model under temperature regimes predicted under a range of emissions scenarios I was able to project the impact of future climate change on the population dynamics and extinction risk in the species.

4.3. Materials and Methods

4.3.1. Life History Data

The parameters used in the study were obtained from long term demographic data collected by the Kenya Rangeland Wild Dog and Cheetah Project, in a study area which covers Laikipia County, Kenya, and parts of the neighbouring counties of Samburu, Isiolo, and Baringo. African wild dogs were monitored between the years 2001 and 2017 using a combination of GPS collars, radio collars and visual observation (Woodroffe, 2011 a; Woodroffe, 2011 b). The number of adults (individuals that are 12 months or older) and juveniles (individuals that are less than 12 months old) in each pack, litter sizes, births, deaths and dispersal events were recorded by researchers throughout the course of the project. Temperature data from a weather station within the study site (Caylor et al., 2017) were used to investigate how temperature correlated with recruitment, survival and dispersal.

4.3.2. Individual based model

4.3.3.1. Purpose

The purpose of this model is to understand how temperature impacts population dynamics and viability in the African wild dog.

4.3.3.2. State variables and scales

Four hierarchical levels make up the individual based model: Individual, territory, population and environment. Individuals are characterised by their dominance status – alpha or sub dominant, and their age – adult (*a*) or juvenile (*j*). Juveniles are defined as individuals between 3 and 12 months, juveniles older than 11 months become adults. Juvenile classification begins at three months as opposed to zero as this is the age at which pups start to move with the pack and can be reliably counted (Woodroffe, 2011b). Prior to this age, as dens are inaccessible, it is difficult to observe wild dogs without disturbance and hence to obtain reliable estimates of litter size. Adult and juvenile wild dogs are in separate age categories as temperature affects adult and juvenile mortality differently, with average maximum temperature during the first three months of life impacting juvenile survival, and average maximum temperature over the previous month impacting adult survival. Another reason for separating adult and juveniles into separate categories is that pack size is often defined as the number of adults in a pack, and pack size influences both adult survival and litter size. Due to the social dynamics of the species, where only the alpha pair breeds and the pack dynamics are influenced by alpha survival, alpha adults are built into the model as a separate dominance category. The model is female only therefore the alpha category contains a single individual, and no individuals move into this category unless the alpha has died. If the alpha dies either a randomly chosen subdominant individual from the same pack inherits alpha status or the whole pack disperses, known as a ‘pack break-up’.

A territory can be occupied by one pack of wild dogs, which consist of one alpha female along with a number of sub dominant adults, and any juveniles born to that pack that have not yet reached 12 months of age. A territory is characterised by: its identity number, the size of the pack present, time since the pack formed, the size of the pack’s last litter and the timing of the packs last breeding attempt. If there are no individuals in the territory it is classified at ‘empty’ and can be occupied by a group of dispersers.

The population is composed of multiple territories and a number of social groups, referred to as ‘packs’. For the purposes of this analysis two different territory numbers are used: 30 territories, which is the maximum number of packs recorded at the Kenya study site, and nine territories, which is the median number of packs per population within the species’ remaining range throughout Africa (Woodroffe and Sillero-Zubiri, 2012). The population is characterised by its size (the number of individuals of all ages) and the number of packs. In addition there is a dispersal pool which comprises of individuals that have dispersed from their pack but have not formed a pack and settled in a territory. When the number of packs in the population is 0 the population is classed as extinct.

Abiotic environment is the highest hierarchical level in the model. As African wild dog recruitment and survival is impacted by mean maximum temperature this is how the abiotic environment is characterised. Temperature, in degrees Celsius, is centred on the mean throughout, therefore the average temperature is represented by 0.

4.3.3.3. Process overview and scheduling

The model proceeds in monthly time steps. Within each time-step six phases occur in the following order: mortality, dispersal, aging, recruitment, inheritance of dominance status or pack break up, re-colonisation of vacant territories.

4.3.3.4. Design concepts

4.3.3.4.1. Emergence

Pack and population level dynamics emerge from individual behaviour in the model, along with the timing of breeding. Individual’s lifecycles and behaviours are defined by empirical rules describing aging, as well as mortality and dispersal probabilities. Adaptation and fitness seeking are not explicitly modelled. They should be captured by the model, however, particularly through the rules describing dispersal, as the higher probability of dispersing at higher pack sizes is likely driven by likelihood of reproduction, and therefore individual fitness.

4.3.3.4.2. Sensing

Individuals are assumed to know their dominance status, age class (juvenile or adult) and pack size in order to inform their dispersal probability. They are also assumed to know the mortality status of the alpha, which informs their ability to change dominance status, and informs whether the pack breaks up.

4.3.3.4.3. Interactions

The interactions modelled explicitly in the models are: adult survival and juvenile survival decrease at higher temperatures, the time between one breeding event and the next is longer at higher temperatures, adult survival increases with pack size, litter size increases with pack size, dispersal probability increases with pack size, the timing between one breeding attempt and the next increases with litter size and juvenile survival increases with litter size. Interactions implicitly modelled are litter size and dispersal probability fall with temperature.

4.3.3.4.4. Stochasticity

Temperature is drawn from a normal distribution to mimic the stochastic variation in temperature observed in the field. In order to determine death a random number is drawn from a uniform distribution between 1 and 0 and if the number was higher than the probability of survival the individual died, if it was lower the individual survived. The same was done for dispersal, but with dispersal probability as opposed to survival probability. To determine the fate of the pack after the alpha died a random number was drawn from a uniform distribution between 0 and 100 and if the number is less than or equal to 40 alpha status was inherited by a subdominant pack member, over 40 and all subdominant individuals left the territory and entered the dispersal pool. 40% probability was used as this is the percentage of pack break-up (as opposed to pack inheritance) observed in the field.

4.3.3.4.5. Observation

For the purposes of model testing each individual is observed process by process. For model analysis only pack and population level variables are recorded, namely: pack size, inter-birth interval, litter size, pack longevity, number of dispersers (the total number of individuals in the dispersal pool in any one time-step), number of packs, population size and time to extinction.

4.3.3.4.6. Initialisation

Each territory is initially occupied by one alpha female and a number of subdominants, determined by selecting a number from a Poisson distribution with a lambda of 3 (the mean number of subdominant females in a pack from the field data). The time until the first breeding attempt was determined by selecting a random number from a uniform distribution of whole numbers between 1 and 11 (the mean inter-birth-interval (in months) from the field data). The initial litter size is set to 4 female pups, and from then on is determined by the litter size submodel. The model is then run for 100 months at a mean (centred) temperature of 0, after which the evaluation of the first run starts.

4.3.3.4.7. Inputs

Temperature is selected from a normal distribution with a mean of 0, representing the mean daily maximum temperature over a period of 30 days, with variance (Ω) matching temperature variance from the weather station at the study site.

$$T_t \sim N(0, \Omega)$$

Table 4.1: Symbols used in the models. Temperature refers to mean maximum temperature throughout.

Symbol	Variable
H	Number of territories in the model
N_t	Total number of adults (alpha and subdominant) at time *t*
$N_{i,t}$	Number of adults (alpha and subdominant) in a pack at time *t*
$N_{D,t}$	Total number of dispersing individuals at time *t*
$N_{iD,t}$	Number of dispersing individuals in a dispersal group at time *t*
$N_{id,t}$	Number of deaths in a pack at time *t*
$N_{ib,t}$	Number of births at time t
α, β, γ, δ, ε, ζ, θ, λ, μ, ξ, σ, φ, ω, Ω	Constants. Further details in Table 4.2.
r_i	Inter birth interval for a pack
$l_{i,t}$	Litter size for a pack at time *t*
$l_{i,r-1}$	Litter size of a pack in the previous breeding event
T_t	Temperature at time *t*
$T_{i,r-1}$	Mean temperature in the denning period prior to the previous breeding event calculated as $\left(\frac{(T_{t-2}+T_{t-1}+T_t)}{3}\right)$ at time *b-1*
$S_{j,t}$	Juvenile survival probability at time *t*
$S_{a,t}$	Adult survival probability at time *t*
$P_{D,t}$	Probability of dispersal at time *t*
$P_{p,t}$	Probability that a dispersal group will occupy an empty territory at time *t*
x,y	Random numbers drawn from a uniform distribution between 1 and 0

4.3.3.5. Submodels

The basic equation population size, that is, the number of African wild dogs in packs in the model (dispersers were excluded from population size estimates) at the next time step (N_t) is a function of the number of territories (H), the number of individuals present in each pack in the previous time step($N_{i,t-1}$); the number of deaths in the current time step ($N_{id,t}$); the number of dispersals from that pack in the current time step ($N_{iD,t}$); and the number of births in that time step ($N_{ib,t}$):

$$N_t = \sum_{i=1}^{H} [N_{i,t-1} - N_{id,t} - N_{iD,t} + N_{ib,t}]$$

If a pack goes extinct ($N_{i,t-1} = 0$) then if there is a group of dispersing individuals (N_D) in the dispersal pool they can join the population and form a new pack.

Model parameters (Table 4.1) were derived from empirical data and functions determining the parameters within the individual based model took the same form as the model from which the estimates were derived, either Cox proportional hazard, in the case of adult survival (S_a) and probability of dispersal (P_D), or generalised linear models, in the case of juvenile survival (S_j), litter size (l) and timing of breeding (b). The function to determine litter size took the form of a Poisson distribution as it was conducted on count data, the function to determine juvenile survival took the form of a binomial distribution and the function to determine timing of breeding took the form of a Gaussian distribution.

4.3.3.5.1. Births

Number of births (N_b) was dependent on the timing of the next breeding attempt (T_{ri}):

$$N_b = \begin{cases} l_i, if\ t = t_{ri-1} + ri \\ 0, otherwise \end{cases}$$

The timing of the each breeding attempt was dependent on the temperature during the previous denning period of that pack ($T_{i,r-1}$) and the previous litter size of that pack ($p_{i,r-1}$), where r_{i-1} is the timestep when the last litter was born. Temperature during the first three months of life ($T_{i,r-1}$) was calculated from the temperature over the three months prior to the juveniles emerging from the den.

$$\left(\frac{T_{t-2} + T_{t-1} + T_t}{3}\right)$$

The inter birth interval was defined by a function of the temperature ($T_{i,r-1}$) and litter size ($l_{i,r-1}$) of the previous denning period:

$$r_i = \alpha + \beta T_{i,r-1} + \gamma l_{i,r-1}$$

α, β and γ are constants defined by the generalized linear model run for inter birth interval.

The estimate for inter birth interval (r_i) was rounded to the nearest whole number to give the number of months between one breeding attempt and the next.

The number of pups at three months of age $(l_{i,t})$ was determined by the number of adults in the pack at that timestep $(N_{i,t})$. The formula used to calculate the litter size is below, and symbol definitions can be found in Table 4.1:

$$l_{i,t} = e^{\delta + \varepsilon N_{i,t}}$$

δ and ε are constants defined by the generalised linear model ran on litter size. The resulting number was then rounded up to the nearest individual to give a whole number.

4.3.3.5.2. Number of deaths

Number of deaths (N_d) was dependent on the survival probability in both adults (S_a) and juveniles (S_j), characterised together as *S*:

$$N_d = \sum_{i=1}^{N_{ai,t-1}} [\begin{cases} 1 & if\ y \sim U(0,1) < S \\ 0 & otherwise \end{cases}]$$

The probability of an individual juvenile's survival at each time-step $(S_{j,t})$ was dependent on the size of that individuals birth litter at the time they permanently left the den $(l_{i,r-1})$ and the mean daily maximum temperature over the denning period following the birth of that individual $(T_{i,r-1})$. As the data from which the survival rate was estimated only contained the number of pups at 3 and 12 months of age, the 9th root was taken to obtain monthly survival rates.

$$S_{j,t} = \left(\frac{\zeta + \theta T_{i,r-1} + \lambda l_{i,r-1}}{1 + \zeta + \theta T_{i,r-1} + \lambda l_{i,r-1}}\right)^{\frac{1}{9}}$$

ζ , θ and λ are constants defined by the generalised linear model ran for juvenile survival (Table 4.2).

The probability of adult wild dog survival, including both alpha and subdominant survival, during that time-step ($S_{a,t}$) was dependent on pack size ($N_{i,t}$) and temperature (T_t) in that timestep. The formula used to calculate the probability of survival for each individual adult is below (Table 4.1, 4.2):

$$S_{a,t} = \mu(e^{\xi T_t + \sigma N_{i,t}})$$

μ, ξ and σ are constants defined by the Cox proportional hazards model on adult survival (Table 4.2).

4.3.3.5.3. Dispersal

Within the model only subdominant adults could disperse, as this is what is observed in the field. Number of dispersers (N_D) was dependent on the probability of dispersal (P_D):

$$\sum_{i=1}^{N_{ai,t-1}} [\begin{cases} 1 & if\ x \sim U(0,1) < P_D \\ 0 & otherwise \end{cases}]$$

Dispersal probability at each time step ($P_{D,t}$) was dependent on pack size in that timestep ($N_{i,t}$). The formula for individual dispersal probability is shown below, and symbol definitions can be found in Table 4.1:

$$P_{D,t} = \varphi(e^{\omega N_{i,t}})$$

φ and ω are constants defined by the Cox proportional hazards model for dispersal.

Once an individual dispersed it entered a dispersal pool, where it remained for two time steps before being lost to the population. Individuals in the model were lost to the population after two months as data from the study site indicates that wild dogs are dispersing for an average of 19.4 days. This is likely to be an underestimate, however, as the parameters are based on models of animals fitted with tracking collars only, but uncollared members of dispersal groups were discovered in new packs after significantly longer time periods (Woodroffe et al In Review b). Individuals also dispersed if the pack breaks up after alpha death. When this happened all juveniles in the pack died.

4.3.3.5.4. Territory inheritance

If any of the packs within the model broke up, leaving an empty territory, a dispersal group could then occupy that territory, starting a new pack. Each individual has an equal probability of occupying a territory and therefore larger dispersal groups have a higher chance of occupying an empty territory. The formula for the probability that a dispersal group would occupy an empty territory (P_p) is shown below, and symbol definitions can be found in Table 4.1:

$$P_{p,t} = N_{iD,t}\left(\frac{1}{N_{D,t}}\right)$$

4.3.3.6. Full model

The above parameters were combined into an individual based model; the formula for the number of individuals of all age classes within packs in the model is shown below:

$$N_t = \sum_{i=1}^{H}[N_{i,t-1} - \sum_{i=1}^{N_{ai,t-1}}[\begin{cases} 1 & if\ x \sim U(0,1) < P_d \\ 0 & otherwise \end{cases}] - \sum_{i=1}^{N_{i,t-1}}[\begin{cases} 1 & if\ y \sim U(0,1) < S \\ 0 & otherwise \end{cases}] + \begin{cases} l_i & if\ t = t_{ri-1} + ri \\ 0 & otherwise \end{cases}]$$

4.3.3. Model parameterisation

In order to parameterise dispersal, recruitment and survival within the individual based model I re-analysed the data from Woodroffe et al (2017), Woodroffe et al (In Review a) and Chapter 3 of this thesis. These re-analyses enabled us to estimate each of the vital rates on a monthly time-step and meant that estimates could be obtained which accounted for variables other than temperature that influenced survival and recruitment which were not included in the IBM such as land use type and rainfall. I used the estimates from these reanalyses to model relationships between pack size (the number of adults in a pack), litter size, inter birth interval (the period between the birth of one litter and the next), juvenile survival, adult survival, probability of dispersal and temperature (outlined below). Adults were defined as individuals over 12 months and juveniles between 3 and 12 months. The models in Woodroffe et al (2017), Woodroffe et al (In Review a) and Chapter 3 showed correlation as opposed to causation, but for the purposes of the individual based model causation has been assumed. In line with the methods in Woodroffe et al (2017) and Chapter 3 maximum daily temperature was used as the measure of temperature. Maximum daily temperature has been found to correlate with the number of hours in the day during which it is cool enough for wild dogs to hunt, and multiple measures of vital rates and behaviour (Woodroffe et al., 2017; Rabaiotti and Woodroffe, 2019).

The relationships between temperature and inter birth interval, litter size, and juvenile survival, were estimated through running generalised linear models using the data from Woodroffe et al (2017). Woodroffe et al. (2017) found that larger packs consistently produced larger litters. In order to obtain the estimates used to parameterise litter size in the individual based model a Poisson distributed generalised linear model with litter size as the dependant variable, and pack size as the independent variable, was run. Temperature was not included in the model as it was not found to have a significant impact (Woodroffe et al., 2017).

Woodroffe et al (2017) showed a positive relationship between temperature in the previous breeding period (the three months in which African wild dogs have pups in the den) and inter birth interval, and a positive relationship between previous litter size and inter birth interval. To estimate the parameters needed to determine timing of breeding I therefore ran a Gaussian distributed generalised linear model, with inter birth interval as the dependant variable, and previous litter size and temperature during the previous breeding period as independent variables.

Litter size and temperature during the first three months of a wild dog's life (equivalent to the three months following the previous breeding period) were found by Woodroffe et al (2017) to influence juvenile survival, with litter size having a positive relationship with survival from 3 to 12 months and high temperatures reducing survival from 3 to 12 months. To obtain estimates of juvenile survival to inform the individual based model I ran a binomial generalised linear model with juvenile survival from 3 to 12 months as the dependant variable and temperature in the first three months of life and litter size as dependant variables.

Adult survival and dispersal datasets were analysed on a monthly time-step, with the mean daily maximum temperature within each month of the year and the mean number of adults in a pack over each month of the year taken.

Chapter 3 found that high maximum temperature was associated with lower adult survival and large pack size was associated with increased adult survival. To obtain estimates for adult survival to parameterise the individual based model I ran a Cox proportional hazards model with survival as the dependent variable and temperature and pack size as the independent variables.

Woodroffe et al (In Review a) found individual wild dogs had a higher dispersal probability at large pack sizes. To obtain estimates for dispersal probability I ran a Cox proportional hazards model with dispersal events as the independent variable and pack size as the dependant variable and these were then used to parameterise the individual based model.

Cox proportion hazards models were carried out using the *survival* package (Therneau and Grambsch, 2000) and generalised linear models were carried out using the *lme4* package (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2015).

4.3.4. Elasticity analysis

I performed an elasticity analysis to determine how robust the model was to uncertainty within the estimates that were obtained from the field data. I independently increased each of the parameters (Table 4.2) in the formulae for inter-birth interval, litter size, juvenile survival, adult survival and dispersal probability, as well as the mean and variance of the distribution from which temperature was drawn, by 1%, meaning positive values were multiplied by 1.01 and negative values by 0.99 respectively (Coulson et al. 2011). After each increase I re-ran the model for 100,000 months, before altering the next parameter. In order to test the impact of number of packs on extinction probability the model was also run with 8 and 10 packs. By independently perturbing each parameter I aimed to determine which parameters contributed the most to the demography of the African wild dog, by observing changes in the parameters of interest (pack size, inter-birth interval, litter size, pack longevity, number of dispersers, number of packs, population size and time to extinction).

I also ran the model under warming of 0.5-5.5 degrees at 0.5 degree intervals, for the model constructed with 9 and 30 packs, to investigate the effect of increased mean temperature on the population. The model was run at for 10 generation to estimate the population extinction risk within 10 generations. It was also run for 100,000 time steps to estimate time to extinction.

Table 4.2: Coefficients in the individual based model that were varied in the elasticity analysis, alongside the parameter value used in the model.

Variable	Coefficient	Symbol	Value
IBI	Intercept	α	8.6404
	Impact of temperature	β	0.9156
	Impact of litter size	γ	0.5198
Litter size	Intercept	δ	0.9622
	Impact of pack size	ε	0.0457
Juvenile survival	Intercept	ζ	-0.8528
	Impact of temperature	θ	-0.5542
	Impact of litter size	λ	0.4413
Adult survival	Intercept	μ	0.0294
	Impact of temperature	ξ	0.1702
	Impact of pack size	σ	-0.1654
Dispersal	Intercept	φ	0.0064
	Impact of pack size	ω	0.10594

4.3.5. Future projections

In order to explore the effect of rising temperature on the population of African wild dogs I ran the model under four future emissions scenarios, for 10 generations, for both 9 and 30 territories. Rasters of current temperature estimates (1975-2013) and future predictions (from the HADGEM-2-ES climate models) of temperature for 2050 and 2070 across the study site were obtained at a resolution of 30 arc seconds from the WorldClim climatic dataset (Hijmans et al., 2005). Raster layers for all four emissions scenarios – representative concentration pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 – were obtained for the years 2050 and 2070. I defined the study area by drawing minimum convex polygons around locations obtained from GPS-collared individuals monitored by the Kenya Rangelands Wild Dog and Cheetah Project, and then merged them to generate a single concave polygon. I then obtained predicted future change in temperature for each pixel across the study site by subtracting the current estimate of mean maximum daily average temperature across 12 months for each pixel from the corresponding future predicted mean maximum daily average temperature in 2070 across 12 months. This series of calculations gave a layer comprising predicted change in temperature between current temperature estimates and future temperature predictions for 2070 for each pixel. This subtraction was repeated for all four representative concentration pathway predictions for 2070. The mean across each layer of temperature change were then taken to give average predicted change in annual temperature in the study site for each RCP.

In order to predict future population trends under climate change the model was run for 600 time-steps, equivalent to ten generations, under all four representative concentration pathways for predicted change in temperature between current estimates and 2070. The model was also run using the estimates plus and minus the standard error from the models of the impact of temperature on juvenile survival, adult survival and inter-birth interval to obtain a high and a low prediction of the impact of temperature under each emissions scenario.

4.3.6. Model Validation

In order to validate the model, I estimated litter size, packs size and inter birth interval for the hottest and coolest 36 months for which I had data on all three variables (2002-2009) using the model constructed with nine territories. To do so I used cross validation, removing three years from the field data and used the remaining data to re-calculate the model parameters. The model was then run 1000 times across 100,000 time steps using the recalculated parameters and the temperature drawn from a normal distribution with a mean of the mean daily maximum temperature during the three years that were removed. I then tested whether the observed mean pack size, litter size and inter birth interval in the removed months fell within the standard error of the mean from the model outputs. A period of 36 months was chosen as it was a long enough time period to include at least two inter-birth intervals and breeding attempts. Model outputs were also visually compared with the empirical data to assess fit.

4.4. Results

4.4.1. Parameter Values

The outputs of the model were realistic. Despite not being explicitly modelled within the IBM mean dispersal group size, mean packs size at formation and mean pack longevity predicted by the model were in line with values observed in the field (Table 4.3, Fig. 4.1). The number of packs remained high, indicating that empty territories were filled quickly (Table 4.3).

Table 4.3: Mean population and pack parameters predicted by the model at mean temperatures across 1000 model runs of 100,000 time steps with 9 territories

Parameter	Value
Pack size	5.40
Pack size on formation	3.62
Litter size	3.92
Inter birth interval (months)	10.95
Pack longevity (years)	4.37
Dispersal group size	3.23
Population size	72.44
Number of packs	8.95

4.4.2. Model Validation

The model fit the field data adequately, with the predicted distributions of pack size, inter birth interval, dispersal group size and the size of the pack at formation approximately matching the distribution of the data (Fig. 4.1). Short lived packs were over-represented in the model predictions, and the distribution of litter sizes was narrower (Fig. 4.1), due to the fact the model was single sex and the number of pups having to be rounded to the nearest whole number.

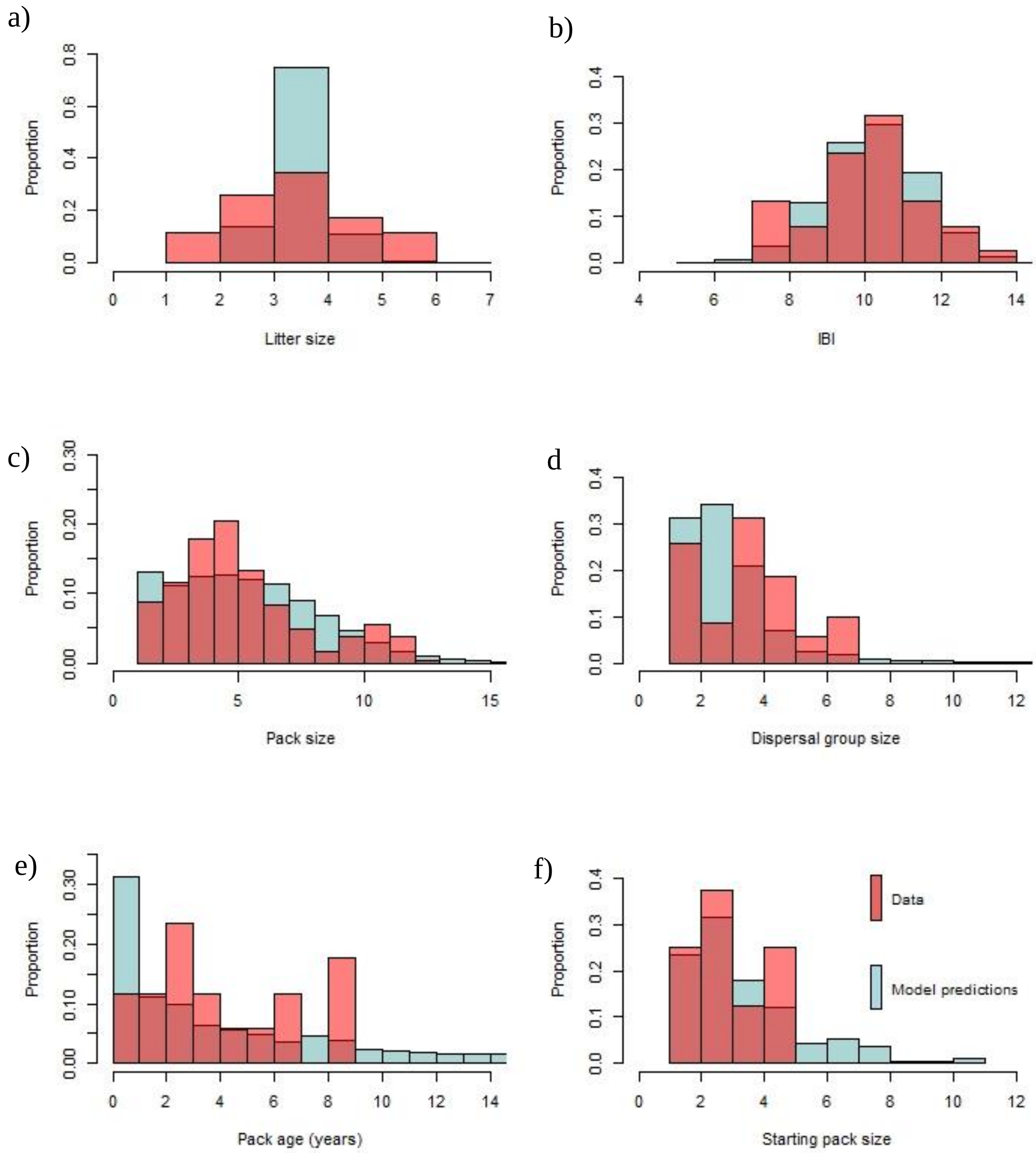


Figure 4.1 Density of model predictions and empirical data for a) pack longevity (years), b) pack size, c) inter-birth-interval, d) litter size, e) dispersal group size and f) size of packs when they are first formed. The empiracle data for litter size, pack size and starting pack size was divided by two to reflect the fact the mode lwas single sex. The empiracle data on dispersal group size was the number of females in th dispersal groups.

Cross validation of the hottest and coolest years produced predictions that were relatively consistent with the pack sizes, inter birth intervals and litter sizes observed in the field (Fig. 4.2), with standard errors overlapping between the field data and predicted values for all cases other than inter birth interval and pack size in the hottest years.

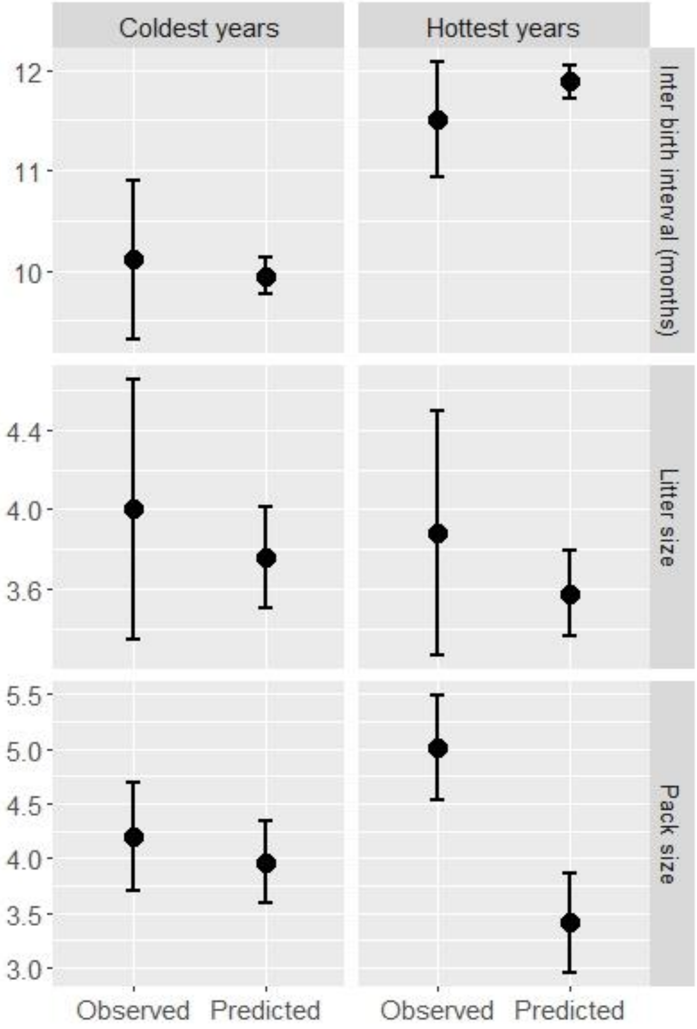


Figure 4.2 Observed and predicted values of inter birth interval, litter size and pack size. Error bars represent the 95% confidence interval.

4.4.3. Elasticity analysis

All model variables were insensitive to 1% changes of the parameters in the model. Pack size and litter size were most elastic to dispersal parameters – both the intercept and the slope of the effect of pack size on dispersal probability, as well as the intercept for inter birth interval (Fig. 4.3). Pack longevity was most sensitive to adult survival due to the link between adult survival, alpha survival and pack break up (Fig.

4.2). The number of packs was most elastic to dispersal parameters and the intercept of inter birth interval (Fig. 4.3). Changing the number of packs in the model by 1 had no impact on extinction risk, and neither did a 1% change in any of the other parameters.

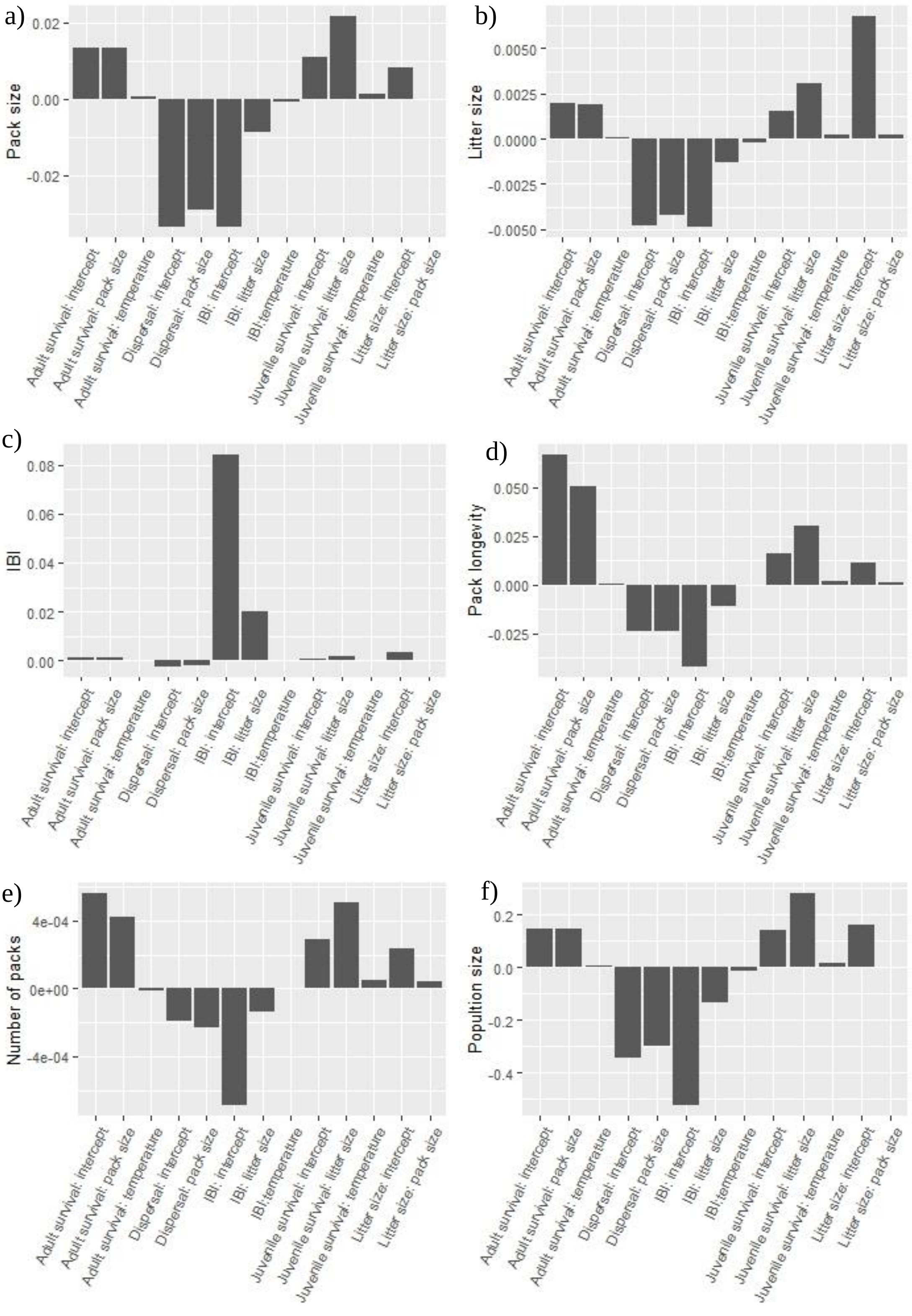


Figure 4.3**:** Elasticity of a) pack size, b) litter size, c) inter-birth interval, d) pack longevity (months), e) number of packs and f) population size to a 1% change in model parameters, and an increase and decrease in pack size by 1. Ten denotes ten packs in the model and eight denotes eight packs.

4.4.4. Impacts of high temperatures

The model predicts that litter size and pack size are expected to be lower at higher temperatures, and there are fewer packs present on average. Individual packs are also predicted to persist for fewer years at high temperatures (Fig. 4.4). At higher temperatures the average predicted population size is lower (Fig. 4.4). Extinction risk within 10 generations for a carrying capacity of 9 packs (i.e. an area equivalent to 9 territories) remains at zero until mean temperatures are on average 2.5°C higher (Fig. 4.5) and when temperatures are 4.5 degrees hotter than current average temperatures extinction risk is 1 (Fig. 4.5). In the model of 30 territories extinction risk remains 0 at 3.5°C and is 100% and 5.5°C (Fig. 4.5). Once extinction risk is greater than one there is a large difference in extinction risk between model runs of temperatures 0.5°C apart for both models run with both 9 and 30 territories (Fig. 4.5).

4.4.5. Future projections

Temperatures across the study site were predicted to rise between 1.6°C and 3.9°C by 2070, in the best (RCP 2.6) and worst (RCP 8.5) case scenarios, respectively. RCP 4.5 was predicted to cause 2.5°C of warming by 2070 and RCP 6.0 was predicted to cause 2.9°C warming by 2070.

When the model was run under the mean temperature increase for the best case emissions scenario (1.6°C warming) there was little change in population persistence over 10 generations for an area encompassing 30 territories, including when the model was parameterised using the high standard error measures for the impact of temperature on survival and inter birth interval (Fig. 4.4). Under the model runs which used the estimates (as opposed to plus or minus the standard error) the predicted inter birth interval was one month longer, at 12 months, under the best case scenario and mean pack longevity fell from 5.4 to 3 years (Fig. 4.4). Predicted pack size was 1.5 adult females lower on average, at 4 dogs as opposed to the 5.7 predicted by the model under current climatic conditions (Fig. 4.4). Lower pack size led to a predicted lower mean population size of 115 individuals as oppose to 175 under current climatic conditions. Number of packs, however, remained high with 30 packs present at the end of the model in the vast majority of runs (Fig. 4.4). There was little difference in litter size between predictions at current temperatures and those under the best case climate scenario (Fig. 4.4).

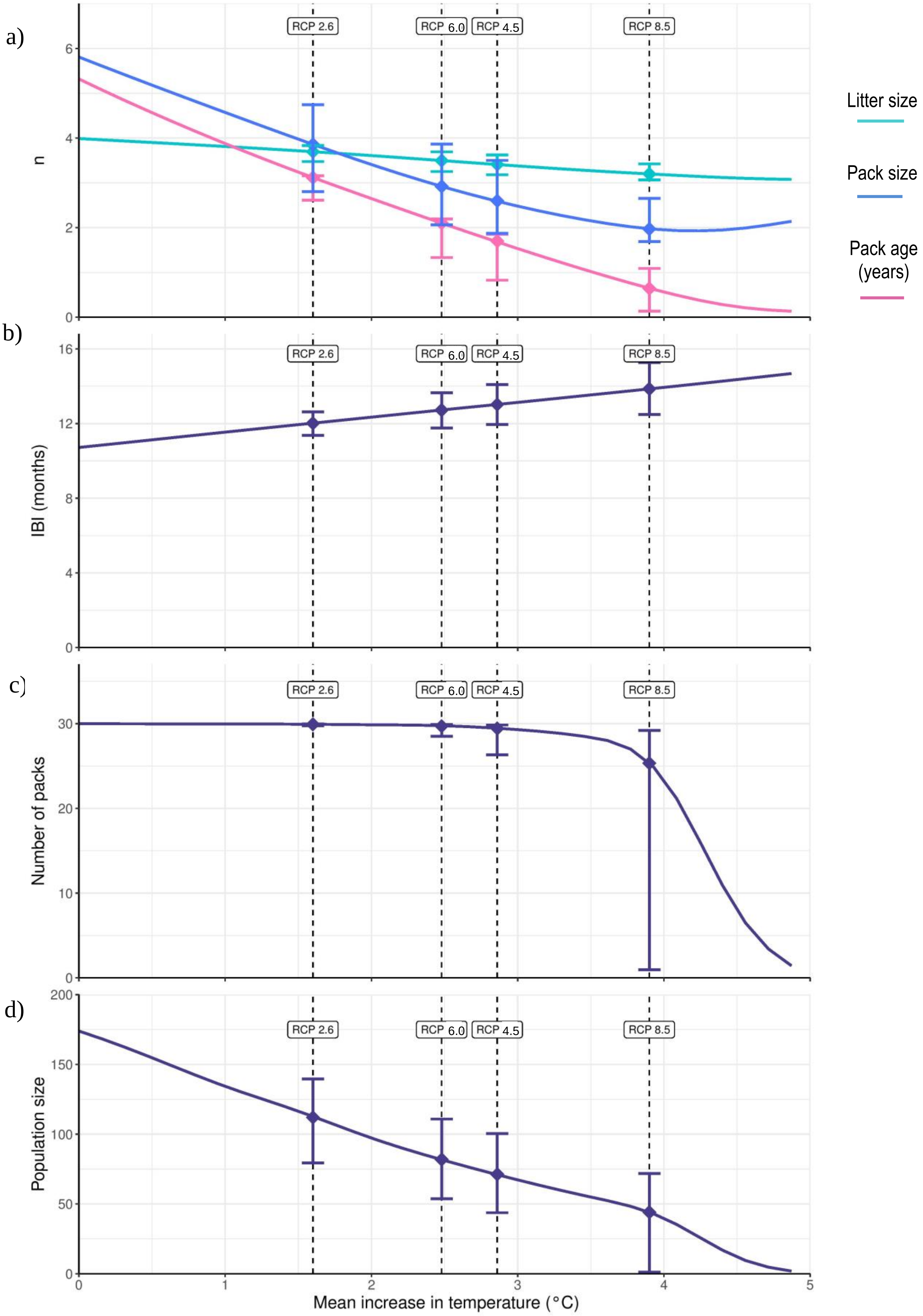


Figure 4.4: The impact of temperature increase (°C) on a) mean litter size, pack age and pack size over 10 generations, b) mean Inter birth interval over 10 generations, c) number of packs remaining 10 generations and d) population size after 10 generations. Curves are splines through predictions made for 0.5 degree intervals of increase in temperature. Points indicate the predictedions of the model under the predicted rise in temperature under four representative concentration pathways, which are marked with a dashed line. Bars represent model predictions based on model runs parameterised using the high and low standard error for the impact of temperature on survival and inter birth interval.

Under RCP 6.0 (2.5°C warming) pack size, pack longevity and litter size were predicted to be smaller than under the best case scenario (Fig. 4.4). Under the model runs which used the predicted inter birth interval was 1.5 months longer, at 12.5 months, and mean pack longevity fell from 5.4 to 2 years (Fig. 4.4). Predicted pack size was 2.5 adult females lower on average, at 3 dogs as opposed to the 5.7 individuals predicted by the model under current climatic conditions (Fig. 4.4). Lower pack size led to a predicted lower mean population size of 80 dogs. Number of packs, however, continued to be high with 30 packs present at the end of the model in the vast majority of runs (Fig. 4.4). Predicted litter sizes were 3.5 as opposed to 4 predicted under current climatic conditions (Fig. 4.4).

The temperature increases predicted under RCP 4.5 (2.8°C) predicted inter birth interval was 2 months longer, at 13 months, and mean pack longevity fell from 5.4 to 1.8 years (Fig. 4.4). Predicted pack size was half the size predicted under current climatic conditions at 2.7 dogs (Fig. 4.4). Lower pack size led to a predicted lower mean population size of 75 individuals, 100 fewer than predicted under current climatic conditions. Predicted number of packs present in the model, remained high but dropped below 30 to 29 (Fig. 4.4). Predicted litter sizes were 3.4 as opposed to 4 predicted under current climatic conditions (Fig. 4.4).

Under RCP 8.5 (3.9°C warming), predicted inter birth interval was 3 months longer, at 14 months, and mean pack longevity fell from 5.4 to 0.9 years (Fig. 4.4). Predicted pack size was less than half the size predicted under current climatic conditions at 2 dogs (Fig. 4.4). Predicted average number of packs present in the model fell to 25 (Fig. 4.4). Lower pack size and number of packs led to a predicted lower mean population size of fewer than 50 individuals, less than a third of the numbers predicted under current climatic conditions. Predicted litter sizes were 3.2 as opposed to 4 predicted under current climatic conditions (Fig. 4.4).

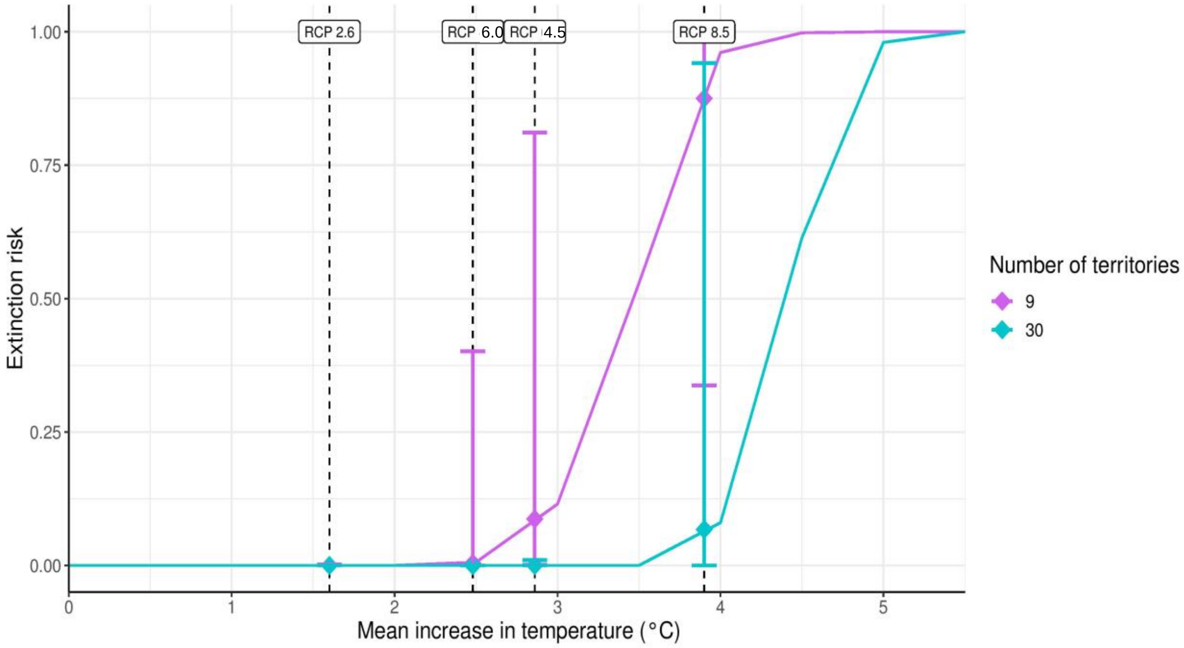


Figure 4.5: The impact of temperature increase (°C) on extinction risk over 10 generations with 9 and 30 oacks in the population. Lines join predictions made for 0.5 degree intervals of increase in temperature. Points indicate the predictedions of the model under the predicted rise in temperature under four representative concentration pathways, which are marked with a dashed line. Bars represent model predictions based on model runs parameterised using the high and low standard error for the impact of temperature on survival and inter birth interval.

Under RCP 2.6 the model predicted an extinction risk of 0 within 10 generations for populations made up of both 9 and 30 territories. Whilst extinction risk was predicted to be above 0 at RCP 4.5 and 6.0 with 9 territories, other than in the model where the low standard error was used, predicted extinction risk remained at 0 with 30 territories in the model (Fig. 4.5). Under RCP 8.5, with 30 territories in the model the predicted extinction risk was11.5% under RCP 8.5 with the high standard error parameters predicting an extinction risk of 93%, and the model parameterised using the low standard error values predicting an extinction risk of 0% (Fig. 4.5). With 9 territories present, with the model parameterised on the low standard error models predicting an extinction risk of 35% and 100% when the high standard error parameters were used (Fig. 4.5).

Table 4.4: Extinction risks and time to extinction over 100,000 time-steps at mean maximum temperatures between 0 and 5.5°C higher than current mean maximum temperatures, for the model run with 9 and 30 territories. Time to extinction was calculated from model runs where the population went extinct only.

Number of territories:	9		30	
Mean daily maximum temperature increase (°C)	Extinction risk	Mean time to extinction (generations)	Extinction risk	Mean time to extinction (generations)
0-2	0	-	0	-
2.5	0.08	85	0	-
3	0.86	59	0.08	1316
3.5	1	12	0.61	284
4	1	11	0.99	130
4.5	1	8	1	19
5	1	7	1	10
5.5	1	6	1	8

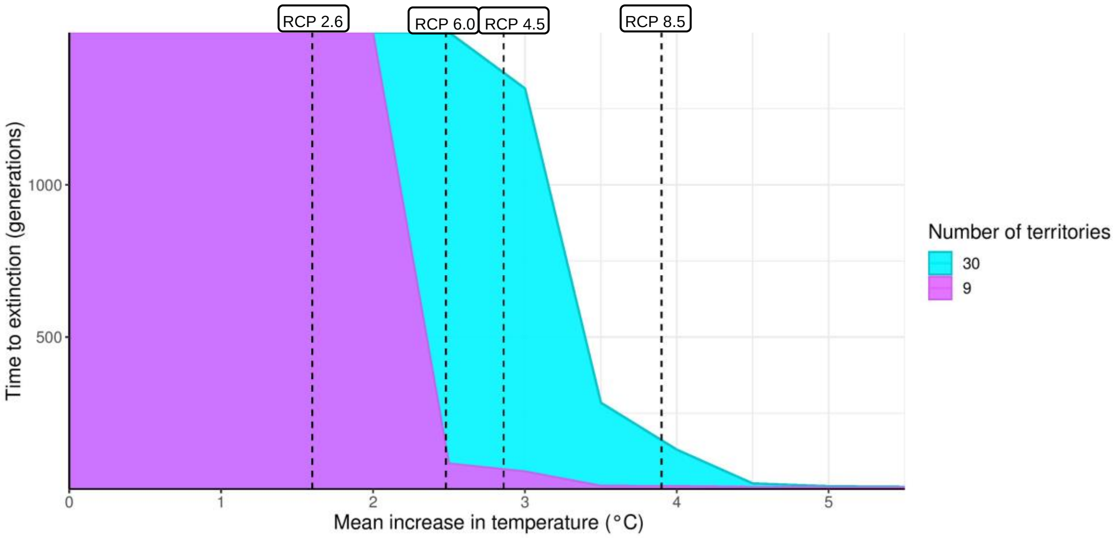


Figure 4.6: The impact of temperature increase (°C) on the number of generations until the population goes extinct, for the model run 9 and 30 packs.

Even over 100,000 time-steps extinction risk remained low until temperatures were 4.5°C higher with 30 territories present in the model, and 3.5°C higher with 9 territories present in the model (Table 4.4). Time to extinction was greater for the model with 30 packs compared to 9 packs across all increases in temperature, and became increasingly smaller over an increase of 0.5°C once temperatures were above 2°C in the model of 9 territories and 3°C in the model of 30 territories (Fig. 4.6). The model of 9 territories predicts comparatively rapid extinction for all RCPs other than 2.6, wheras the model of 30 territories only predicted this at RCP 8.5 (Fig. 4.6).

4.5. Discussion

Ambient temperature had widespread impacts on the outcomes of the individual based model, at both a pack and population level. Packs were predicted to be smaller, and to persist for less time, at higher temperatures through a combination of temperature impacts on survival and recruitment. At a population level, population size, defined as the number of individuals present in all packs in the model, was predicted to be lower at higher temperatures and extinction risk was predicted to be higher at temperature increases of 2.5°C or greater. Whilst a high number of territories within a population buffered the impacts of high temperatures, a 300% increase in carrying capacity of a population only increased temperature resilience by half a degree, and high temperatures resulted in smaller, shorter lived packs, and population declines, even when pack numbers were high.

Climate change impact predictions which rely solely on species traits or correlations between distribution and climate are likely to underestimate threats to species facing demographic climate change impacts (Sinclair et al., 2010; Urban et al., 2016). The underestimation of these threats is likely to be particularly acute for highly mobile species which have in recent history become highly range restricted due to human activities, but have wide climatic niches. In contrast with my model results, trait-based assessments would be expected to classify wild dogs as relatively invulnerable to climate change because of the fact they have high reproductive rates (potentially facilitating recover from perturbation), they are highly mobile (potentially allowing them to shift their geographic range to newly-suitable habitat unaided) and historically lived across a wide range of climatic conditions (expected to indicate flexibility to cope with a range of climatic conditions) (Foden et al., 2013; Urban et al., 2016). My model incorporating the demographic impacts of temperature indicates the impact of rising temperatures on population viability is likely to be more severe than has previously been assumed. My model shows that impacts of high ambient temperatures on reproduction (Woodroffe et al., 2017) and survival (Chapter 3) can combine to threaten population viability.

Our IBM predicts that African wild dog populations are likely to be sensitive to climatic conditions, with the empirically observed impacts of high temperatures on adult survival, juvenile survival and timing of breeding predicted to reduce population sizes and ultimately to increase population extinction risk. In my model, lower adult and juvenile survival at high temperatures, combined with a longer period between one breeding attempt and the next, was together predicted to reduce the size of each pack in the population. Pack size effects, presumed to be generated by cooperative behaviour, amplified the effects of high temperature: lower adult and juvenile survival at high temperatures lead to smaller packs, which produce fewer pups and also experience still-lower adult survival. Moreover, smaller packs produced fewer dispersal groups, reducing the chance of any empty territory becoming occupied. When the population was simulated under 4.5°C of warming, the population eventually became extinct 100% of the time, even with 30 territories in the model. Even at 2.5°C of warming however, extinction risk within 10 generations was higher than under current temperatures, and was predicted to be over 50% at 3.5 degrees warming when there were 9 territories available to the population, consistant with the median population size across the speceis' range.

When these finding are applied to the temperature increases that African wild dogs are projected to experience in the Kenya study site by 2070, it becomes clear that climate change is likely to have negative impacts on this population. Even under the best case scenario the IBM predicts population changes, with smaller, shorter-lived packs, and a consequent fall in population size. Under the middle scenarios, RCP 4.5 and RCP 6.0, the predicted number of packs present in the population at any one time is predicted to be lower, the population size was greatly reduced and when the population was modelled with 9 territories the extinction risk is predicted to be higher than under the current temperature regime within 10 generations. In the worst case scenario for 9 territories the population died out within 10 generations in 95% of simulations and mean populations sizes across 10 generations were just 12% of those predicted under current temperatures. Even with 30 packs in the model extinction risk was significantly higher within 10 generations under the worst case emissions scenario, and 92% after 100,000 time-steps.

With 30 territories in the model extinction risk was greater than 0 at 3.5 °C, 1°C higher than with 9 territories in the model. When the model was run for a longer time period, however, the difference between the temperatures at which extinction risk was above 0 was only 0.5°C. Nontheless, the higher temperature at which extinction risk rises and the longer time to extinction with 30 packs in the model indicate that increasing the size or connectivity of populations may have a buffering effect on the impacts of high temperature on wild dog populations. Only four remaining populations of wild dogs contain 30 packs or more, however (Woodroffe and Sillero-Zubiri, 2012), as the Kenya population has been reduced to a much lower number of packs since a disease outbreak in 2017.

Our results show that most population characteristics were insensitive to the demographic parameters in the model, which is unsurprising due to the feedback between recruitment, mortality, pack size, and dispersal, meaning that group level parameters change relatively little under small shifts in other demographic parameters, as an increase in recruitment leads to an increase in dispersal, and a decrease in survival leads to a decrease in dispersal, offsetting the impacts of survival and recruitment on group size. Population size was most sensitive to recruitment parameters, particularly those informing the inter birth interval, as a smaller inter birth interval means recruitment keeps packs larger, and also parameters informing dispersal probability, likely due to the fact dispersers which did not occupy a territory only survived for 2 months in the model. Number of packs in the population was equally sensitive to adult survival and recruitment. An increase or decrease in the number of packs in the model by 1 did not impact extinction risk, suggesting that populations can remain stable with one greater or fewer packs.

The IBM predictions fit the data adequately, even for demographic variables for which the model was not parameterised, such as dispersal group size. The variance of litter size was lower than in the empirical data, due to the fact that litter size was not stochastic, and simply a whole number dependant on pack size. There were a greater number of small, shorter-lived packs predicted by the model than were found in the data. This difference is likely due to an element of survival or reproduction in the first year of a packs existence that is not captured in the model. Cross validation showed that the model made predictions within one standard error of the observed data for the mean pack size, litter size and inter birth interval in most cases, however in the hottest years the mean inter birth interval was lower and the mean pack size higher than predicted. As I had limited observation time during which all three parameters were available it means that the time period used for validation, 3 years, was quite short, and therefore sensitive to stochastic events unrelated to temperature.

As my model was female only, the impacts on populations may be conservative, as the presence of male dispersers for the females to start a pack with was assumed. In reality, a suitable group of males may not be present in the population, or may be relatives of the group of females, and therefore a dispersal group may be unable to form a pack. Inbreeding avoidance is very strong in wild dogs, and packs will generally not breed if there are no unrelated individuals of the opposite sex present. The model also ignores the impact that the death of the alpha male may have on a pack; packs within a real population would be expected to break up when the alpha male dies if there were no suitable males to take over. This means that the modelled population is likely to be more stable than real populations of the African wild dog. There were no population density parameters in the model, and the population density had a maximum density of the number of territories within the population. There have been few studies into how population density impacts the number of packs that can be supported in a population in African wild dogs populations, however previous work has found that increases in population density lead to greater range overlap as opposed to reduction in the size of territories (Woodroffe, 2011a). This has the potential to impact the species' dispersal behaviour and pack formation.

This model highlights the potential of individual based demographic models to identify environmental conditions under which population viability is reduced. This approach could then be combined with projections of future climate to determine areas where the species is most likely to persist under climate change. By identifying areas where a species has the highest and lowest population viability under future climatic conditions models such as this can be used to target conservation interventions, for example areas where increasing adult or juvenile survival rates would improve population viability in the species. As the model was parameterised using data from a single population, the results may not be as representative of other populations, particularly as in most of the species' range breeding is seasonal, with inter birth interval fixed at approximately 12 months (McNutt et al., In Review). For species with multiple long term study sites, as is often the case for both charismatic megafauna and economically important species, it would be possible to parameterise simple individual based models using data from different sites.

These results demonstrate how long term field data can be used to predict population level effects of environmental change on species, revealing where species are most likely to undergo the largest and smallest impacts, and where they are most likely to persist under future environmental conditions. It can also be used to identify how much environmental change a species is resilient to, determining "tipping points" after which populations are likely to go extinct. The findings of this study have implications for how researchers predict climate change impacts on species, and highlight the extent to which relatively simple mechanistic population models can be used to predict the impacts of climate change on population viability. My findings also raise further concerns about declines in long term field based studies across conservation biology as a whole (Hughes et al., 2017) as, without long term monitoring across a range of weather conditions, mechanistic predictions are not possible. In cases where long term field data are available mechanistic individual based population models can shed new light on climate change threats and enable predictions of future population trends of species.

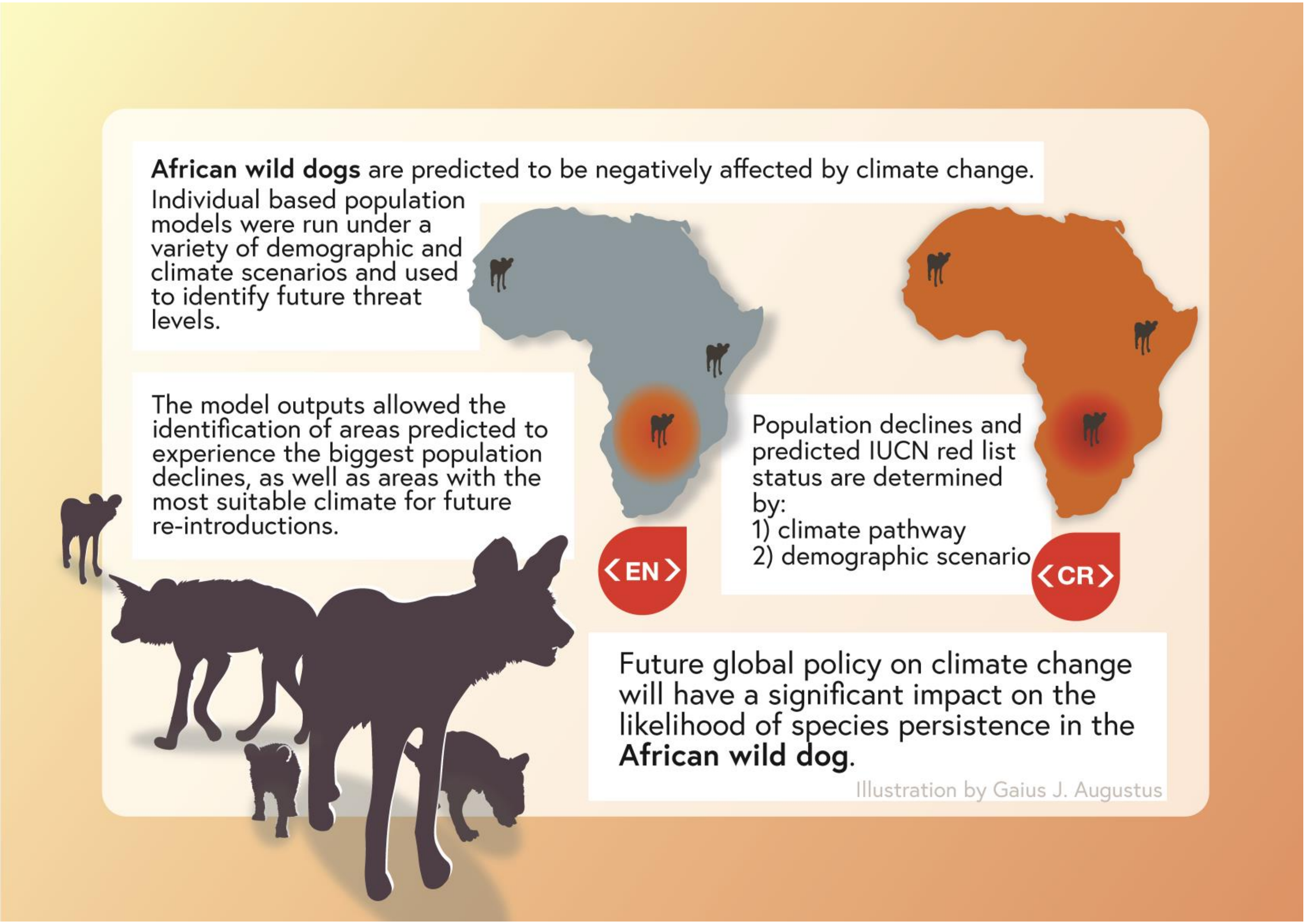
Plate 5: Juvenile African wild dog, Mpala Ranch.

Chapter 5 Emissions scenario determines extinction risk for an endangered species, the African wild dog

5.1. Abstract

Previous studies have shown that climate change is likely to have a negative demographic impact on the African wild dog, *Lycaon pictus*. Here, I use an Individual-Based Model, parameterised for three demographic scenarios, to make spatially-explicit predictions of the impact of climate change on population sizes and extinction risk throughout the species’ range. Wild dog populations were simulated for the year 2060 under four representative concentration pathways of global carbon emissions. Simulations predict declines over all of both the historic and current range of the species. Areas in the current, possible and recoverable range which are predicted to undergo the smallest population declines were concentrated in East Africa, whereas the areas predicted to undergo the largest future declines were in Southern African, specifically Botswana, South Africa, Namibia and Angola. Quantitative differences in the predictions from each demographic scenario suggest that other threats, such as human-wildlife conflict and domestic dog disease, likely plays a role in determining the climatic threat to populations. These findings have implications for conservation planning for the African wild dog, as well as how the risk of climate change to species can inform estimation of threat status for the IUCN Red List.

Graphical abstract



African wild dogs are predicted to be negatively affected by climate change.

Individual based population models were run under a variety of demographic and climate scenarios and used to identify future threat levels.

The model outputs allowed the identification of areas predicted to experience the biggest population declines, as well as areas with the most suitable climate for future re-introductions.

Population declines and predicted IUCN red list status are determined by:
1) climate pathway
2) demographic scenario

Future global policy on climate change will have a significant impact on the likelihood of species persistence in the **African wild dog**.

Illustration by Gaius J. Augustus

5.2. Introduction

Climate change, long acknowledged as a future threat to species, is rapidly becoming a current threat, with the extinction of species such as the Bramble Cay melomys, *Melomys rubicola* (Waller et al., 2017), and the golden toad, *Incilius periglenes* (Pounds and Crump, 1994), heralded as the early signs of an increasing trend in climate-caused extinctions. The scale of climate change impacts on biodiversity have been predicted to overtake those of land use change by 2070 (Newbold, 2018). Climate change differs from many other species threats, including land use change, in that even well enforced protected areas provide little protection, unless those areas are specifically placed to mitigate the effects of climate change. On top of this, climate change is a threat which is both gradual and difficult to reverse, occurring over time scales that do not lend themselves to evaluation under established extinction risk assessments (Thomas et al., 2004; Thuiller et al., 2005). Identifying which species are most at risk from climate change, and the most suitable areas for species persistence into the future, are essential for informing future conservation interventions if they are to be successful in preventing climate-driven species extinctions (Correia et al., 2015).

A myriad of methods for assessing climate change risk to species have emerged within the scientific literature. These aim to identify which species are at risk from climate change, as well as where species are most likely to persist under future climatic conditions. One of the most established of these methods is correlative ecological niche models, which identify which areas will have a suitable climate for species under future climate projections. Whilst these models are convenient in cases where there is a need for assessment of species where data are limited (Pearson and Dawson, 2003), or when ecologists aim to assess multiple species relatively rapidly (Sinclair et al., 2010), multiple drawbacks of this methodology have been raised (Green et al., 2008; Kearney and Porter, 2009). Models including the mechanism by which species are impacted by climate change have increasingly been found to outperform correlative models both in terms of sensitivity and when tested on simulated datasets (Yates et al., 2000; Pagel and Schurr, 2012; Zurell et al., 2016), and as a result there have been increasing calls for the incorporation of these mechanisms into models predicting climate change risk (McMahon et al., 2011; Urban et al., 2016). The mechanisms recommended for inclusion include, but are not limited to, dispersal ability, species interactions, evolution, environment, physiology and demography (Urban et al., 2016). By explicitly incorporating such traits, models assessing climate impact can better predict which sites will be more or less suitable under future climatic conditions, and can potentially take into account resilience of both species and ecosystems to climatic impacts through demography, physiology, species interactions or adaptation – either through phenotypic changes or evolutionary shifts.

Demographic impacts on species are of particular importance as they present the most direct way in which threats impact extinction risk. Demographic impacts of climate change have been recorded for a myriad of species, including impacts on recruitment, survival and dispersal (Doak and Morris, 2010; Dybala et al., 2013; Merow et al., 2014; McCauley et al., 2017; Velarde and Ezcurra, 2018). Studies are increasingly combining impacts on these different vital rates into population models which predict population persistence under future climatic conditions. These models rarely have a spatial element (Keith et al., 2008), however, despite the fact that the inclusion of both spatial and demographic factors has been found to be important in determining population extinction risk under climate change (Pearson et al., 2014). Where studies of the impact of climate change on population trends do include a spatial component they are rarely spatially explicit, and where they are they are often applied to a single population (Keith et al., 2008; Anderson et al., 2009), meaning that population trends and extinctions risk are estimated for a specific population only, rather than for the species as a whole.

The IUCN Red List is the most widely used method for assessing the threat status of species worldwide. It categorises species based on the size of the area they inhabit, population trends and extinction risk (Mace et al., 2008). The IUCN Red List criteria have been found to be an effective method for assessing the extent of threats to species and have been shown to be useful in identifying specific threats (Hayward, 2011; Harris et al., 2012). There have been a number of concerns raised, however, that the criteria may not be well placed to assess extinction risk resulting from climate change due to the fact that impacts of climate change are both pervasive and gradual, meaning that identifying the risks may come at a point where it is too late to implement effective conservation interventions (Thomas et al., 2004; Thuiller et al., 2005; Akçakaya et al., 2006). Species with short generation times were thought to be particularly likely to be assessed as having a lower risk from climate change than their true risk (Akçakaya et al., 2006). Despite these issues, and biases in which species are assessed as being threatened by climate change (Trull et al., 2018), the IUCN Red List has still been used to rank the ‘importance’ of threats to species, leading to claims that ‘only 19% of threatened or near threatened species face threats from climate change’ (Maxwell et al., 2016).

A number of studies have found that the Red List criteria do in fact, counter to concerns, provide sufficient warning of extinction risk resulting from climate change, allowing conservation actions to be identified and implemented (Keith et al., 2014). Work establishing the criteria’s ability to predict extinction risk in time to implement action is still sparse, however, and has focused on single, small-bodied species with short generation times, where conservation actions such as captive breeding programmes are likely to be relatively swift to implement (Keith et al., 2014; Stanton et al., 2015). Stanton et al (2015) highlighted that although the Red List should provide decades of warning of climate induced extinctions, conservation interventions should be implemented once a species is listed as Vulnerable, as 50% of modelled species became extinct within 20 years of being classified as Critically Endangered. The proposal that conservation interventions need to be implemented once a species is listed as Vulnerable would mean that establishing climate change threats to species already classified as threatened is likely to be particularly important.

The African wild dog (*Lycaon pictus*) is a social carnivore currently listed as Endangered on the IUCN Red List (Woodroffe and Sillero-Zubiri, 2012). Once found throughout most of Sub-Saharan Africa, today it is restricted to just 7% of its historic range, with less than half of their current range falling within protected areas (Woodroffe and Sillero-Zubiri, 2012). Although the main threats to the species have previously come from habitat loss, disease and deliberate and accidental killing by people (Woodroffe and Sillero-Zubiri, 2012), recent findings have highlighted demographic impacts of high temperatures, which suggest that climate change might also threaten species persistence (Woodroffe et al., 2017). African wild dog recruitment is lower when air temperatures are higher (Woodroffe et al., 2017) and adult survival has also been shown to fall after spells of hot weather (Chapter 3). When the effects of ambient temperature on vital rates at one site in Laikipia, Kenya, were simulated using an individual based model, profound demographic effects were predicted, with population size expected to fall and extinction risk to rise at high temperatures (Chapter 4). However, assessing the potential impacts of climate change on the entire species requires expanding this modelling effort to account for geographical variation in both demography and climate.

In this chapter, I use the individual based model used in Chapter 4 to project the effects of future climate change on wild dog populations throughout the species' geographic range. I represent varying levels of other human impacts by simulating three different demographic scenarios, and varying levels of global carbon emissions by simulating four Representative Concentration Pathways (RCPs). Finally, I use the findings to predict changes in population size and extinction risk in the species' current range under future climate change, comparing my findings with the IUCN red list criteria.

5.3. Materials and Methods

5.3.1. Model Structure

The model took the form of a single sex, individual based model (IBM) based on the one described in Chapter 4. The model consisted of nine territories, reflecting the median number of wild dog packs found in populations across the species' current range (Woodroffe and Sillero-Zubiri, 2012). Each territory could contain one wild dog pack, consisting of a single dominant female, plus subdominant adult females and juvenile females. Individuals in the model were characterised by their age and dominance status. Juveniles were aged 3 to 12 months and adults were over 12 months of age. Individuals were not included prior to 3 months of age, as measuring litter size at birth is challenging when dens are difficult to access (Woodroffe et al., 2017). Number of pups leaving the den at three months of age was therefore used where most models would use births in the model. Individuals were characterised as either dominant or subdominant, and only a single individual was dominant in each pack at any time step.

Unlike in the model outlined in Chapter 4, the timing between one breeding attempt and the next was fixed at 12 months, and occurred seasonally as, in the majority of the African wild dog's range, breeding occurs seasonally at the coolest time of year (McNutt et al., In Review). Sub models for recruitment and adult survival within the IBM were parameterised based on data from three sites, to represent three demographic scenarios.

5.3.2. Demographic scenarios

The model was modified to give three demographic scenarios, representing different levels of human impact. Each demographic scenario was then evaluated using predicted temperature data across the entire historic range of the species. The demographic parameters for the population models were obtained from datasets covering African wild dog recruitment, mortality and dispersal, and were used to create three demographic scenarios based on three field sites. Recruitment data, *i.e.*, data on litter size and juvenile survival, for sites in Kenya, Botswana and Zimbabwe were obtained from Woodroffe et al (2017). Across all three sites, juvenile survival was higher at higher litter sizes and litter size was higher at higher pack sizes (Woodroffe et al., 2017). Adult mortality and pack size data for the same three sites were obtained from Chapter 3 of this thesis. Data on dispersal were obtained from Woodroffe et al (in Review a), however this data was only available for the Kenya site, meaning that the dispersal dynamics in all three demographic scenarios followed those in Chapter 4, with higher dispersal probabilities at higher pack sizes. All models were run on a monthly time step.

5.3.2.1. Demographic Scenario 1

Demographic Scenario 1 was based on data from the Kenya study site. As outlined in Chapter 4, because temperature over a 30 day period was found to influence adult survival at the Kenya site, temperature was drawn from a normal distribution with a mean of the mean maximum temperature for that month (T_n).

$$T_t \sim N(T_n, \Omega)$$

Unlike in the model outlined in Chapter 4, which was based on an aseasonal site, seasonality was simulated in the model by drawing the mean temperature from a vector which cycled between the hottest and coldest months, determined by the difference between the hottest and coldest moths, referred to in this paper as the seasonality. The mean temperature in each time step (T_n) was therefore determined by the month (n), the mean annual temperature(T_c) (which was centred on the mean, and so always 0 under current climatic conditions) and the seasonality (T_v), which was the temperature difference between the hottest month and the coldest.

$$T_n = \; T_c + \frac{m_n}{6}\, T_v, n = 1, \ldots, 12,$$

$$\text{where } \{m_n\}_{n=1}^{12} = \{0,1,2,6,2,1,0,-1,-2,-6,-2,-1\}$$

Adult survival, as in Chapter 4, was lower when the temperature in that time step was higher, and higher at larger pack sizes. Pups permanently left the den at three months of age, and this occurred in the month following the denning period, and therefore juveniles were defines as individuals between 3 and 12 months of age. Denning season temperature was determined by the mean of the temperature in previous three months, as in Chapter 4. Also in line with the model outlined in Chapter 4, denning season temperature negatively impacted juvenile survival (Table 5.1).

5.3.2.2. Demographic Scenario 2

Demographic Scenario 2 was based on data from the Botswana study site. The structure of the Botswana demographic scenario only differed from scenario 2 in the scale at which temperature impacted adult survival. Temperature in the Botswana scenario was determined in the same way as in the Kenya demographic scenario, however adult survival in the Botswana demographic model was impacted by the mean daily maximum temperature over the current and previous two time steps, the equivalent of temperature over 90 as opposed to 30 days. Adult survival was lower when the mean temperature across the three months was higher, and, as with the Kenya demographic scenario, higher at higher pack sizes (Table 5.1), but constants were changed in line with the datasets from the Botswana site.

5.3.2.2. Demographic Scenario 3

Demographic Scenario 3 was based on data from the Zimbabwe study site. At the Zimbabwe site, adult mortality was not associated with ambient temperature and so, for the Zimbabwe scenario, I modelled adult mortality as a constant probability, and temperature was determined simply by drawing a random number from a normal distribution with a mean of the difference between current and future temperatures in the denning period (T_w) . Large litter size at three months was associated with low ambient temperatures during the denning period in Zimbabwe, and so the litter size sub model included both denning season temperature, defined as the mean temperature of the three months prior to birth, and pack size. Juvenile survival was dependant on litter size only (Table 5.1). Constants were changed in line with the datasets from the Zimbabwe site.

Table 5.1: Population variables and their influence on other population variables in the three scenarios based on data from Kenya, Botswana, and Zimbabwe

	Contributing variables (direction)		
Demographic Scenario:	1: Kenya	2: Botswana	3: Zimbabwe
Temperature	Mean maximum temperature over 1 month	Mean maximum temperature over 3 months	Mean maximum temperature over 3 months
Litter Size	Pack size (+)	Pack size (+)	Pack size (+) Temperature during the first three months of life (-)
Juvenile survival	Litter size (+) Temperature during the first three months of life (-)	Litter size (+) Temperature during the first three months of life (-)	Litter size (+)
Adult survival	Pack size (+) Temperature (-)	Pack size (+) Temperature (-)	-
Inter birth interval	Fixed at 12 months	Fixed at 12 months	Fixed at 12 months
Dispersal	Pack size (+)	Pack size	Pack size (+)

5.3.3. *African wild dog range*

The historic, current, recoverable and possible range of the African wild dog was obtained from the Range Wide Conservation Program for Cheetah and African Wild Dog's (RWCP) estimates, which were determined by the RWCP to assess population declines and persistence in the species range (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016). The historic range is where the species is believed to have lived before wide-spread human caused extirpations and is the area across which the models were ran. The current range is where the species has been verified to still live today, the possible range is where experts have determined that the species may still be living but it has not been verified, and recoverable range is where experts have determined to be suitable for the recovery of the species.

5.3.4. Climate change projections

5.3.4.1. Data on current climate conditions

I evaluated two commonly used global climate datasets, CHELSA (Karger et al., 2017) and WorldClim (Hijmans et al., 2005), against meteorological data from the three sites for which the demographic scenarios were parameterised. The CHELSA dataset was chosen over WorldClim as its estimates of current temperature conditions matched the meteorological data across the three study sites more closely (Fig. 1). The CHELSA dataset includes mean daily maximum temperatures for each month of the year, averaged across the years 1979-2013, and interpolated across the globe at a resolution of 30 arc seconds. Rasters of current mean maximum temperatures for each month of the year were extracted from the CHELSA dataset to cover the historic range for the African wild dog (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016) using the raster package (Hijmans, 2017) in R version 3.3.2 (R Core Team, 2016), which was used for manipulating spatial data and spatial calculations throughout.

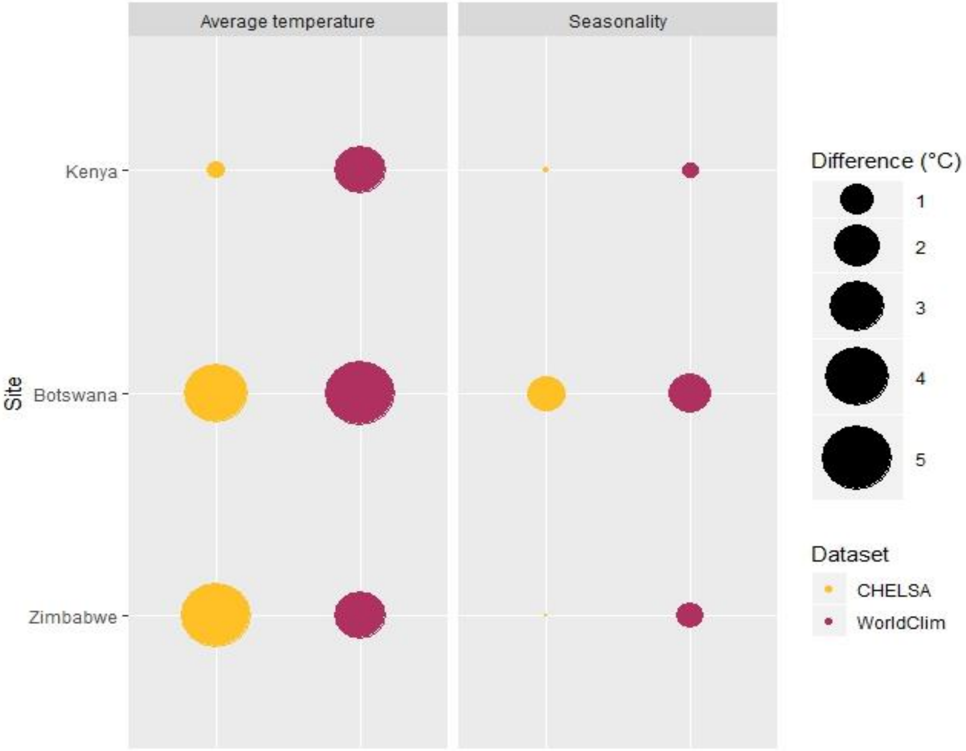


Figure 5.1: The difference in the mean annual daily maximum temperature and the seasonality between data from the weather stations at the study sites and the CHELSA and WorldClim current temperature estimates. Seasonality was defined as the difference between the mean daily maximum temperature in the hottest and coldest month.

5.3.4.2. Projections of future climate

Rasters of projected mean maximum temperatures for 2061-2080 across the historic range of the African wild dog were also extracted from the CHELSA dataset. The layers extracted were predicted future mean daily maximum temperature for each of the 12 months of the year. Predictions from the HADGEM-2-ES climate model were chosen as these predictions are commonly used in mechanistic species distribution models under climate change (McQuillan and Rice, 2015; Gouveia et al., 2016; Courtois et al., 2016; Fourcade, 2016; Gül et al., 2018). All four available representative concentration pathways (RCPs), 2.6, 4.5, 6.0 and 8.5, were used as I wished to obtain results for all potential future policy angles which will impact future global temperatures.

5.3.4.3. Change in temperature

Models were run on the difference between current temperatures and future projections as I assumed adaptation of African wild dogs to local temperature regimes. I created a series of rasters representing the projected temperature change between the present time and 2061-2080, by subtracting, for each raster square across the species' historic range, and each month of the year, the estimated mean daily maximum temperature under current conditions, from the projected mean daily maximum temperature in the same month under future conditions. This process was repeated for each of the RCPs, to give an array of 48 rasters, corresponding to 12 months and four RCP scenarios. I used the 12 temperature change layers representing change for each month of the year to calculate the mean annual temperature variable (T_c) for input to the demographic model, giving four temperature change layers, one for each RCP.

In addition to these monthly rasters, I generated another array of rasters corresponding to projected temperature changes during the denning season. First, a layer was created to represent current denning-season temperatures, by averaging the mean daily maximum temperatures for the three coolest months of the year (June, July and August for the Southern hemisphere, and November, December and January for the Northern hemisphere). This process was then repeated for the predicted temperature datasets for each of the four RCPs. The current denning-period temperature layer was then subtracted from each of the four future denning-period temperature layers, to give four layers of predicted change in denning season temperature (T_w) under the four different RCPs.

Each of the 8 rasters, the four of T_c and the four of T_w, were then resampled to give a pixel size of 9000km^2.

5.3.4.4. Projected annual range in maximum temperature

Projected annual range in maximum temperature (T_v,) was defined as the difference in temperature between the months with the highest and lowest mean daily maximum temperature. I first generated raster layers representing the highest and lowest monthly mean maximum daily temperatures in the year for 2061-2080. The coldest layer was then subtracted from the hottest layer to produce the future T_v raster. This layer was then re-sampled to give a pixel size of 9000km^2. The values in this layer were then rounded to the nearest 0.5°C as the model was relatively insensitive to changes in seasonality lower than this, and to reduce the number of model runs needed for each temperature value (Fig. 5.2).

I used these temperature change layers to calculate T_v for input to the demographic model.

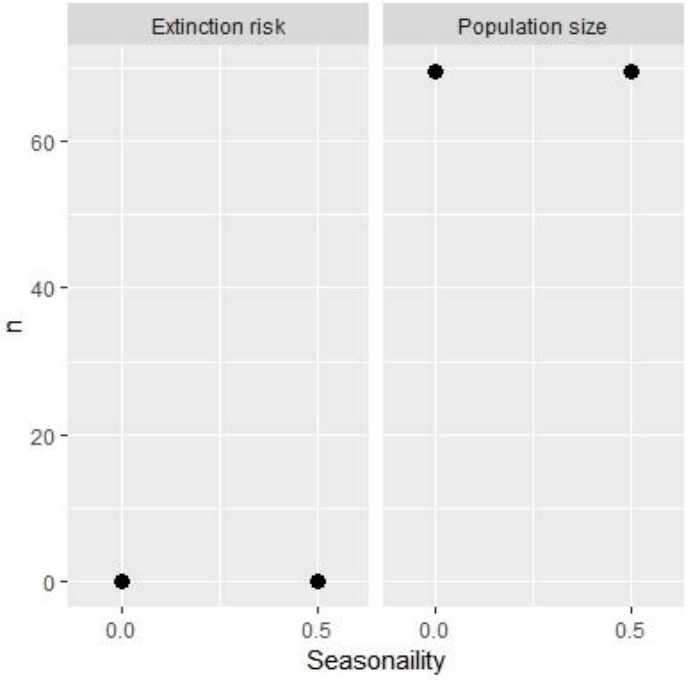


Figure 5.2 Predicted extinction risk and population size values at 0 an 0.5 °C T_v.

5.3.5. Projecting the demographic impacts of climate change

I explored geographical variation in climate change impacts on wild dog populations by running the demographic model for an array of values for T_c and T_v.

This array was chosen to represent the temperature variation projected to occur across the species' historical range. To identify the temperature values to include in the array, the minimum and maximum values of T_c, T_w and T_v, were extracted from all 16 raster layers representing T_c , T_w, and T_v, under four future climate change scenarios. These minimum and maximum values were then used to create a matrix representing combinations of projected changes in T_c and T_v, at 0.1°C and 0.5°C intervals respectively, spanning the range of observed values, and a vector of all possible values of T_w, at 0.1°C intervals.

For each set of relevant temperature values, I ran the model 1000 times, for 600 time steps, equivalent to 10 generations. As in Chapter 4 the model was burnt in for 100 time-steps at an average temperature of 0°C (denoting no change in temperature from present day). The models for Demographic Scenarios 1 and 2 were run for each combination of change in T_c and T_v. As the only environmental variable needed for Demographic Scenario 3 was temperature in the denning period, the model for this scenario was run for each predicted value of T_w. All three demographic scenarios were run for values representing the historic range as the driver of demographic impacts were unknown, and each site not only varied in climate but also in human pressure and lion density, among other variables. By running all three scenarios for temperatures representing the historic range this enabled us to project the full range of future population responses to rising temperature for each location within the historic range, regardless of future changes in human and predation pressure.

Population size was extracted from all models at the start of the model, and after 120, 180, and 600 time steps, equivalent to two, three, and ten generations (Woodroffe and Sillero-Zubiri, 2012). Extinction risk, defined as the proportion of runs in which the population went extinct, was calculated for 180, 300 and 600 time steps, equivalent to three, five and ten generations (Woodroffe and Sillero-Zubiri, 2012). The numbers of generations after which the data were extracted was chosen to be in line with those needed for comparison with the IUCN Red List category criteria (Woodroffe and Sillero-Zubiri, 2012). A generation was considered to be 5 years long in line with the IUCN Red List assessment for the species (Woodroffe and Sillero-Zubiri 2012)

For each set of input variables (T_c and T_v), the mean starting and remaining population sizes across the 1000 runs at those values was taken and converted to percentage remaining population. The proportion of times the simulated populations went extinct was converted to an extinction risk on a scale of 0 to 1.

These model outputs were then used to generate maps of projected population decline and extinction risk, by matching the input variables in the model (T_c and T_v for Demographic Scenarios 1 and 2, T_w for Demographic Scenario 3) with the values of the raster pixels for the layers across the species' historical range. The resulting layers of percentage population remaining at two, three and ten generations and extinction risk at three, five and ten generations were then clipped to the current, possible and recoverable range of the species. Mean values of predicted remaining population were taken across each polygon in the current, recoverable and potential ranges to give predicted population declines in these areas. As in the model in Chapter 4, wild dogs could disperse between territories, however they could not disperse between populations, represented by a single raster square in the generated maps.

5.3.6. Comparison with Red list criteria

The species is currently classified as Endangered, based on the size of the global population and the size of the largest subpopulation (Woodroffe and Sillero-Zubiri, 2012). Based on this information a number of criteria do not apply, and therefore the relevant Red List criteria are: A, which considers declines in population size, Area of Occupancy or Extent of Occurrence, over 3 generations; C, for the Endangered category only, which considers the number of mature individuals combined with population declines over 2 generations; and E, which considers modelled extinction risk over 3 and 5 generations.

The currencies used in IUCN Red List species assessments are global population decline, global extinction risk, area of occupancy and extent of occurrence. I calculated predicted global population decline across the current species range by summing the starting population sizes from all the pixels within the species' resident range, and likewise summing the ending population sizes, then dividing one by the other, for each of four emissions scenarios and all three demographic scenarios. I calculated global extinction risk for the species by taking the lowest extinction risk predicted for any pixel in the species' current range, for each of the four emissions scenarios and each of the three demographic scenarios.

Area of occupancy is the size of the geographic area that the species occupies. To calculate this measure, I used the maps of extinction risk to calculate the total geographic area covered by pixels in which extinction risk (over three and five generations) was estimated to be lower than 0.5. The percentage decline in area of occupancy was calculated by expressing future predicted species range as a percentage of current species range. This calculation was performed for all 12 climate and demographic scenarios.

The extent of occurrence is defined as a standardised measure of the area within which all occurrences of a species exist (IUCN, 2019). To calculate predictions for future extent of occurrence I drew a minimum convex polygon around all pixels where extinction risk was estimated to be below 0.5 and calculated the area of this polygon.

I used these estimates to predict the Red List threat category for the African wild dog for the climatic conditions predicted for the year 2060. My assessment is not, therefore, equivalent to a formal IUCN Red List assessment, which would use population trends over future generations starting in the present day. Moreover, threats other than temperature, such as predicted future land use change and future human population trends, were not taken into account within my informal assessment. Nevertheless, the assessment has heuristic value in quantifying the extinction risk to the species using a widely-recognised set of criteria, and in evaluating how well those criteria perform in evaluating climate change impacts.

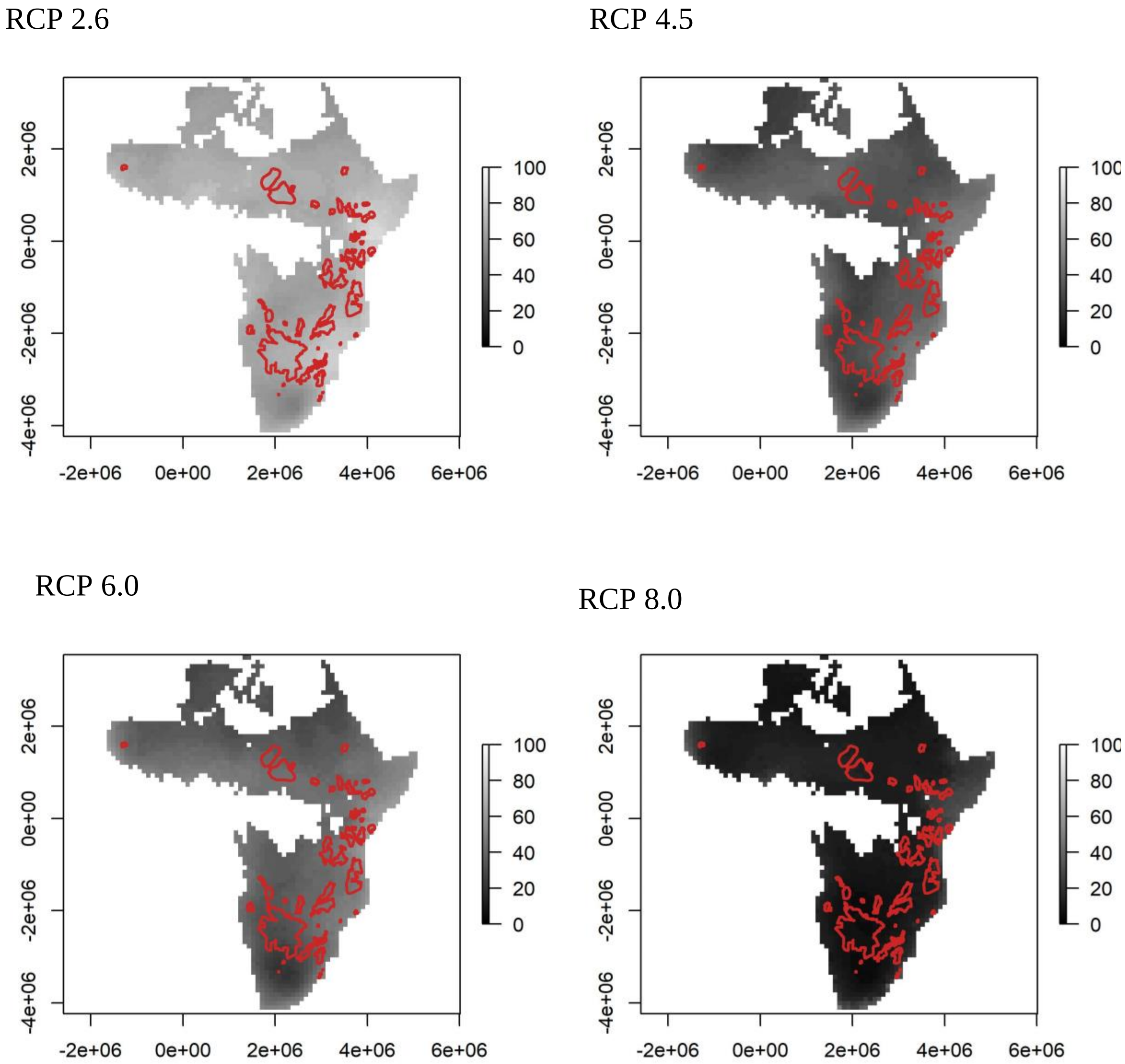
5.4. Results

5.4.1. Population trends and persistence

5.4.1.1. Demographic scenarios and emissions scenarios

Population sizes were predicted to decline across the species range under all four emissions scenarios in all three demographic scenarios (Fig. 5.3 and 5.4, Appendix 2.1). As expected, declines projected under the best case emissions scenario, RCP 2.5, were the smallest, and declines projected under the worst case pathway, RCP 8.5, were the largest, under all four demographic scenarios (Fig 5.3).

In Demographic Scenario 1, which was based on data from the site in Kenya, outside protected areas, all areas of the current range were predicted to have declines of between 10 and 20%, with the majority of pixels projected to have future population declines of around 30% (Fig 5.4, Appendix 2.1). The middle emissions scenarios, RCPs 4.5 and 6.0, had a wide distribution in predicted population declines, with declines of between 45% and 95% under RCP 4.5 and declines of between 30% and 90% under RCP 6.0 (Fig 5.4, Appendix 2.1). Projections of temperature increase by 2060 are greater under RCP 4.5 than 6.0 as emission under RCP 4.5 are above those of RCP 6.0 until the year 2060 (Barros et al., 2014). The projections under the worst case scenario in Demographic Scenario 1 showed extensive declines of up to 100%, with most areas of the historic and current ranges showing declines of 90% or more (Fig 5.4, Appendix 2.1).


RCP 2.6

RCP 4.5

RCP 6.0

RCP 8.0

Figure 5.3: mean predicted percentage remaining population across the historic range of the African wild dog after 10 generations under the climatic conditions predicted for RCP 2.6, 4.5, 6.0 and 8.5 across all three demographic scenarios. Current confirmed range is marked in red.

In Demographic Scenario 2, which was based on data from the site with the lowest human impact (in Botswana), population declines were projected to be lower than those in Demographic Scenarios 1 and 3. In Demographic Scenario 2 under the RCP 2.5 emissions scenario population declines of between 10 and 40% were projected across the range, with median population decline of 24% (Fig 5.4). The middle emissions scenarios, RCP 4.5 and 6.0, gave similar projections, with declines of between 55 and 75%, however the median percentage declines were around 5% higher under RCP 4.5 (Fig 5.4). In Demographic Scenario 2.under the worst case emissions scenario, RCP 8.5, population declines of between 45 and 85% were projected, but all populations were predicted to persist even under RCP 8.5, with as population declines of under 100% were predicted across the historic range (Fig 5.3, Fig 5.4).

Declines projected under Demographic Scenario 3 were similar in magnitude to projections under Demographic Scenario 1. Larger declines across the current range of between 10 and 55% were projected under the best case emissions scenario, however, with most areas in the species current range projected to experience declines of around 45% (Fig 5.4, Appendix 2.1). Under the middle emissions scenarios declines of between 40 and 95% were predicted. The distribution of the declines under RCP 4.5 showed projected declines around 63% and 80% were most common within the current range, and declines of around 60% were most common under RCP 6.0. Under the worst case emissions scenario, RCP 8.5, most declines in the current range were around 95%.

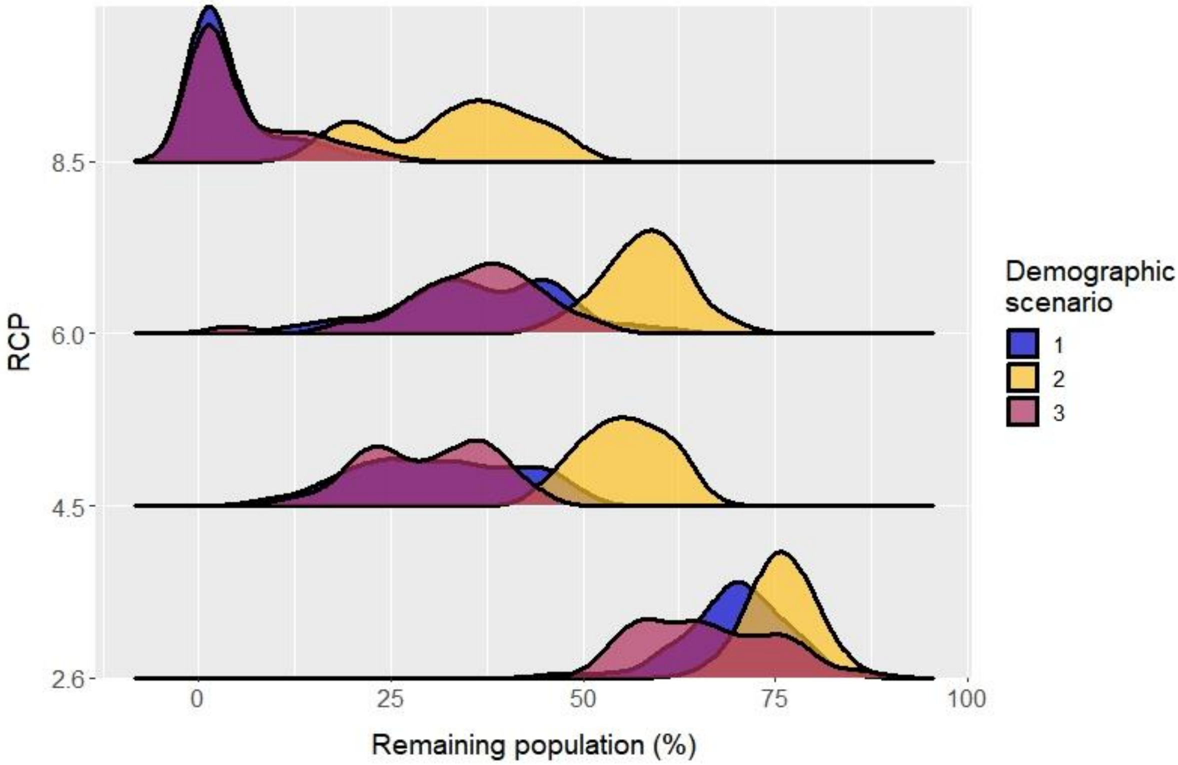


Figure 5.4: Predicted percentage remaining population across the current of the African wild dog after 10

Although marked population declines were predicted throughout the species range under most scenarios, predicted extinction risks were low other than in the worst case emissions scenario (Fig. 5.5, Appendix 2.2). Demographic Scenario 1 predicted an extinction risk of 100% across large areas in the North and South of the historic range, including across multiple sites in the current species range (Fig. 5.5). Under RCP 8.5 44% of the current range was predicted to have an extinction risk of over 50%. In Demographic Scenario 2, extinction risk remained relatively low with the highest extinction risk of a single pixel predicted to be 15% even under the worst case emissions scenario. In Demographic Scenario 3, extinction risks of up to 95% were predicted within the historic range and extinction risks of between 10 and 75% were predicted across the current range. 20% of the current range was predicted to have an extinction risk of over 50% (Figure 5.5, Appendix 2.2).

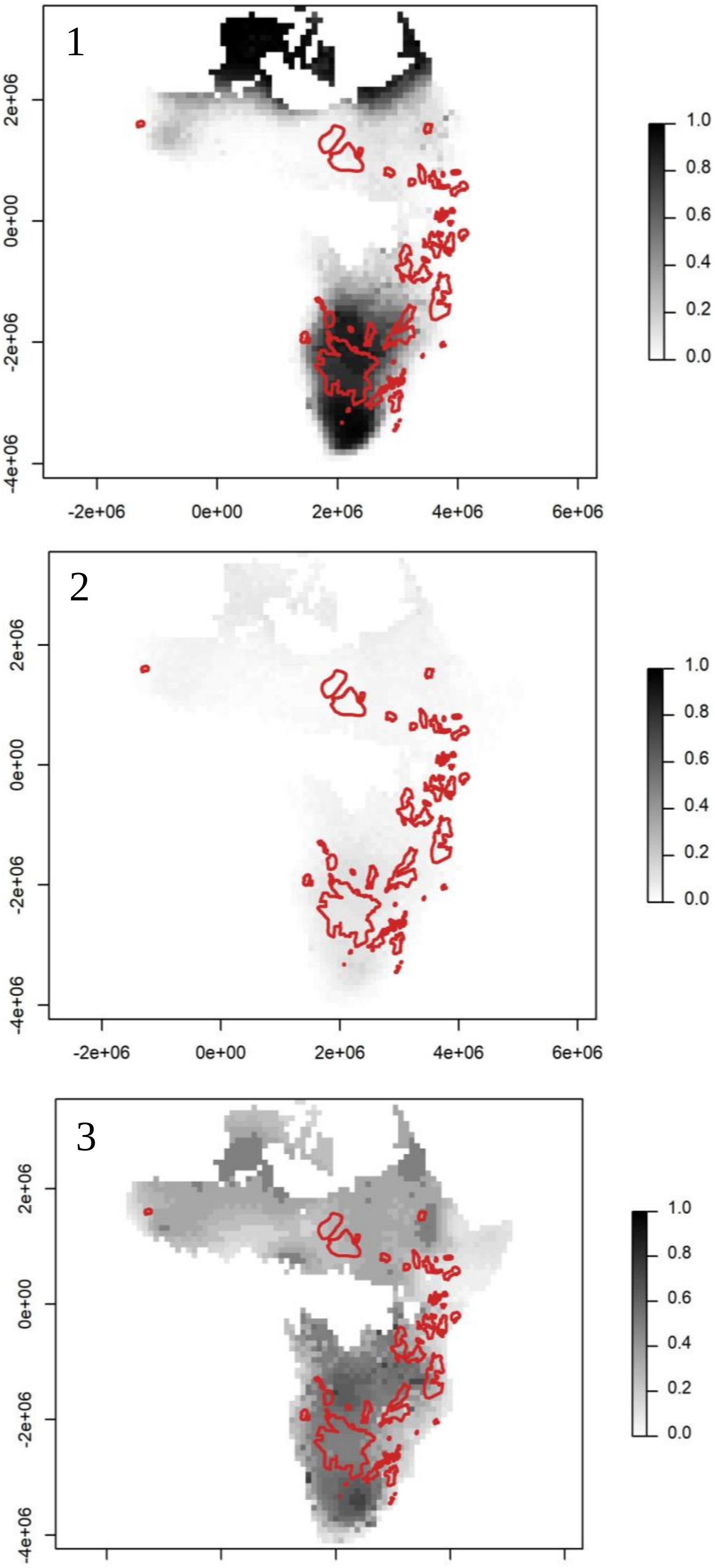


Figure 5.5: Predicted local extinction risks within the historic range of the African wild dog after 10 generations under the climatic conditions predicted for RCP 8.5 in Demographic Scenarios 1, 2 and 3. Current confirmed range is marked in red

5.4.2. 5.4.2. Projected population declines in the current, possible and recoverable range

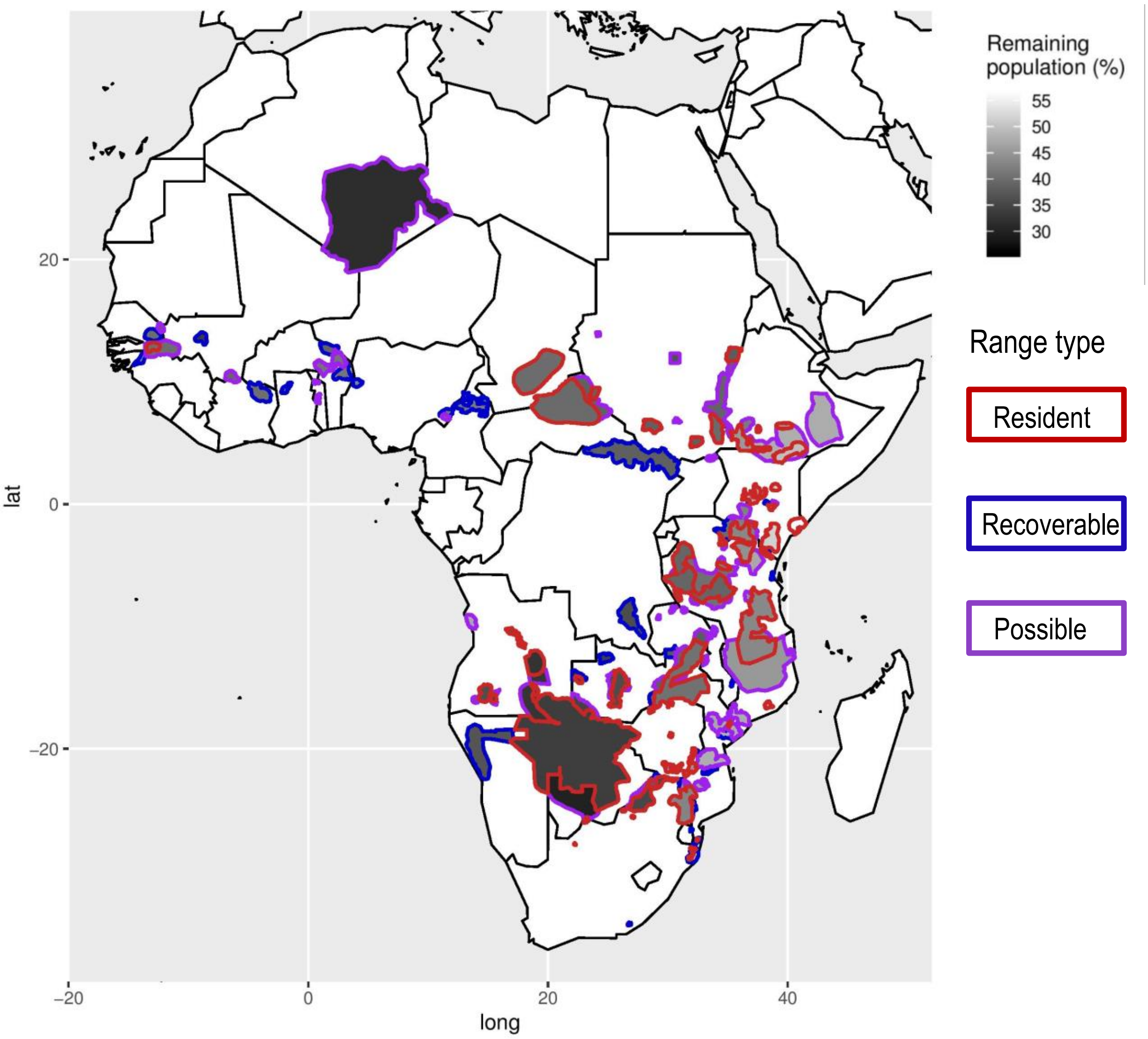


Figure 5.6: Map of population declines in the resident, recoverable and possible ranges of the African wild dog. Shading indicates mean predicted remaining population across all demographic scenarios and emissions scenarios. Outline colour indicates range type.

5.4.2.1. Projected population declines with the species' current range

There are currently 54 wild dog populations within the species current range (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016). Of these, 48 (89%) were predicted to undergo mean declines of over 50% across all representative concentration pathways and demographic scenarios, with 52 (96%) predicted to undergo declines of this magnitude in Demographic Scenario 1, 11 (20%) in Demographic Scenario 2 and 52 (96%) in Demographic Scenario 3 when a mean was taken across all emissions scenarios. The populations predicted to have the largest declines are all located in Southern Africa, with all eight of the populations with predicted declines of over 65% located in the Southern part of the continent, specifically in Botswana, Zambia, Namibia, Angola and Botswana (Fig 5.6). The largest remaining population of African wild dogs, that is, the resident population in the Grater KAZA landscape at the nexus of northern Botswana, Western Zimbabwe, NE Namibia, SW Zambia and SE Angola, was predicted to experience a decline of 67% and the second biggest population, found in the Selous-Niassa area of southern Tanzania and northern Mozambique, was predicted to experience a decline of 57% (Fig 5.7). The combined wild dog population inhabiting the eight populations predicted to experience the greatest declines at the time of the IUCN Red lists previous assessment in 2012 was 1832, comprising 24% of the global total at that time.

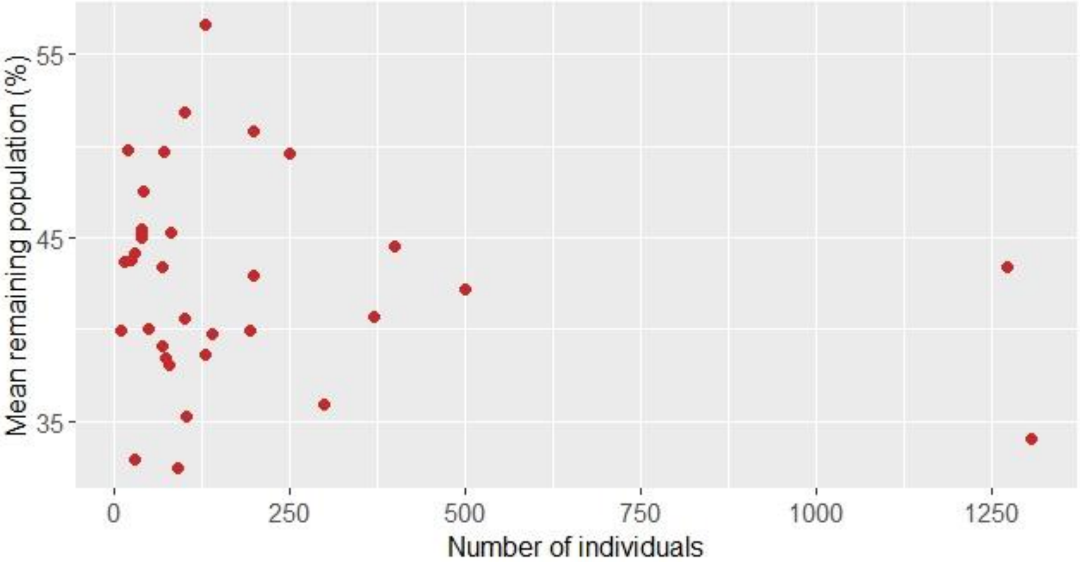


Figure 5.7: Scatter plot of the estimated size of each extant wild dog population according to the 2012 IUCN Red List assessment *vs* the predicted mean future population declines across demographic scenarios and climate change pathways.

The populations in the confirmed current range predicted to experience the smallest declines were mostly in East Africa, particularly Kenya, with some towards the East coast of Africa as far south as KwaZulu-Natal in South Africa (Fig. 5.6). Of the eight populations predicted to have mean population declines of 50% or less, six were in Kenya, The number of individuals in these populations at the time of the IUCN Red lists previous assessment in 2012 was 640, representing 8% of the estimated global population. However, the impact of temperature on the inter-birth interval was not included in the models, and would lead to larger predicted declines at sites with aseasonal breeding. These populations include Tsavo, Samburu-Laikipia, the Serengeti-Mara and potentially populations in the south of Ethiopia and South Sudan. When the model for Demographic Scenario 1 was run for the average temperature change across these sites with IBI included, greater population declines were predicted under all four emissions scenarios, particularly in the worst case scenario where predicted population declines were 20% higher than in the model when this variable wasn’t included (Table 5.2). There was also a large difference in predicted extinction risk in the worst case emissions scenario (Table 5.2).

Table 5.2 Mean percentage population declines predicted by the model with and without the inclusion of temperature effects on IBI.

	Without IBI		With IBI	
Emissions scenario	Extinction risk	Projected population decline	Extinction risk	Projected population decline
2.6	0	2%	0	3%
4.5	0.002	8%	0.005	13%
6.0	0	6%	0.001	10%
8.5	0.29	63%	0.76	83%

5.4.2.1. Potential for wild dog persistence within possible range

The patterns of projected declines among populations which might remain, currently undetected, in the possible range (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016) followed those predicted in the current range, with greater declines in Southern Africa and lesser declines in Eastern Africa and along the coasts. Six of 58 (10%) possible remaining populations of wild dogs were predicted to experience declines of over 65%, if indeed these populations are still extant (Fig 5.6). Of these six, the majority were in Southern Africa, with three in Angola, one in Botswana, and one in Zambia, as well as a large area of potential range in Algeria (Fig. 5.6). If populations were assumed to be persisting, undetected, in all of the areas currently designated as "possible range", only two populations were predicted to undergo declines of less than 50% in the future, namely Rahole in Kenya and Morene-Borana in Ethiopia (Fig 5.6).

5.4.2.1. Potential for wild dog restoration within the Recoverable range

Of 36 areas designated as recoverable range (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016), the areas predicted to be the least suitable for African wild dogs under future climatic conditions were located in Southern and West Africa. Three sites currently considered potentially suitable for wild dog recovery are predicted to undergo declines of 65% of greater, should wild dogs become re-established in those areas; of these, two were located in Zambia and one in Mali (Fig 5.6). The Serengeti-Mara ecosystem and the Bili-Garambara range which spans the northern region of the Democratic Republic of the Congo were also predicted to undergo declines of 65% or more if wild dogs still persist there (Fig. 5.6). The areas predicted to undergo the smallest declines should wild dogs become re-established there were along the East coast of the continent, with two of the four recoverable ranges predicted have mean declines of 50% or less on the coast of South Africa – namely a small population in Zululand and the Greater Fish River, and in East African, namely The Kenyan border near Mkomazi in Kenya and Saadani in Tanzania (Fig 5.6).

5.4.3. Assessment using Red List criteria

The two currencies used to assess Criterion A of the IUCN Red list were population declines and area of occupancy declines over 3 generations. Only Demographic Scenario 1 under predicted future climatic conditions in the RCP 8.5 pathway reached the threshold for vulnerable when using the decline in area of occupancy as the criterion for assessment. All other declines in area of occupancy were too small to qualify under any of the three categories.

When decline in population numbers was used as the measure of likely extinction risk, however, 11 out of the 12 scenarios showed population declines in line with an IUCN Red List category of Vulnerable or higher, with the exception being Demographic Scenario 2 under the best case emissions scenario, RCP 2.5 (Table 5.2). Under RCP 4.5 and 6.0 the population declines predicted for Demographic Scenario 2 met the criteria for classification as Vulnerable under criterion A, and under Demographic Scenarios 1 and 3 they met the criteria for classification as Endangered. Under the climatic conditions predicted under RCP 8.5, the model predicted population declines sufficient to meet the criteria for classification as Endangered under Demographic Scenario 2, and sufficient to meet the criteria for classification as Critically Endangered in Demographic Scenarios 1 and 3 (Table 5.2).

Table 5.3: Assessment against red list criterion A2, if applied to the current global population in the year 2060 – projected population decline across the current range in three generations

Demographic Scenario	Emissions scenario	Projected population decline (%)	Red List Status
1 (Kenya)	2.6	30.23	V
	4.5	63.93	EN
	6.0	59.63	EN
	8.5	94.53	CR
2 (Botswana)	2.6	21.85	-
	4.5	40.40	V
	6.0	38.15	V
	8.5	59.01	EN
3 (Zimbabwe)	2.6	32.30	V
	4.5	64.79	EN
	6.0	59.45	EN
	8.5	90.49	CR

Only the criteria for Endangered status could be assessed for Criterion C as there are more than 250 individuals of the African wild dog remaining in the wild, meaning that the species was not suitable for assessment as critically endangered. The models of Demographic Scenarios 1 and 3 predicted population declines meeting the criteria for a species to be categorised as Endangered under RCPs 4.5, 6.0 and 8.5, with Demographic Scenario 1 also predicting declines in line with classification as Endangered under RCP 2.6. Demographic Scenario 2 did not predict declines in line with the endangered category under any emissions scenario, however (Table 5.3).

Table 5.4: Assessment against red list criterion C2, if applied to the current global in the year 2060 – percentage population decline across the current range in two generations.

Demographic Scenario	Emissions scenario	Projected population decline (%)	Endangered
1 (Kenya)	2.6	24.77	Yes
	4.5	52.28	Yes
	6.0	49.09	Yes
	8.5	78.08	Yes
2 (Botswana)	2.6	0.00	No
	4.5	1.00	No
	6.0	2.00	No
	8.5	5.10	No
3 (Zimbabwe)	2.6	19.26	No
	4.5	42.68	Yes
	6.0	39.66	Yes
	8.5	57.57	Yes

As the model under all demographic scenarios predicted an extinction risk above 0.5 for at least one subpopulation of the current range under all RCPs none of the predictions met the required standard for classification under Criterion E.

5.5. Discussion

My model predicted global population decline of the African wild dog under all four emissions scenarios, in all three demographic scenarios. The regions expected to experience the greatest population declines include Southern Africa, particularly around the Kalahari Desert. The emissions scenario had a strong impact on the magnitude of the projected declines, determining both population persistence and extinction risk across much of the current range. Unlike previous studies, which found little impact of emissions scenario on threat status (Keith et al., 2014; Stanton et al., 2015), the emissions scenario determined the predicted future IUCN Red List category. For example, when assessed in 2060 under Red List criterion A under Demographic Scenarios 1 and 3, the global population would be classified as Vulnerable under the best case emissions scenario but Critically Endangered under the worst case emissions scenario. This finding indicates that the future global policy on climate change is likely to have a significant impact on the likelihood of species persistence in the African wild dog.

The level of predicted population declines across all three demographic scenarios was dependant on representative concentration pathway, with greater declines predicted for emissions scenarios representing higher emissions scenarios. The mean population declines across both the current and historic ranges of the African wild dog was over 20% lower in the best case emissions scenario compared to the middle emissions scenarios. The worst case emissions scenario resulted in catastrophic declines across all demographic scenarios, with declines of up to 100% in Demographic Scenarios 1 and over 90% in Demographic Scenario 3, resulting in high extinction predicted extinction risk across much of the current and historic range

Projected declines varied between the three demographic scenarios. Demographic Scenario 2, based on data from the Botswana study population, which had the lowest human impact, was associated with smaller predicted declines in population size than were Demographic Scenarios 1 and 3, based on data from Kenya and Zimbabwe, which are sites experiencing higher human impact. Under RCP 8.5 in

Demographic Scenarios 1 and 3, population extinctions were predicted across large parts of the species range. Extinction risk under Demographic Scenario 1 remained low, however, with a maximum extinction risk of 15% in any 9,000km^2 grid cell. It is conceivable that the lesser population declines and lower extinction risks predicted under Demographic Scenario 2 might reflect local adaptation to high temperatures at the Botswana study site from which the demographic parameters were estimated. In contrast the Kenya study site (on which Demographic Scenario 1 was based), is an aseasonal site where the temperature is more consistent and local adaptation to high temperature might be less likely. The Zimbabwe site that informed the Demographic Scenario 3 is also seasonal, however, and experiences peak temperatures even higher than those at the Botswana site (Woodroffe et al., 2017), which would suggest that the lower human impacts or higher connectivity at the site are what reduces the impact of temperature on populations.

The Zimbabwe population is smaller, has greater human pressure and higher lion density than the Botswana site (Woodroffe et al., 2017). The fact that high temperatures impact the number of pups living to 3 months, unlike the other two sites where it impacts pup survival from 3-12 months, may be due to a separate mechanism by which recruitment is impacted by high temperatures, or the fact that this site has the highest denning season temperatures (Woodroffe et al., 2017). The site characteristic which drives the early loss of pups, combined with higher baseline adult mortality than the other two sites, is likely to be what is driving higher predicted declines in Demographic Scenario 3 when compared to Demographic Scenario 2.

The finding that the demographic scenario based on parameters from the site with the highest connectivity and lowest human impacts is associated with smaller impacts of rising temperatures suggests that lower human pressures may be beneficial to African wild dog resilience in the face of climate change. Where other studies have found that protected areas may not prevent population declines in mammals resulting from climate change (Geldmann et al., 2013; Spooner et al., 2018), these findings suggest that areas with lower human impact may play a role in protecting the African wild dog from climate change-induced population declines. The Botswana population on which from which the Demographic Scenario 2 parameters were estimated is also large with high connectivity, containing around 24% of the worlds remaining African wild dogs (KAZA TFCA, 2019). As human population increases across Africa and habitat fragmentation may reduce the ability of wild dog populations to cope with rising temperatures. These findings provide further evidence (O'Neill et al, In Review) that improving connectivity between remaining populations of African wild dogs is an important conservation intervention, which is likely to increase the species resilience. The scenario was parameterised on data from individuals inhabiting the centre of the greater KAZA landscape, however, where there is particularly low human impact and little interaction with humans or livestock. This demographic scenario may be optimistic for other parts of the population even within the Greater KAZA landscape, and areas with this low level of human impact which are suitable habitat for the African wild dog exist in very few parts of Africa (Woodroffe and Sillero-Zubiri, 2012).

The areas of the current range predicted to face the greatest population declines were in Southern African, in particular Angola, Botswana, Namibia and South Africa. This finding has important implications for the persistence of the species, as Botswana currently supports almost a quarter of the remaining wild dog population (KAZA TFCA, 2019). KAZA is home to the largest remaining population of African wild dogs but is predicted to one of the areas hardest hit, with declines predicted for that subpopulation of between 30% (Demographic Scenario 2, RCP 2.5) and 100% (Demographic Scenario 1, RCP 8.5), with average declines of over 65% across all demographic and climatic scenarios. 90% of current wild dog populations reside in areas predicted to experience mean population declines of over 65% in the future, and 28% of the remaining wild dog population lives in areas predicted to have mean population declines of over 90% in the future. My findings in Chapter 3 indicated, however, that large populations may have a small amount of buffering from climate induced population declines, so the connectivity in the Greater KAZA region (Marsden et al., 2012) may somewhat dampen the predicted impacts.

Areas predicted to experience the smallest declines were mostly located in East Africa, in particular Kenya, Ethiopia and Tanzania. Demographic Scenario 1, which showed the greatest magnitude of declines, was parameterised on a study site in this region, however, and therefore may be the most appropriate scenario for the region. Most of the sites in the region, unlike the Kenya site the model was parameterised on, are protected areas, however, so human threats are likely to be lower, which would mean temperature impacts are likely to be lower. This model is likely to be somewhat conservative in some areas of East Africa, specifically those between around 7°N and 7°S where populations breed aseasonally. When impacts of temperature on inter-birth interval were included predictions of population declines in the region the predicted population declines were closer to those predicted for Southern Africa, meaning that those populations in East Africa that have aseasonal breeding may be hit harder despite lower levels of projected climate change. This highlights the importance of taking into account localised adaptation when predicting climatic impacts on species.

If wild dogs continue to inhabit the areas designated as possible range (IUCN/SSC, 2008; IUCN/SSC, 2012; IUCN/SSC, 2016), the potential populations in Kenya and Ethiopia were predicted to undergo the smallest declines. This finding suggests that the species may have a greater chance of persisting in these areas under future climatic conditions, especially populations in Ethiopia with seasonal breeding. These regions should be prioritised for surveys aimed at identifying potentially important wild dog populations which are not currently being conserved or monitored. On the other hand, South Africa, Zambia, Angola and Algeria appear to present lower priorities for identifying remaining populations, based on climate change risk.

If wild dogs were assumed to have been re-introduced to the sites identified by experts as potentially recoverable range, the populations in East Africa and coastal areas were predicted to be impacted by climate change to a much lesser extent than those elsewhere, suggesting that recovery opportunities may exist in this region. The majority of the recoverable range of the species that was predicted to have the smallest population declines as a result of climate change, should populations be assumed to have been reintroduced to these areas, were in East Africa and along the Eastern coast of the continent, so these areas should be considered a potential priority for future reintroductions, however there are not large areas of recoverable range in these regions.

The emissions scenario determined which IUCN Red List category the species was predicted to be placed in under future climatic conditions. Population reductions predicted under the best case emissions scenario (RCP 2.6) met the criteria for Endangered status under assessment for criteria A2 and C2 only for Demographic Scenario 1. Under the middle emissions scenarios, however, the predicted future IUCN Red List threat status was as Endangered under criteria A2 and C2 in Demographic Scenarios 1 and 2. Under the worst case emissions scenario (RCP 8.5), the predicted IUCN Red list category was Critically Endangered for the Demographic Scenarios 1 and 3 under Criterion A2. Whereas other studies have found that RCP has little influence on the likelihood of population persistence and threat status of species

(Raxworthy et al., 2008), the level of carbon emission is predicted to play a key role in determining the threat status in the African wild dog.

My model predicted that RCP 8.5 would be expected to lead to extreme population declines under all three demographic scenarios, and multiple population extinctions in the species under two out of three demographic scenarios. It is clear that temperature increases at this level would have very significant impacts on the suitable range remaining for the species. Even under the middle two RCP scenarios, population declines of 40% or higher are predicted across most of the species range within three generations.

The predictions made by these models are conservative, for three reasons. First, they assume a stable temperature from now until 2060 before a change in temperature in line with future predictions. In reality, the temperatures will rise slowly, and whilst declines will happen earlier, they will also happen more gradually, which means the declines related to climate change may not meet the IUCN Red List criteria, which are assessed over just three generations. This further highlights challenges in using the IUCN Red List criteria for assessing climate change threat, and means that threat level is unlikely to change early enough to allow time for successful conservation actions to be carried out. Second, the predictions of extinction risk and population declines do not take into account changes in weather variables other than temperature. Specifically, they assume that rainfall patterns will remain unchanged, when in fact many of these areas are expected to experience changes in rainfall patterns under future climate change predictions. Southern Africa, where I predict the greatest temperature impacts, is also predicted to experience lower rainfall (Niang et al., 2014), potentially exacerbating the impacts I predict. Third, my model ignores future land use change and increases in human population density. Currently, the biggest threat to African wild dogs is habitat loss, and therefore for lands outside very large protected areas it is likely that human activity, and not climate change will be the primary threat to those populations. These three factors mean that my estimates of threat level and extinction risk are likely to be conservative. Combining these models with future predictions of land use change would help shed further light on the likely future extinction risk of remaining populations, and would likely show greater population declines.

The model implicitly assumes localised adaptation to temperature conditions, by using current temperatures as the base temperature and only taking into account future increases. Whilst localised adaptation has been widely studied in pathogens (Laine, 2008; Sternberg and Thomas, 2014; Mariette et al., 2016), and considered several species of invertebrates (Declerck et al., 2001; Valladares et al., 2014; Roy et al., 2015) and plants (Souther and Mcgraw, 2011; Bocedi et al., 2013), little work has been done on this phenomenon in mammals (Bocedi et al., 2013). Whilst adaptation of African wild dogs to local climate conditions would be expected, particularly as temperature variability at seasonal sites is far greater than that in aseasonal sites, levels of adaptation may be lower than assumed by the model. Localised adaptation should be investigated further as it has implications for species re-introductions – wild dogs taken from East Africa might be unlikely to survive if translocated to Southern Africa, for example. Likewise, wild dogs reintroduced to the East African recoverable areas might be less well adapted to East African temperature regimes if transplanted from Southern Africa.

The threat from climate change differs from many other threats in that climate change affects species across their range, regardless of the level of other, more localised, human impacts. A wild dog pack living deep inside a larger, well-maintained protected area might be unaffected by anthropogenic killing, domestic dog disease, or habitat degradation. But it would nevertheless suffer the human impacts caused by climate change. This paper presents predictions of the impacts of climate change in isolation from other threats such as habitat destruction, and therefore the results presented provide a conservative estimate of future population declines, based on the current occupied range remaining stable. For species that have undergone extensive range contraction, such as the African wild dog, models of demographic effects in their current range are likely to be crucial for establishing where the species is most likely to persist in the future, and to establish where conservation efforts should be focused to ensure species survival.

Plate 6: Uncollared adult African wild dog, Laikipia, Kenya

Chapter 6 Discussion

6.1. General discussion

In this thesis, I explored how rising temperatures under future climate change are likely to impact African wild dog populations and examined the species' potential for behavioural adaptation to high temperatures through shifting their timing of activity. In this final chapter I will summarise my findings and discuss their wider relevance to the fields of global change ecology and conservation science.

In Chapter 2, I demonstrated that African wild dogs are unlikely to be able to compensate fully for high temperatures by shifting their timing of hunting and becoming more active at night. Nocturnal hunting was constrained by moonlight, which will not become more available as the climate changes. Failure to compensate for high daytime temperatures by hunting at night was particularly marked during the denning period, when the adults have pups to guard and feed. The inability of African wild dogs to compensate for high temperatures during the denning period likely explains the observed fall in recruitment following hotter denning periods.

In Chapter 3, I demonstrated that African wild dogs have lower adult survival at high temperatures across 3 sites. The impact of high temperatures varied between sites and was related to the level of human pressure and seasonality. The principal cause of death in Zimbabwe was snaring, and mortality due to this cause was not associated with ambient temperature. Mortality from non-human causes was higher when ambient temperatures were high at the sites in Botswana and Zimbabwe. In contrast, in Kenya the principal causes of death were infectious disease and direct human killings, and mortality due to these causes was higher at high ambient temperatures.

In Chapter 4, I used an Individual-Based Model to examine the effects of high temperatures on African wild dog population dynamics in Laikipia, Kenya, and to predict the effects of future climate change. The model predicted that pack sizes, number of packs in the population and litter sizes would all fall at high ambient temperatures. This fall in population size was associated with a large increase in extinction risk once temperature increases were above a certain threshold. The worst case emissions scenario had very high rates of extinction for population sizes comprised of both 9 and 30 territories, however extinction risks were lower with 30 territories in the model, particularly over 10 generations, and the larger populations went extinct at temperatures half a degree higher than populations made up of 9 territories (the median population size for the species (Woodroffe and Sillero-Zubiri, 2012)). The emissions scenario impacted the extinction risk in both population sizes, with worse emissions scenarios resulting in larger predicted population declines and shorter times to extinction.

In Chapter 5, I identified the geographic areas most likely to remain suitable for African wild dogs under future climate change scenarios. Three population models, representing different patterns of seasonality and human pressures, were run under four different future emissions scenarios. I found that individual based models can be used to identify where populations of a species are most and least likely to persist under predicted future climatic conditions. These models highlighted that remaining populations in Southern Africa are likely to experience the greatest population declines, however the demographic model parameterised on the largest population of wild dogs in this region showed the smallest declines. Emissions scenario determines predicted future IUCN Red List status in the species.

These results have specific implications for the conservation of the African wild dogs under future climate regimes, as well as more general implications for the assessment of climate change threat and the identification of conservation measures most likely to mitigate climate change impacts.

6.2. Implications for methods used to assess climate change threats to species

Models predicting the impact of climate change on species have predominantly taken two approaches. Firstly, characterising the species' climatic niche, and using it to predict which areas will be suitable for that species in the future, and secondly using a broad-brush, often trait-based, multi-species approach, where the characteristics of that species are used to estimate its level of climate change risk. Models which build in the mechanism by which high temperatures impact species inevitably perform better (Kearney and Porter, 2009), and can shed new light on species threats from climate change that would not be highlighted by trait-based or correlative models (Urban et al., 2016). There is a trade-off, however, between how much a model is tailored to an individual population or species, and the applicability of the results.

The challenge when building data-driven, mechanistic models of species under climate change is that they require large amounts of data (Kearney and Porter, 2009). In order to disentangle how climatic variation impacts species the dataset needs to either be sufficiently long-term or to cover an area with sufficient climatic variation. Similarly, it is important the entire life-cycle of the species is understood, including social structure, survival and reproduction rates, and dispersal (Adahl et al., 2006; Pagel and Schurr, 2012; Tye et al., 2018). Long term data-sets are of particular importance in obtaining these data, as variation of habitat in time is often less than that in space. This means that there are often other environmental conditions that can obscure climatic effects in cases where climatic variation in space is used to predict changes over time. Long term field data will play a key role in building more mechanistic climate models, and it is therefore important that existing long term projects continue to be funded (Hughes et al., 2017).

For many species, much data on their life-cycle, dispersal and even distribution is not available as collecting datasets of enough detail require large amounts of both time and money. However extensive datasets already exist for many species of economic importance, such as species targeted for harvest, as well as of cultural importance for ecologists historically, such as large mammals and European birds and insects. It is important that both conservation organisations and those involved with the economic utilisation of species assess which species have datasets available, and identify priority species for which data driven mechanistic models should be built. This will help identify gaps in the data, both in existing datasets, and for species identified as being of particular economic, cultural or ecological importance – such as keystone species or fish stocks. Focus should be on both filling these gaps and identifying existing underutilised datasets which can be used to inform mechanistic models under climate change.

This work also highlights challenges in assessing species threat from climate change. Where population models often assess trends on a scale of 10 generations or more the method by which species threat status is assigned utilises a timescale of two or three generations. With climate change this presents a unique challenge, as the impacts are ubiquitous and non-reversible, so when future impacts are predicted it is more difficult to implement actions to prevent them. For species that can’t be bred in captivity and then re-released this can present a particular challenge, as conservation measures for these species are often more costly and take longer to implement, and they cannot be removed from unfavourable habitats in the wild. On top of this, declines factored into the IUCN Red List must be predicted to happen over the next 2-5 generations. While climate changes more slowly than this for most species, the slow pace of climate change relative to species generation times does not make climate change any more avoidable or easier to reverse. Unlike other threats, climate can be represented in global circulation models and used to predict local changes in weather patterns within species ranges decades into the future. That other threats are less predictable should not mean that climate change threats are side-lined in the process of red listing. Whilst it is possible to interpolate climatic changes between now and 2060, it adds another layer of uncertainty, and will likely under-represent the threat posed to the species. The ability to factor in expected declines would assist in assigning to species to a more practical threat status, whereby money and resources can be allocated accordingly.

Evolution is likely to be an important way in which many species adapt to changing climatic conditions. While large mammals are unlikely to evolve at a pace fast enough to keep track with climate change, the same is not true for other species, and evolution is likely to be in important factor in how many species adapt. Shifts in species traits, whether through plasticity or evolution, are an important way in which species may persist despite changes in their environment. The ability of species to adapt to climatic conditions through both plasticity and evolution should be investigated and incorporated into models of species responses to climate change where possible.

Similarly, where known, species physiology can play an important role in thermoregulation, and subsequently fitness at different temperatures. Getting a detailed understanding of the physiology of species under high temperatures is very challenging however, as it often requires relatively intrusive work, particularly when compared to demographic modelling. The use of captive animals in this work will be key for many species. Linking behavioural changes to energetic outputs and species physiology would provide a more detailed picture of the true mechanism behind species responses to climatic conditions. Coupling species physiology to models of demographic impacts in mechanistic models under climate change is important if we are to build truly mechanistic models and obtain a complete picture of how and why species respond to rising temperatures. Models of this kind can also help pinpoint conservation measures that may relieve physiological stress on species at high temperatures, such as increasing microclimate availability.

This thesis focuses solely on direct impacts of climate on a single species, however many impacts of climate will be indirect, through changes to vegetation structure, or changes in species interactions resulting from demographic or behavioural impacts on predators or prey. Many of the large scale multi-species models make assumptions about species interactions based around a single system – for example the Madingley model assumes predation rate increases as temperatures increase as this is what happens in insect systems (Newbold, 2018). This is the opposite of what is suggested by this work, however, where energy expenditure and time spent hunting fell at higher temperatures.

Species interactions have been previously found to drive climate change responses in some species, and the majority of extinctions where climate was implicated as a factor have involved species interactions. Whilst obtaining data on many species can prove challenging, it is important that these kinds of interactions are investigated, as incorporating them into climate change impact models is likely to improve their accuracy. There are a number of research stations globally where work is done on numerous species, and even ecosystems, and in these cases the data can be used to produce multi-species, or potentially even ecosystem scale models, which include species interactions.

6.3. Implications for conservation and future conservation research

Climate change, unlike many other threats to species, is ubiquitous, affecting species regardless of their location inside or outside a protected area. Whilst habitat loss is undoubtedly the greatest threat faced by species globally, species which have already lost much of their habitat, leaving them confined mostly to protected areas, climate change prevents a unique conservation challenge. This is because these species cannot move to areas that are more suitable climatically, and, unlike many other threats, climate change will still impact species inside protected areas. Even for species with currently stable populations, in pristine habitat, with few human threats, climate change may make that habitat increasingly less suitable in the years to come. For species which require large areas in which to survive, and are difficult to both breed in captivity and translocate, climate change poses a particularly acute problem. Many such species are large mammals, which, due to their comparatively long generation times, are unlikely to be capable of evolutionary change at a fast enough pace to adapt to rising temperatures. That means it is crucial that climate change risk to these species is assessed and incorporated into future conservation strategies.

This thesis began by examining whether wild dogs can adapt their behaviour to compensate for high temperatures by hunting more at night, when temperatures are cooler. Whilst there is some flexibility in the timing of their hunting behaviour there is clearly a mechanism through which wild dogs are prevented from hunting at night, particularly during the denning period. Identifying why wild dogs are not leaving the den to hunt at night, despite the fact they are under much higher energetic pressures, may enable conservation scientists to implement measures that can help support populations in periods of hot weather, preventing the fall in recruitment that was found to drive population declines at high temperatures in later chapters of this thesis. Identifying shifts in the timing of activity at high temperatures in other species could help identify how they are likely to respond to climate change and therefore indicate where conservation interventions should be targeted.

I only investigated one possible mechanism by which wild dogs might adapt to higher temperatures. Whilst changes to wild dog phenology are not likely to prevent climate change impacts, as in most areas they already breed at the coolest time of year (Woodroffe et al., 2017), and most colonisation of areas outside their current range would likely require human managed re-introductions, there are a variety of other changes in behaviour and physiology by which wild dogs may be able to adapt. These include, but are not limited to: changes in habitat use; prey preferences; pelage properties, including colour and thickness; and changes to their physiology to encourage more efficient heat loss. Their ability of these ‘shifts in self’ to keep pace with climate change is unclear however; changes due to phenotypic plasticity may occur rapidly, but evolutionary change is likely to happen too slowly to protect the species from the impacts of climate change. Identifying other mechanisms by which the species may avoid demographic effects of high temperature may enable better predictions of the species’ response to climate change, as well as potentially identifying targeted conservation actions that may help mitigate the effects of high temperatures on African wild dogs.

The negative impact of high temperatures on adult survival shown in Chapter 3 suggest that the impact of high temperatures on African wild dog fitness through reduced activity across a 24h period translate to demographic impacts even outside the denning period. Where high temperatures have the greatest impact on mortality, it appears to specifically increase deaths due to disease and direct killing by humans. These are two major threats to the species throughout its range (Woodroffe and Sillero-Zubiri, 2012) and these findings suggest that implementing conservation measures to reduce these threats could simultaneously reduce the impact of high temperatures. Measures such as vaccination of wild dogs or domestic dogs can potentially reduce the risk of disease and hence lower African wild dog mortality (Prager et al., 2011) . Similarly, programmes which aim to help people reduce predation of livestock by African wild dogs may bring down the number of direct killings (Woodroffe et al., 2005) and likewise reduce the impacts of climate change on adult mortality. It appears, however, from the findings in Chapter 4, that the temperature impacts on wild dog recruitment play a greater role in driving demographic impacts than those on adult survival.

The combined impact of temperature on adult survival and recruitment on the population African wild dogs in Laikipia, Kenya are predicted to cause not only population declines, but also potentially the extinction of the population. Whilst extinction risk after 10 generations remained relatively low under all potential future emissions scenarios for the population of wild dogs that was made up of 30 packs, the highest number of packs recorded in the region, the smaller population of 9 packs, the median across the species' range, had an extinction risk of 10% under the second worst case scenario, and 88% in 10 generations under the worst case scenario. This is significant as the population is now much smaller than 9 packs after a disease outbreak in 2017 reduced the population to a single surviving pack. Large population declines were predicted over 10 generations in the simulated population of 9 packs compared with 30 packs at both starting population sizes across all four emissions scenarios, and even over longer time scales the population of 30 packs persisted under temperatures half a degree greater than the population of 9 packs. These findings have implications for how the population of wild dogs in Laikipia is managed, as well as the management of wild dog populations more widely. Population of 30 packs or more only exist in 4 areas with in the wild dog's current range (Woodroffe and Sillero-Zubiri, 2012). The fact population size impacts extinction risk highlights the importance of connectivity in mitigating the impacts of climate change on the species. Efforts to connect existing isolated ranges will become increasingly important as the climate warms, however these will become increasingly difficult as population growth across the continent continues. It is key that measures which will help lessen the impacts of high temperatures on wild dogs are established, for example reductions in disease levels.

By using the demographic model to simulate three demographic scenarios, and running it in space under future emissions scenarios in Chapter 5, I was able to highlight areas where climate change was likely to have the smallest and greatest impact. Most of the areas predicted to undergo the greatest population declines under climate change were in Southern Africa, particularly concentrated around Botswana, Namibia, South Africa and Angola. This finding is cause for great concern, because the largest remaining wild dog population currently inhabits the Kavango-Zambezi Trans-Frontier Conservation Area (KAZA) spanning northern Botswana, eastern Namibia, Western Zimbabwe, South-West Zambia and South-East Angola. This population is unique in its size, extent, and genetic connectivity (Marsden et al., 2012) and any threat to this population is a threat to the entire species. The demographic scenario based on data from this area however, and therefore the most appropriate to use for future predictions, showed a much smaller decline in population size relative to the other demographic scenarios. The connectivity of the population and the lack of human pressures will buffer this population, however for surrounding, smaller, populations, such as those in and around the Kalahari, the future looks bleak.

Most of the areas predicted to face a smaller risk from climate change were along the East coast of Africa, particularly in East Africa, as well as a small number of sites towards the West coast. Most of these populations are small, however, and the demographic scenario based on East Africa showed severe declines in population numbers, and this was worsened by the inclusion of seasonal breeding in the model. This shows the need to be cautious when using models of this kind to direct conservation efforts and ensure localises adaptations are taken into account.

There are a number of implications of these predicted climate change impacts for conservation. Firstly, they can help guide where conservation efforts are focused. In Chapter 5, I identified several areas suspected to support resident wild dog populations, in regions expected to suffer smaller impacts of climate change than some of the known resident range. Surveys of these areas (such as Rahole and Morene-Borana) are a priority for conservation action. Areas identified as recoverable for the African wild dog that are predicted to be most climatically suitable in the future should be targeted for reintroductions – particularly in West Africa, where smaller declines were predicted and there is seasonal breeding. Finally, these maps can help target conservation actions to areas where the species are most likely to persist under climate change. It may be that the future on the species will rely on extensive habitat restoration outside of areas currently identified as recoverable. This has happened in areas of their current range, such as Savé Valley, which until the 1990s was primarily used for cattle ranching. Integrating such projections with the assessment of other risks is key, and measures which alleviate more than one risk, such as increasing the connectivity of populations, should be prioritised over other conservation measures.

I predict that future climate change will have an impact on the African wild dog’s threat status according to the IUCN Red list. Other papers assessing the suitability of the Red List for predicting risk of extinction from climate change have highlighted the importance of bringing in conservation measures once the species is listed as Vulnerable. As the African wild dog is already listed as Endangered I would highly recommend that conservation interventions, or, at the very least, research into which interventions help mitigate temperature impacts, starts as soon as possible. Without appropriate conservation action the species is likely to be under serious threat of extinction.

Whilst models predicted a significant fall in population size under all emissions scenarios throughout the species range, higher emission pathways produced larger population decline predictions. I predict that the amount of greenhouse gasses emitted will be key in determining the threat posed by climate change to the African wild dog, and that RCP 8.5 will cause catastrophic declines in this species. Beyond focused conservation actions, political action, or inaction, on climate change has the potential to determine the African wild dog’s fate. The greater our efforts to curb carbon emissions, the more likely we are to guarantee the survival of African wild dogs into the future.

Appendices

Appendix 1

Appendix 1.1. Monitoring periods for GPS-collared African wild dogs at our Kenya study site.

Monitoring started when GPS-collars were fitted, and ended when the collar was removed, the battery expired, or contact was lost. Two dogs – WDF120 and WDF126 changed packs during monitoring, moving to the Truant pack on the 29/09/14 and the Toucan pack on the 29/03/15 respectively.

			GPS-collar monitoring		
ID	**Pack 1**	**Sex**	*start*	*end*	*Number of days*
WDM91	Tui’s	M	27 Jul 13	01-Aug-14	370
WDF96	Loisaba	F	15 Mar 12	31-Jan-13	322
WDM97	Rat	M	27 Apr 11	27-May-11	30
WDF105	Loisaba	F	14 Sep 11	25-Nov-11	72
WDF109	Lebai	F	07 Apr 11	12-Aug-11	127
WDM111	Loisaba	M	02 Mar 12	10-Jun-12	100
WDM112	Tui’s	M	8 Mar 12	08-Dec-12	275
WDM118	Bahati	M	24 Jul 13	25-Jan-14	185
WDM119	Loisaba	M	3 Aug 13	30-Sep-14	423
WDF120	Tui’s	F	31 Jul 14	28-Nov-14	120
WDF123	Crocodile	F	23 Apr 14	23-Jan-15	275
WDF126	Katu	F	1 Aug 14	03-May-15	275
WDF130	Ol Pejeta	F	27 Aug 14	14-Dec-14	109
WDM131	Crocodile	M	24 Apr 15	13-Jun-15	50
WDM132	Bahati	M	25 Apr 15	21-Jun-15	57

Appendix 1.2. Times of GPS fixes of each wild dog GPS-collar used in the study

X denotes a GPS fix that was included in the distance analyses. ○ denotes a GPS fix that was discarded from the dataset. Day was considered to be 6:00 or 6:30 to 18:00. Night was considered to be 18:00 to 06:30. Dogs not used in the night analysis due to having too few nocturnal GPS fixes are highlighted in grey.

WD	**01:00**	**02:15**	**03:30**	**05:00**	**06:00**	**06:30**	**07:00**	**07:30**	**08:00**	**10:00**	**13:00**	**16:00**	**18:00**	**18:30**	**19:30**	**20:00**	**20:45**	**22:00**	**23:30**
WDM91	X		○			X	○		X		X	○	X		X			○	
WDF96	X					X	○	○	X		X	○	X	○	X				
WDM97	X					X			X		X	○	X		X				
WDF105	X					X	○	○	X		X		X	○	X				
WDF109	X					X			X		X		X		X				
WDM111	X					X	○	○	X		X		X	○	X				
WDM112	X					X	○	○	X		X		X	○	X				
WDM118	X		○			X	○		X		X		X		X			○	
WDM119	X		○			X	○		X		X		X		X			○	
WDF120	X		○			X	○		X		X		X		X			○	
WDF123	X					X	○	○	X		X		X	○	X				
WDF126	X		○			X	○		X		X		X		X			○	
WDF130	X		○			X	○		X		X		X		X			○	
WDM131	X	○	○	○		X	○		X		X		X		X		○	○	○
WDM132	X	○	○	○		X	○		X		X		X		X		○	○	○

Appendix 1.3. Number of days and nights of data included in the analyses per GPS-collared wild dog

Individual identity	Daytime activity	Daytime distance travelled	Night-time activity	Night-time distance travelled	24 hour activity	24 hour distance travelled
WDM91	332	269	333	277	332	244
WDF96	260	195	261	200	260	152
WDM97	30	22	23	21	23	18
WDF105	71	56	72	54	71	34
WDF109	127	79	127	85	122	57
WDM111	4	92	5	87	4	49
WDM112	274	187	275	187	274	133
WDM118	13	166	13	164	13	145
WDM119	349	275	349	274	348	233
WDF120	120	98	121	91	120	66
WDF123	273	131	273	139	273	74
WDF126	273	273	273	252	273	212
WDF130	148	134	148	131	148	120
WDM131	108	70	109	59	108	35
WDM132	50	36	50	37	50	23
Total	**2432**	**2089**	**2432**	**2058**	**2419**	**1595**

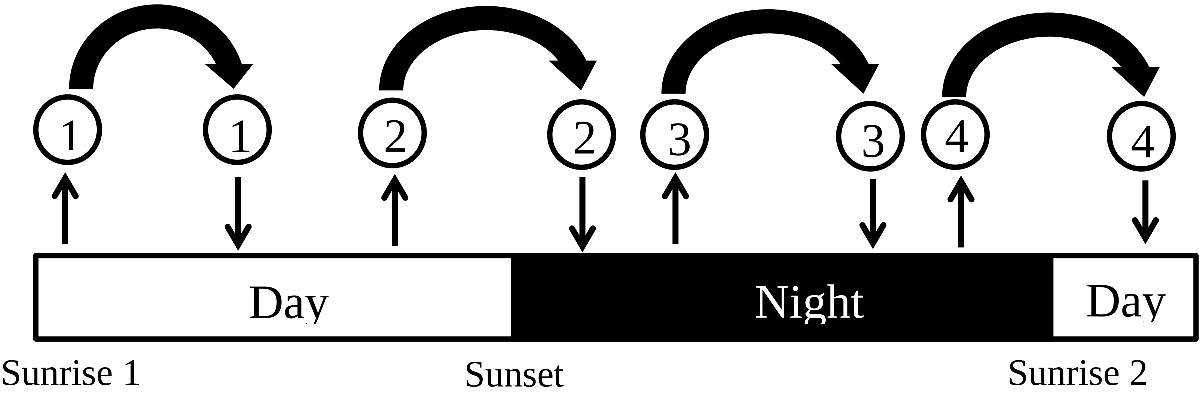
Appendix 1.4. Reasons for including explanatory variables and expected outcomes.

+ indicates an expected increase in activity and distance travelled and – indicates an expected decrease.

Variable	**Reason**	**Expected outcome**	
		Day	**Night**
Daily maximum temperature	Maximum temperature was chosen as it has been found to be the ecologically relevant temperature variable impacting wild dog behaviour in a number of other studies which have also included other variables such as average daily temperature (Woodroffe et al 2011a, Woodroffe, Groom and McNutt 2017). Woodroffe, Groom and McNutt (2017) found that high daily maximum temperatures during the denning period were associated with low pup survival.	-	+
Daily rainfall	Woodroffe, Groom and McNutt (2017) found that rainfall had an effect on pup survival. We wanted to investigate if this was a result of impacts on adult behavior.	Due to inconsistent effects of rainfall on pup survival we were unsure of how rainfall would impact wild dog behavior.	
Level of moonlight	Cozzi *et al* (2012) found a positive relationship between night-time wild dog activity and levels of moonlight. Including this variable allowed us to investigate whether constraints of moonlight levels prevent wild dogs from hunting at night.	NA	+
Denning	Woodroffe, Groom and McNutt (2017) found that wild dogs have greater energy demands when they are denning, and travelled further during a 24 hour period.	+	+
Age of pups	As pups grow they require more food and therefore greater energy expenditure by the adults.	+	+
Days at den site	During the denning period the pack typically moves its den site a number of times in response to threats and prey depletion around the area of the den. Ford et al found that as wild dogs spend time at a den site prey becomes locally depleted (Ford et al., 2015), which forces them to travel further for food (Woodroffe, Groom and McNutt, 2017).	+	+
*Daily maximum temperature * Daily rainfall*	Rainfall often mediates the impacts of high temperatures.	+	-
*Daily maximum temperature * Denning*	To test if responses differ significantly inside compared to outside the denning period	Unknown	Unknown
*Daily maximum temperature * Days at den site*	Dogs may need to increase their activity on hot days as prey becomes locally depleted at a den site.	+	+

Appendix 1.5. Diagram and description of moonlight calculations.

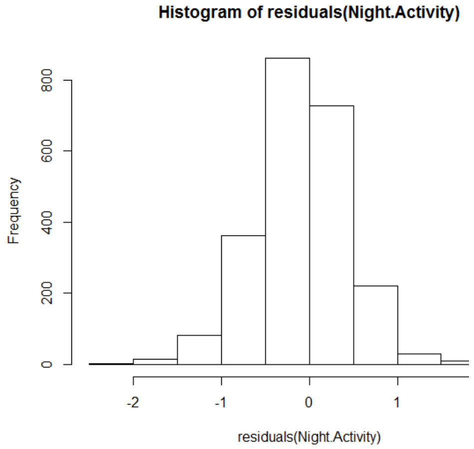
Circles indicate the moon, ↑ indicates moonrise, ↓ indicates moonset. Numbers correspond to scenarios in the below table.



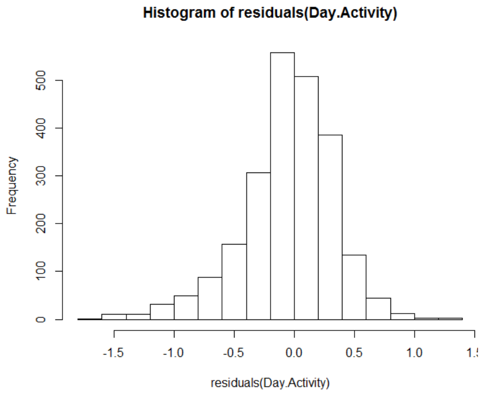
Scenario number	**Scenario**	**Calculation for hours of moonlight**	**Calculation to give final moonlight value**
1	Moon rises and sets the day before.	0 moonlight.	Multiply by percentage illumination of the moon that night
2	Moon rises the previous day and sets during the night.	moonset - sunset	
3	Moon rises and sets during the night	moonset - moonrise	
4	Moon rises at night and sets the next day	sunrise 2 - moonrise	

Appendix 1.6. Histograms of residuals

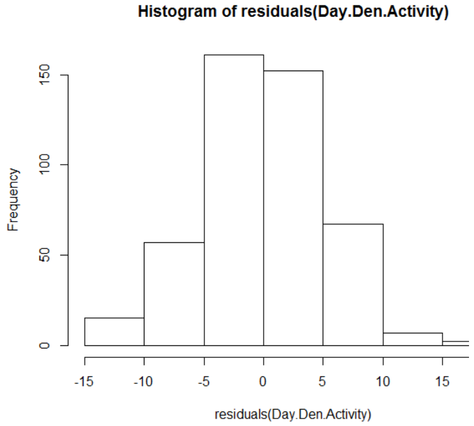
Night-time activity (denning and non-denning)



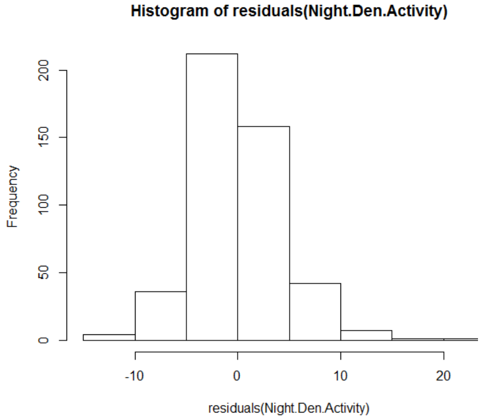
Daytime activity (denning and nondenning)



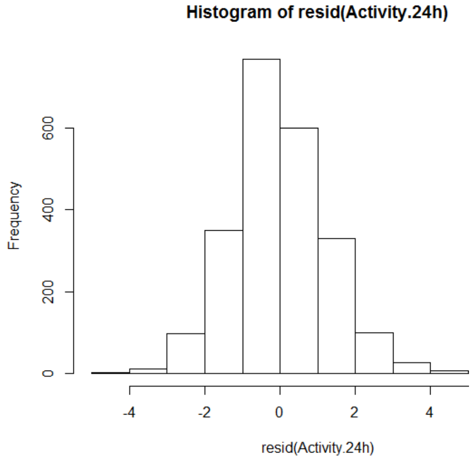
Day-time activity (denning)



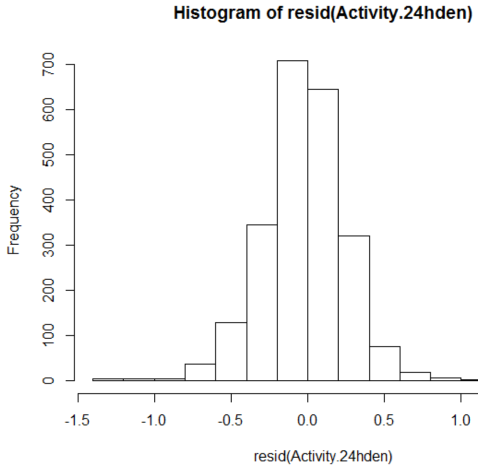
Night-time activity (denning)



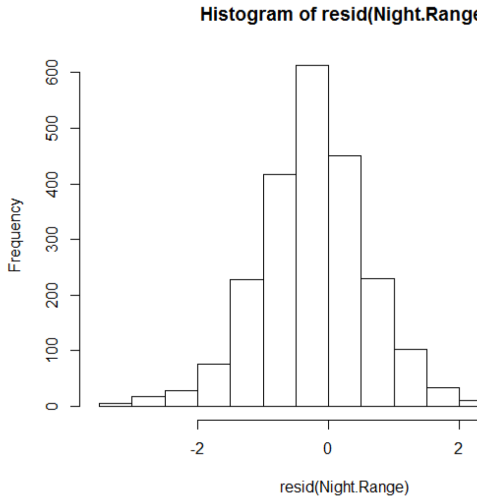
24 hour activity (denning and non-denning)



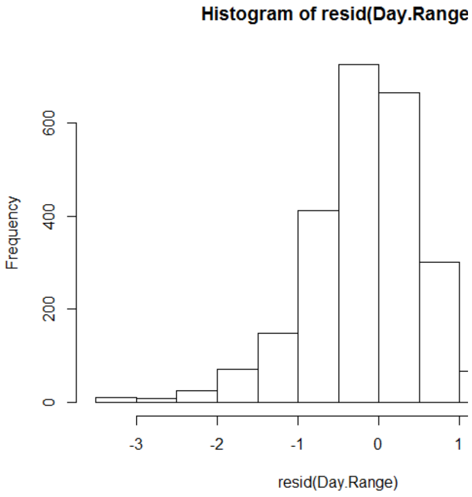
24 hour activity (denning)



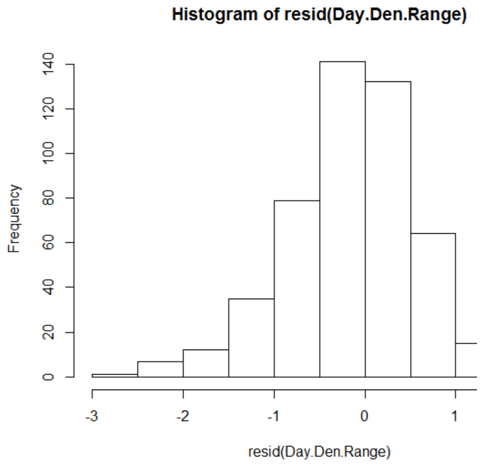
Night-time range (denning and non-denning)



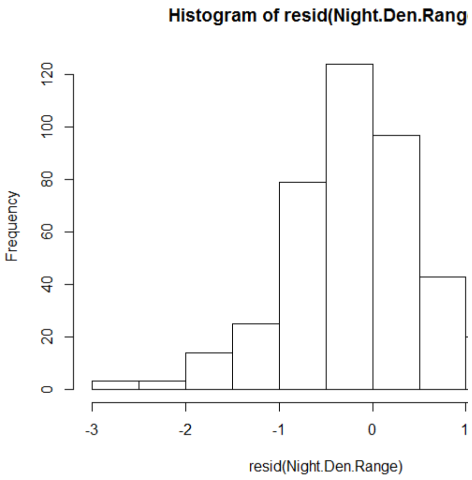
Daytime range (denning and nondenning)



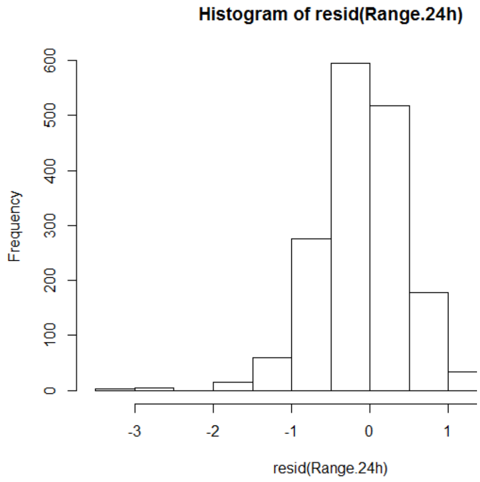
Day-time range (denning)



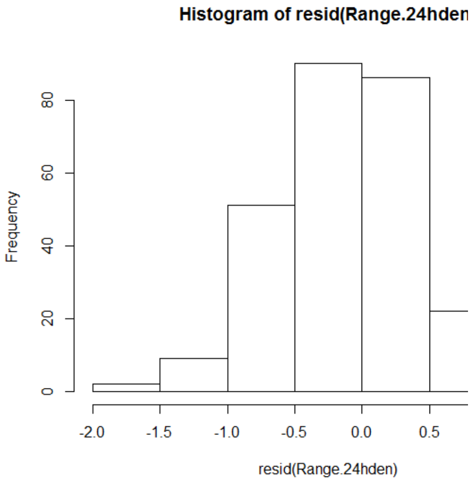
Night-time range (denning)



24 hour range (denning and non-denning)

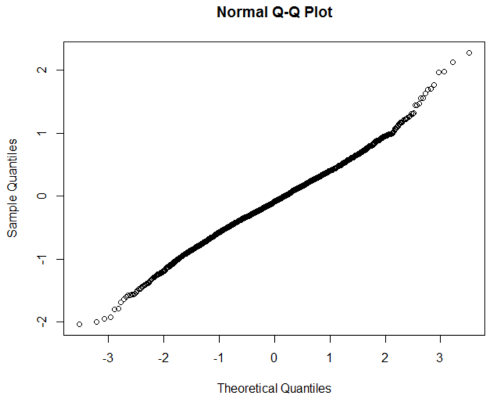


24 hour range (denning)

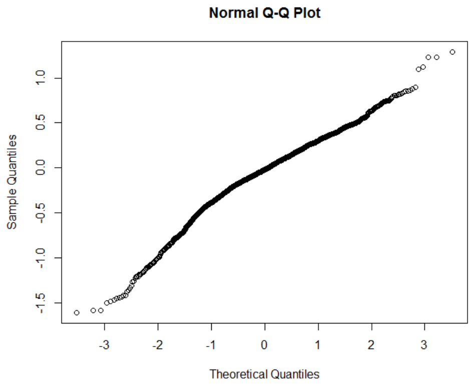


Appendix 1.7. Q-Q plots of model residuals

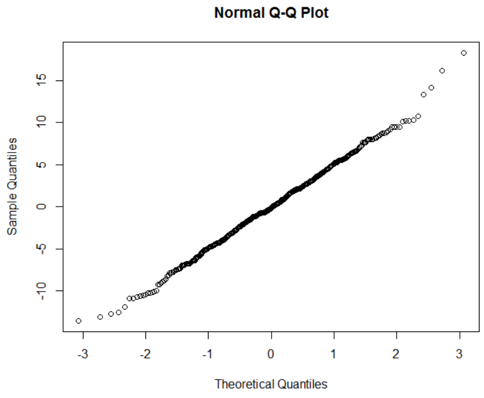
Night-time activity (denning and non-denning)



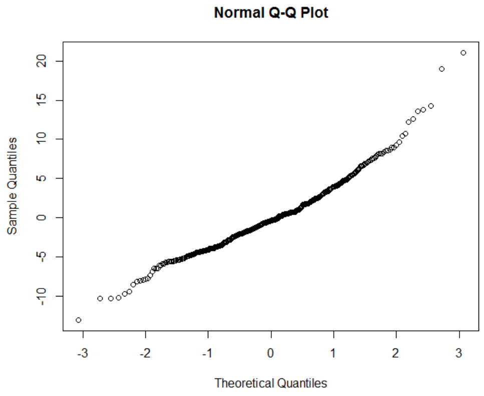
Daytime activity (denning and nondenning)



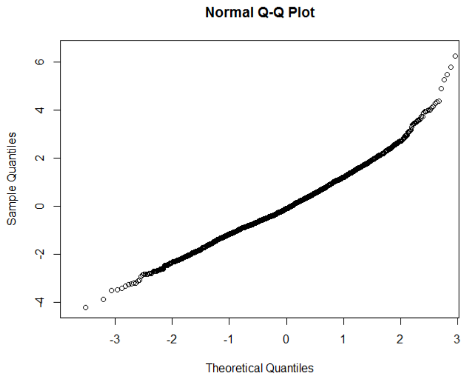
Day-time activity (denning)



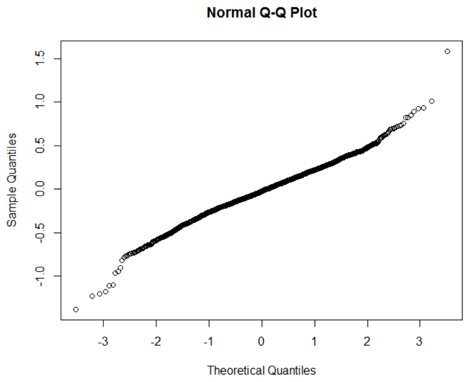
Night-time activity (denning)



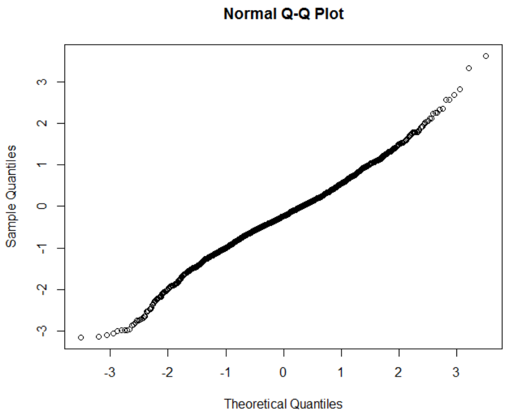
24 hour activity (denning and non-denning)



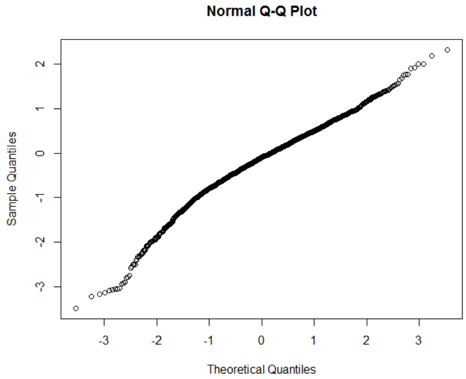
24 hour activity (denning)



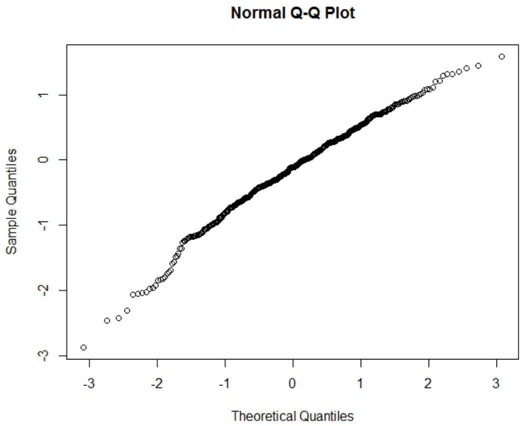
Night-time range (denning and non-denning)



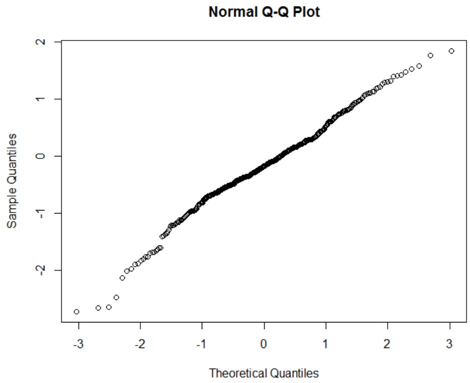
Daytime range (denning and nondenning)



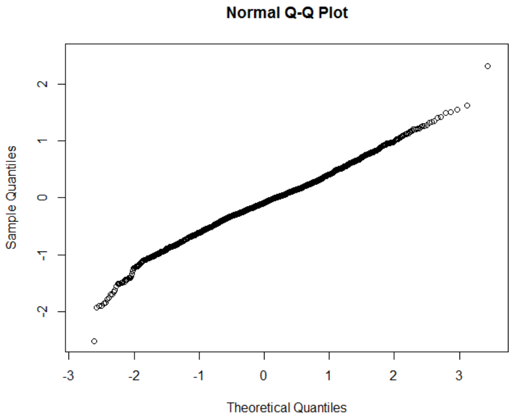
Day-time range (denning)



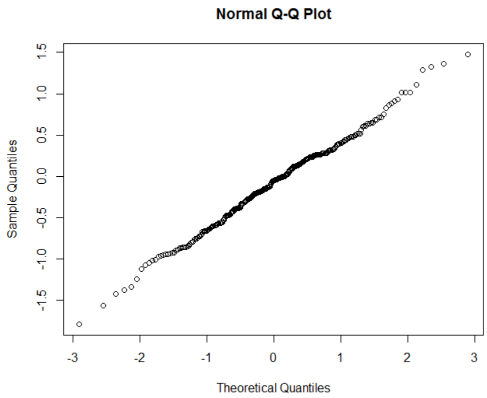
Night-time range (denning)



24 hour range (denning and non-denning)



24 hour range (denning)



Appendix 1.8. Table of top models

Table OR8.1: list of models for **daylight hours** where delta < 5.

1= Maximum temperature	2= Rainfall	3=Denning (Yes)
4=Maximum temperature*Rainfall	5=Maximum temperature*Denning (Yes)	6=Days at den
7=Pup age	8=Days at den*Maximum temperature	

Dependent variable	**Time period**	**Independent variables**	***AICc***	***Delta***
Activity	All	1 2 3 4	14709.12	0.00
		1 2 3 4 5	14711.14	2.01
		1 2 3	14713.71	4.58
	Denning	1 2 4 6 7	3281.10	0.00
		1 2 6 7	3281.92	0.82
		1 2 4 6 7 8	3283.09	1.99
		1 6	3283.82	2.73
		1 2 6 7 8	3283.83	2.74
		1 2 6	3285.14	4.04
Distance travelled	All	1 2 3	9679.18	0.00
		1 2 3 5	9680.09	0.91
		1 2 3 4	9680.12	0.93
		1 2 3 4 5	9680.87	1.69
		1 3	9683.28	4.10
	Denning	1 6 7	1592.40	0.00
		1 6	1592.82	0.43
		6 7	1594.30	1.90
		1 2 6	1594.35	1.96
		1 2 6 7	1594.44	2.04
		1 2 4 6 7	1595.08	2.68
		6	1595.61	3.21
		1 2 6 7 8	1595.97	3.58
		2 6 7	1595.99	3.60
		1 2 4 6 7 8	1596.64	4.24

Table OR8.2: list of models for **night-time hours** where delta < 5.

1= Maximum temperature
2= Rainfall
3=Denning (Yes)
4=Maximum temperature*Rainfall
5=Maximum temperature*Denning (Yes)
6=Days at den
7=Pup age
8=Days at den*Maximum temperature
9=Moonlight

Dependent variable	**Time period**	**Independent variables**	***AICc***	***Delta***
Activity	All	1 2 3 4 5 9	13401.64	0.00
		1 2 3 4 9	13403.49	1.85
		1 2 3 5 9	13404.91	3.27
	Denning	9	2571.20	0.00
		1 9	2571.56	0.36
		6 9	2573.24	2.04
		1 2 9	2573.62	2.42
		1 2 5 6 9	2574.63	3.43
		1 6 7 9	2575.01	3.80
		1 2 7 9	2575.05	3.85
		1 2 6 9	2575.68	4.48
Distance travelled	All	1 2 3 5 9	10733.09	0.00
		1 3 9	10733.51	0.42
		1 2 3 4 5 9	10734.28	1.20
		1 2 3 9	10735.28	2.20
		1 2 3 4 9	10736.23	3.14
	Denning	6	1555.51	0.00
		1	1556.16	0.65
		9	1556.29	0.79
		7	1556.30	0.79
		2	1556.30	0.80
		1 6	1556.46	1.96
		6 9	1556.55	2.05
		1 9	1556.19	2.68
		1 2 9	1556.25	4.75
		1 2	1556.29	4.78

Table OR8.3: list of models for the **24 hour period** where delta < 5.

1= Maximum temperature
2= Rainfall
3=Denning (Yes)
4=Maximum temperature*Rainfall
5=Maximum temperature*Denning (Yes)
6=Days at den
7=Pup age
8=Days at den*Maximum temperature
9=Moonlight

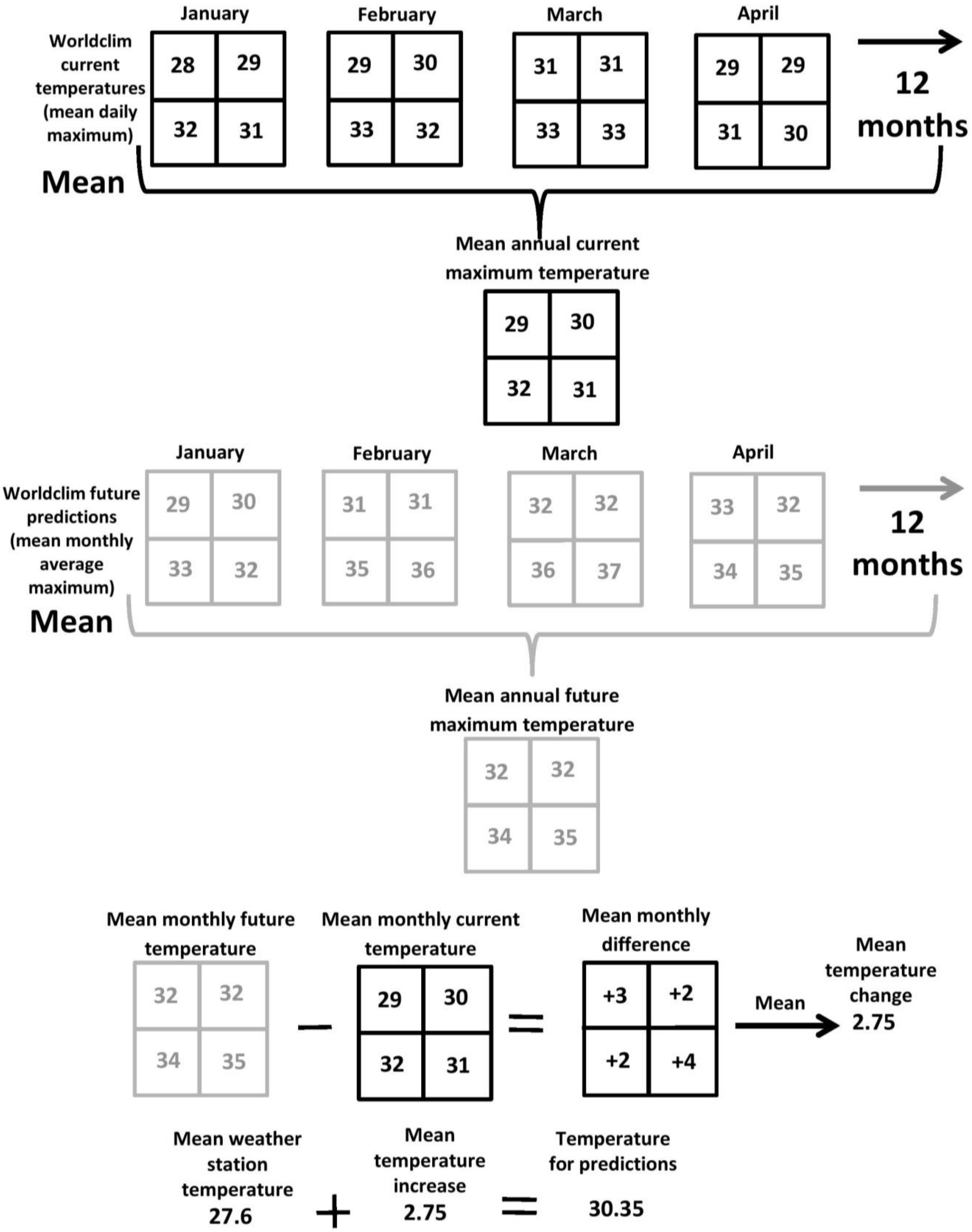
Dependent variable	**Time period**	**Independent variables**	***AICc***	***Delta***
Activity	All	1 2 3 5 9	12312.72	0.00
		1 2 3 4 5 9	12312.97	0.25
		1 2 3 9	12314.25	1.52
		1 2 3 4 9	12314.82	2.09
		2 3 5 9	12316.82	4.10
	Denning	1 2 6 7 8 9	2747.22	0.00
		1 2 6 9	2747.64	0.42
		2 6 9	2747.81	0.59
		1 2 4 6 7 8 9	2748.70	1.48
		1 2 6 7 9	2749.07	1.85
		2 6 7 9	2749.10	1.88
		1 2 6	2749.29	2.08
		1 2 4 6 7 9	2750.27	3.05
		1 6 9	2750.94	3.72
		1 2 6 7	2750.98	3.77
		1 6	2751.04	3.82
		1 2 7 9	2751.84	4.63
Distance travelled	All	1 2 3 5 9	9416.02	0.00
		3 9	9416.91	0.89
		9	9417.38	1.36
		1 2 3 4 5 9	9417.82	1.80
		2 3 9	9418.19	2.16
		3 9	9418.55	2.53
		3	9419.01	2.99
		1 9	9419.34	3.31
		1 2 3 9	9419.91	3.89
		1 3	9420.50	4.48
		1 2 9	9420.65	4.62
		2	9420.92	4.89
	Denning	1 6	1308.19	0.00
		6	1308.25	0.06
		1	1308.33	0.13
		6 7	1308.52	0.32
		1 2 6	1310.20	2.01
		7	1310.25	2.06
		1 9	1310.29	2.09
		1 2	1310.33	2.13
		1 6 7 9	1310.43	2.24
		2	1310.67	2.48
		1 2 6 7	1310.74	2.55
		9	1311.03	2.83
		1 2 6 9	1312.12	3.93
		1 2 9	1312.29	4.10
		1 2 6 7 9	1312.56	4.36
		2 6 9	1312.57	3.37

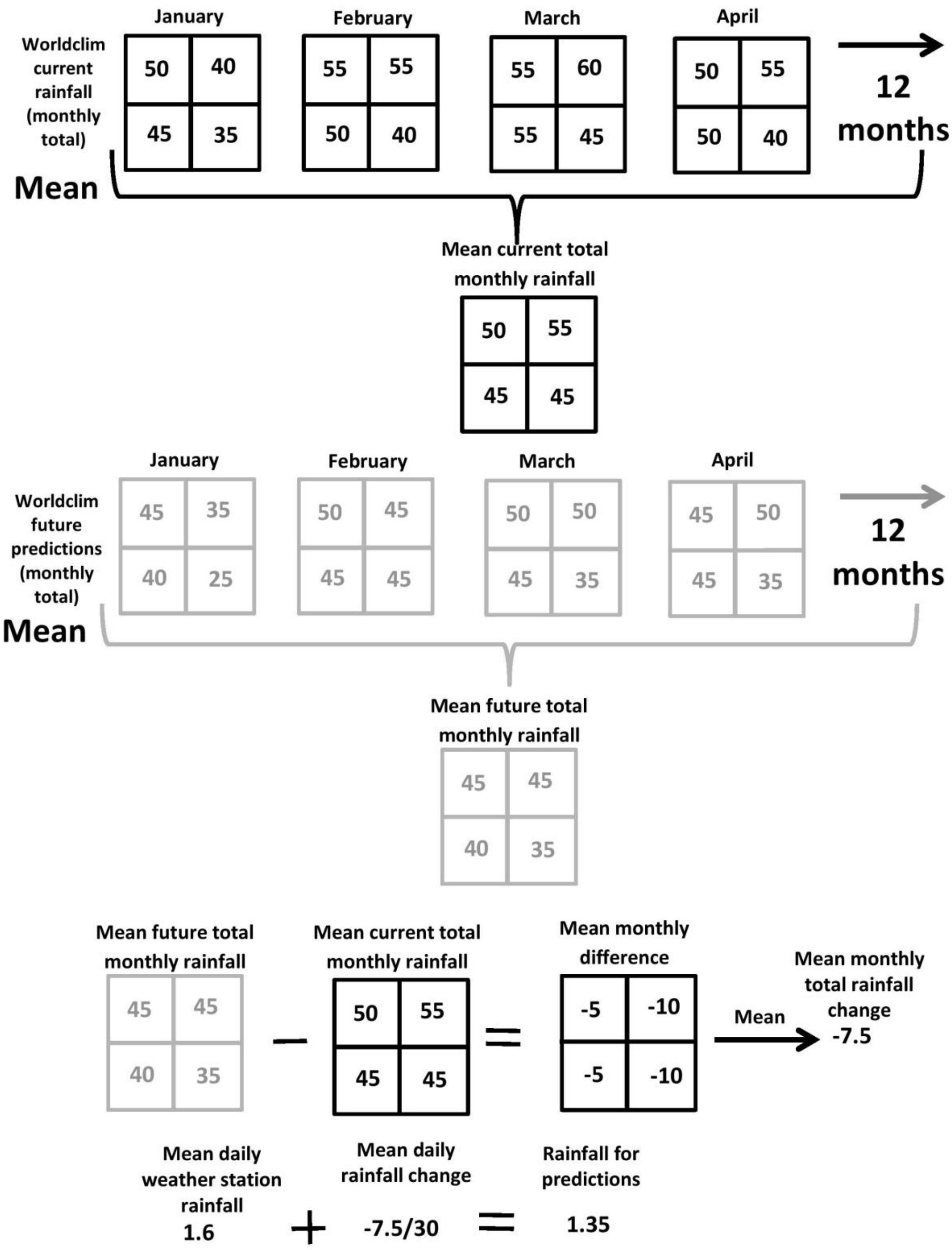
Appendix 1.9. Table of correlations between explanatory variables

Variable 1	**Variable 2**	**Correlation**
Days at den	Pup age	0.23
Days at den	Maximum temperature	-0.12
Days at den	Rainfall	-0.06
Days at den	Moonlight	0.02
Pup age	Maximum temperature	0.04
Pup age	Rainfall	-0.16
Pup age	Moonlight	-0.13
Maximum temperature	Rainfall	-0.14
Maximum temperature	Moonlight	-0.07
Rainfall	Moonlight	0.02

Appendix 1.10. Diagrams showing the calculations performed on the Worldclim temperature and rainfall data

Diagrams showing the calculations performed on the Worldclim temperature and rainfall data to obtain the values that were entered to obtain future projections of activity and distances travelled. Numbers used are examples and do not reflect the data.




Worldclim current rainfall (monthly total)
January
50 40
45 35
February
55 55
50 40
March
55 60
55 45
April
50 55
50 40
12 months
Mean
Mean current total monthly rainfall
50 55
45 45
Worldclim future predictions (monthly total)
January
45 35
40 25
February
50 45
45 45
March
50 50
45 35
April
45 50
45 35
12 months
Mean
Mean future total monthly rainfall
45 45
40 35
Mean future total monthly rainfall
45 45
40 35
Mean current total monthly rainfall
50 55
45 45
Mean monthly difference
-5 -10
-5 -10
Mean
Mean monthly total rainfall change
-7.5
Mean daily weather station rainfall
1.6
Mean daily rainfall change
-7.5/30
Rainfall for predictions
1.35

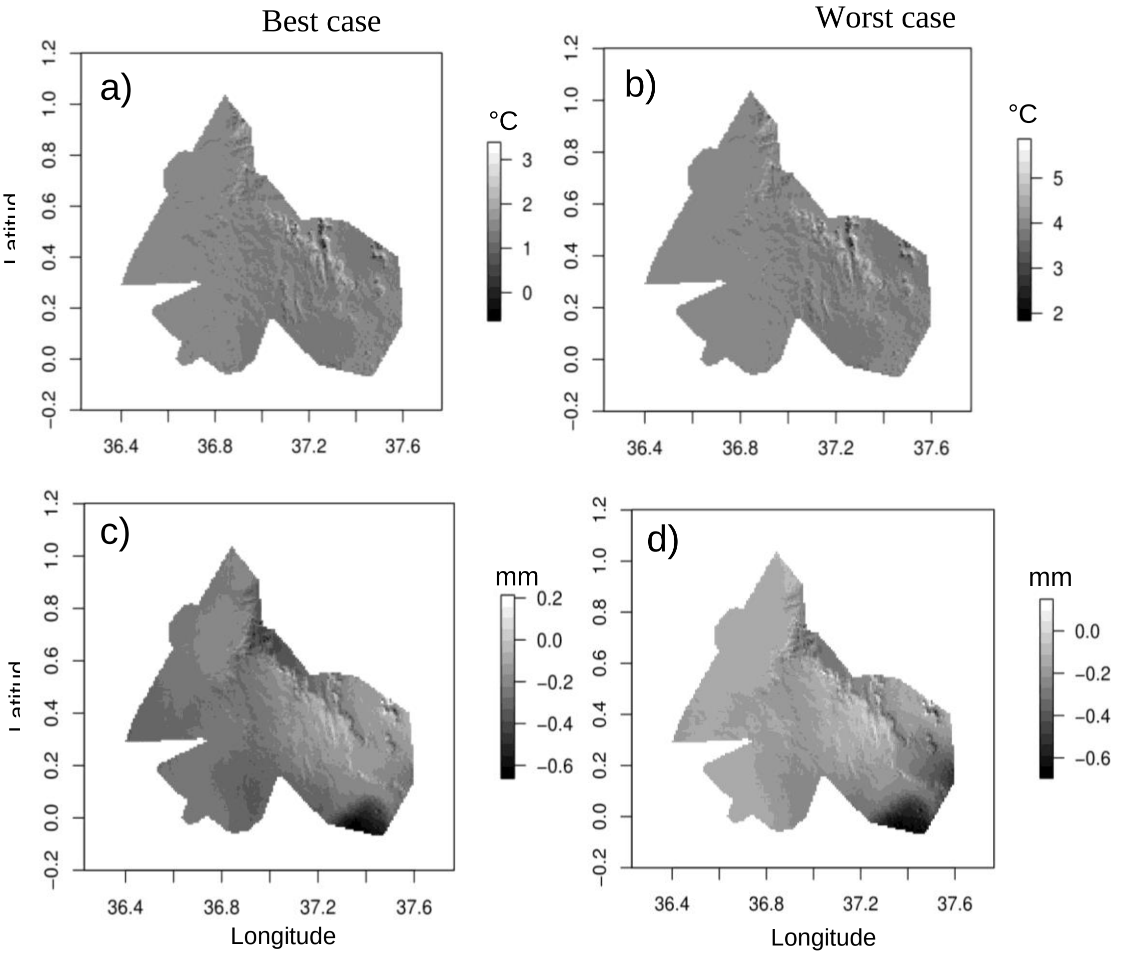
Appendix 1.11. Predicted differences in precipitation temperature

Predicted minimum, mean and maximum differences in daily total precipitation and mean maximum temperature across the study site in the best (RCP 2.6) and worst case (RCP 8.5) HADGEM2 emissions scenarios from Worldclim 1.4 between 2010 and 2070.

		Minimum	Mean	Maximum
Temperature (°C)	Best case	-0.6	1.6	3.3
	Worst case	1.8	3.9	5.9
Rainfall (mm)	Best case	-0.6	-0.2	0.2
	Worst case	-0.7	-0.5	0.1

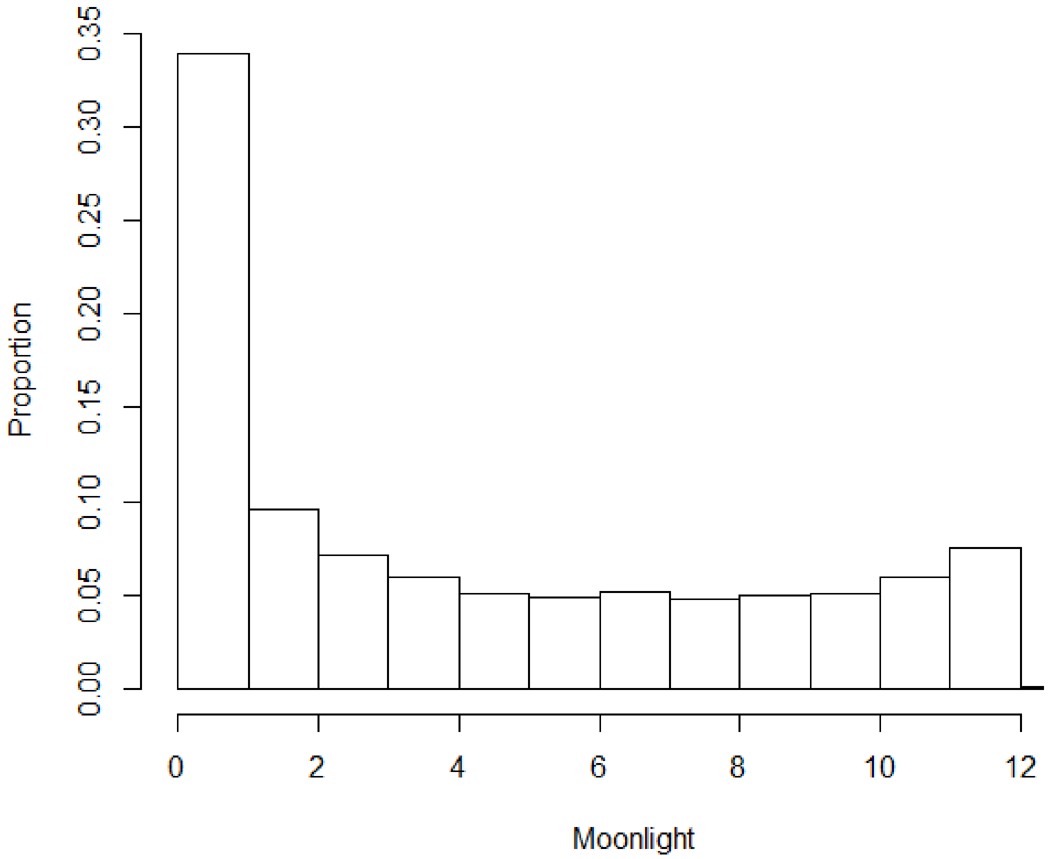
Appendix 1.12

Study area maps showing projected change in mean maximum temperature (°C) and average total daily precipitation (mm) between 2010 and 2070 for the best (Representative Concentration Pathway 2.6) and worst (Representative Concentration Pathway 8.5) case IPCC scenarios: a) predicted change in temperature under RCP 2.6; b) predicted change in temperature under RCP 8.5; c) predicted change in precipitation under RCP 2.6; d) predicted change in precipitation under RCP 8.5. RCP 2.6 indicates the best case IPCC scenario, and RCP 8.5 the worst case. Predicted future temperatures are from the HADGEM2 climate model.



Appendix 1.13. Histogram of moonlight

Histogram of moonlight showing a high proportion of nights have low levels of moonlight

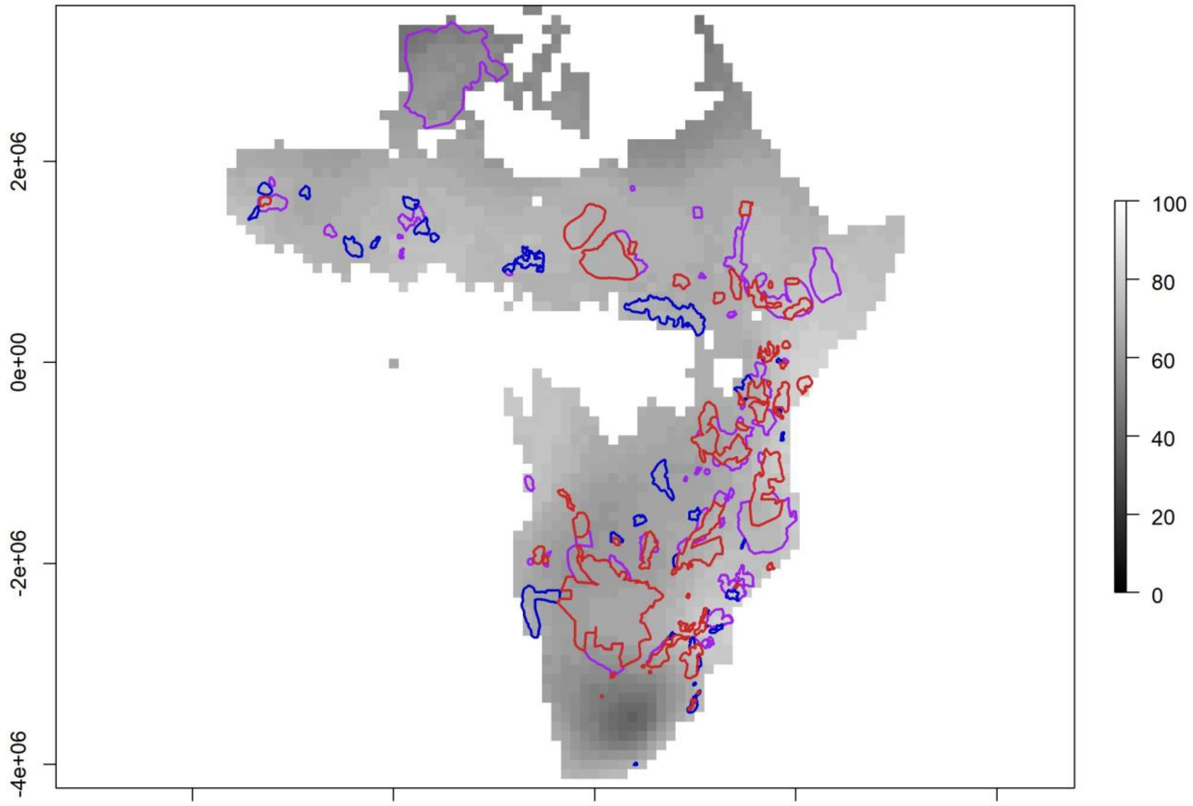


Appendix 2

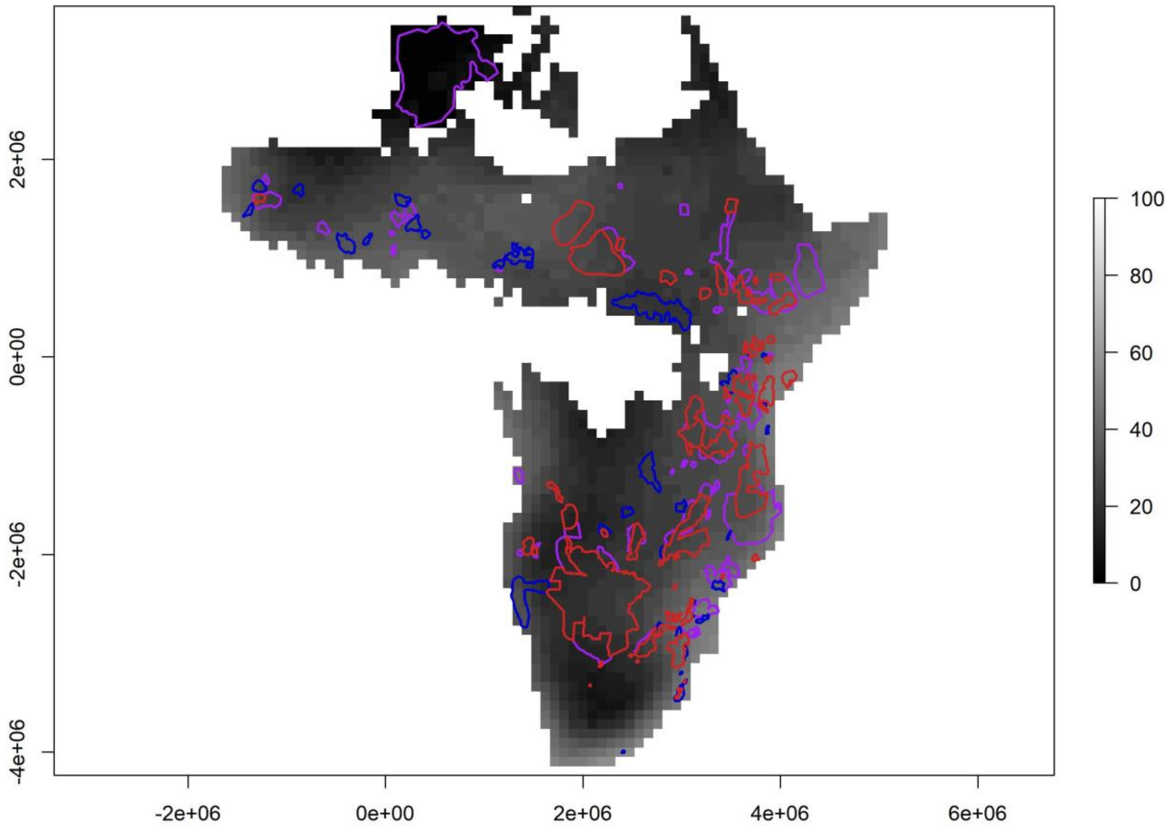
Appendix 2.1 Maps of remaining population

On all maps current range is denoted by a red outline, recoverable range by a purple outline and possible range by a blue outline. Scale denotes predicted percentage remining population after 10 generations.

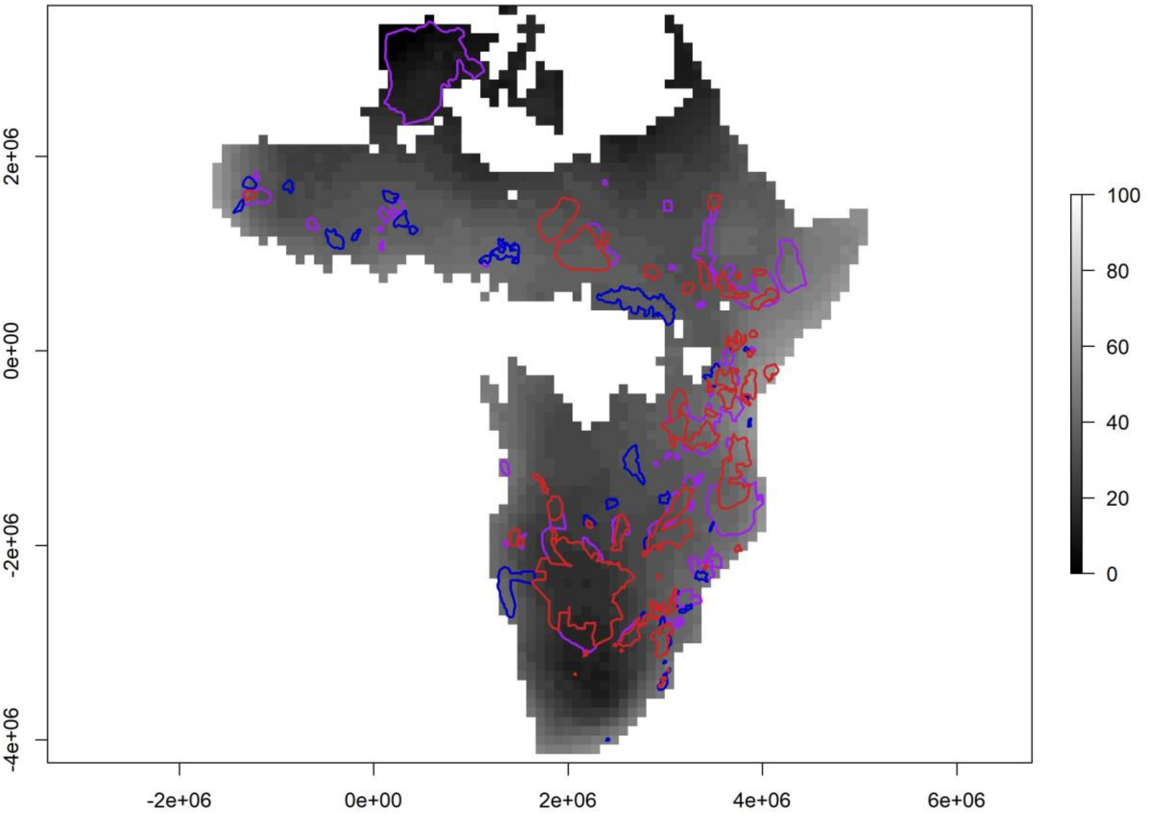
2.1.1 Demographic scenario 1 RCP 2.6



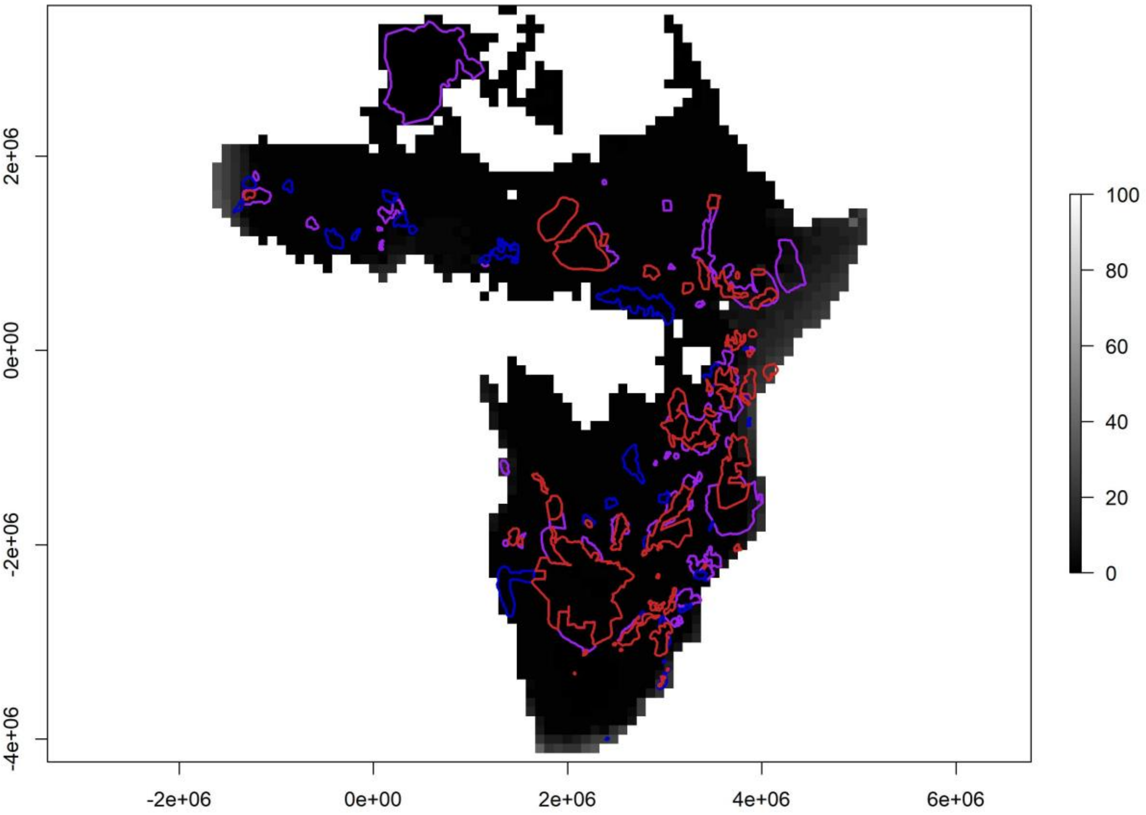
2.1.2 Demographic scenario 1 RCP 4.5



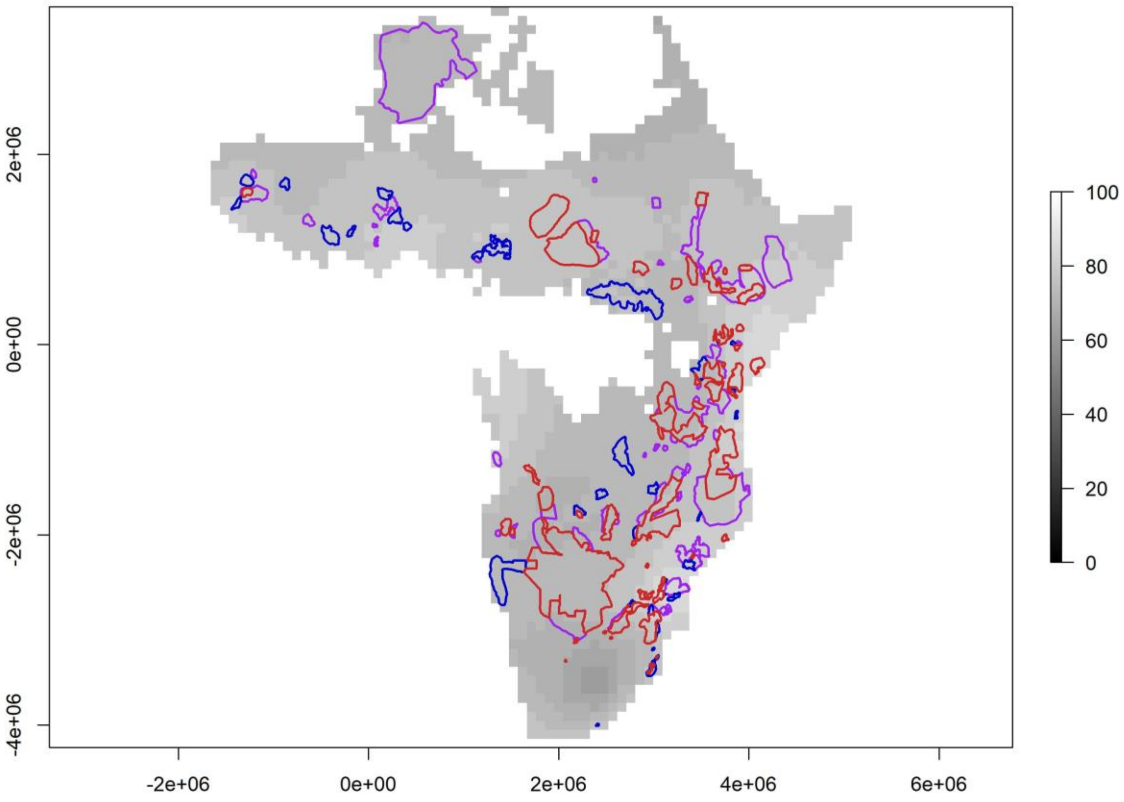
2.1.3 Demographic scenario 1 RCP 6.0



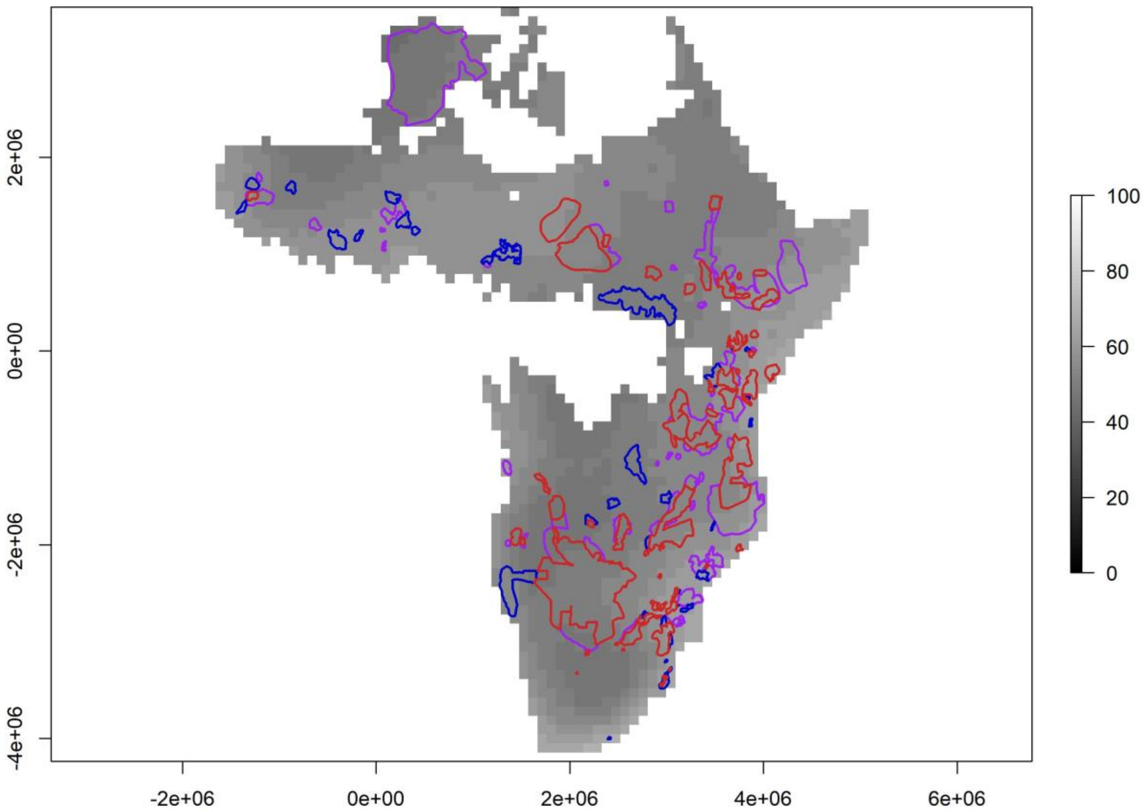
2.1.4 Demographic scenario 1 RCP 8.5



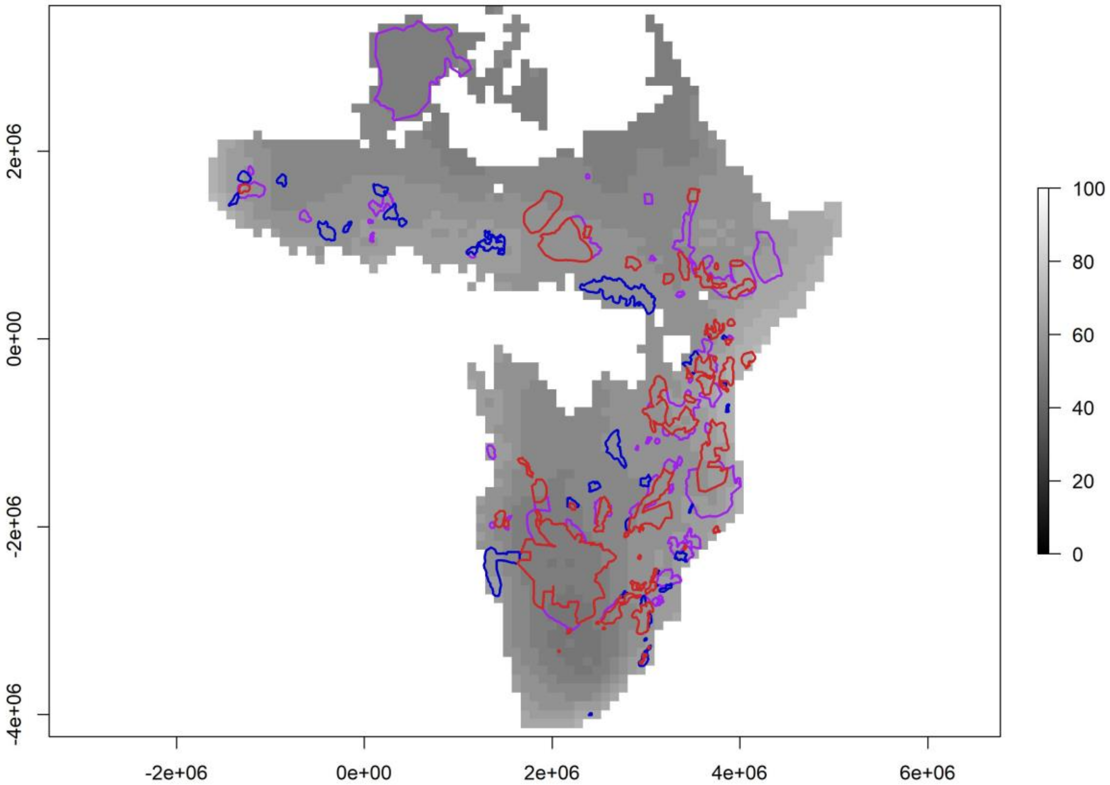
2.1.5 Demographic scenario 2 RCP 2.6



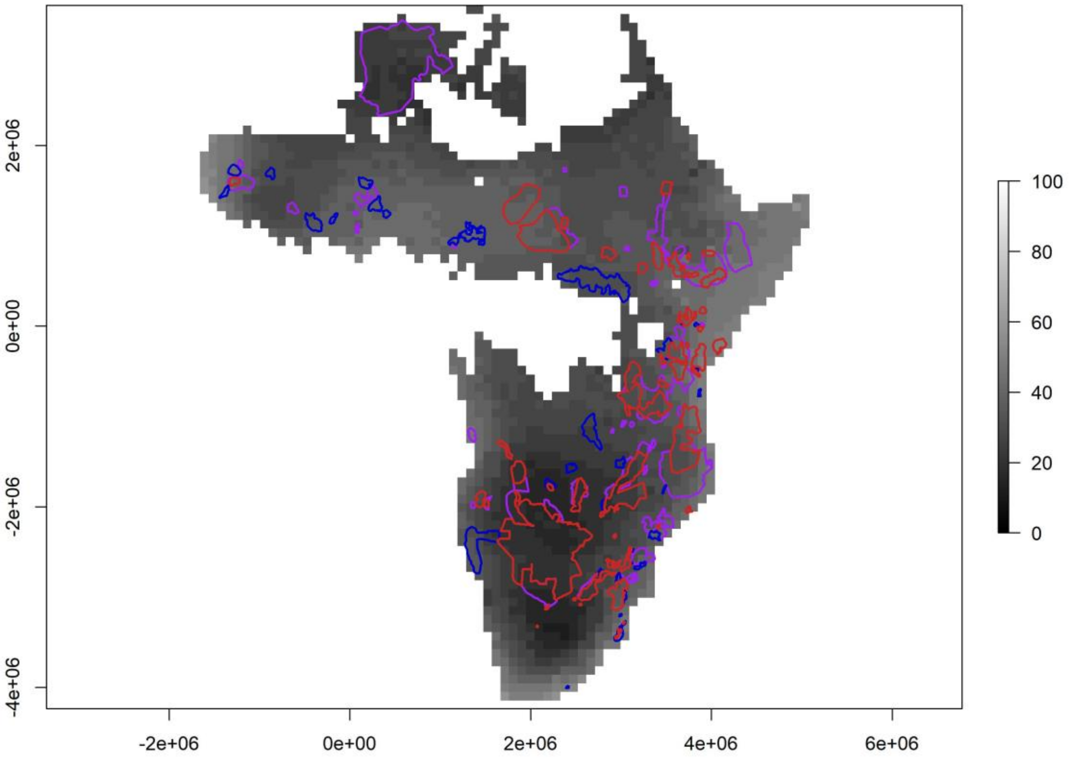
2.1.6 Demographic scenario 2 RCP 4.5



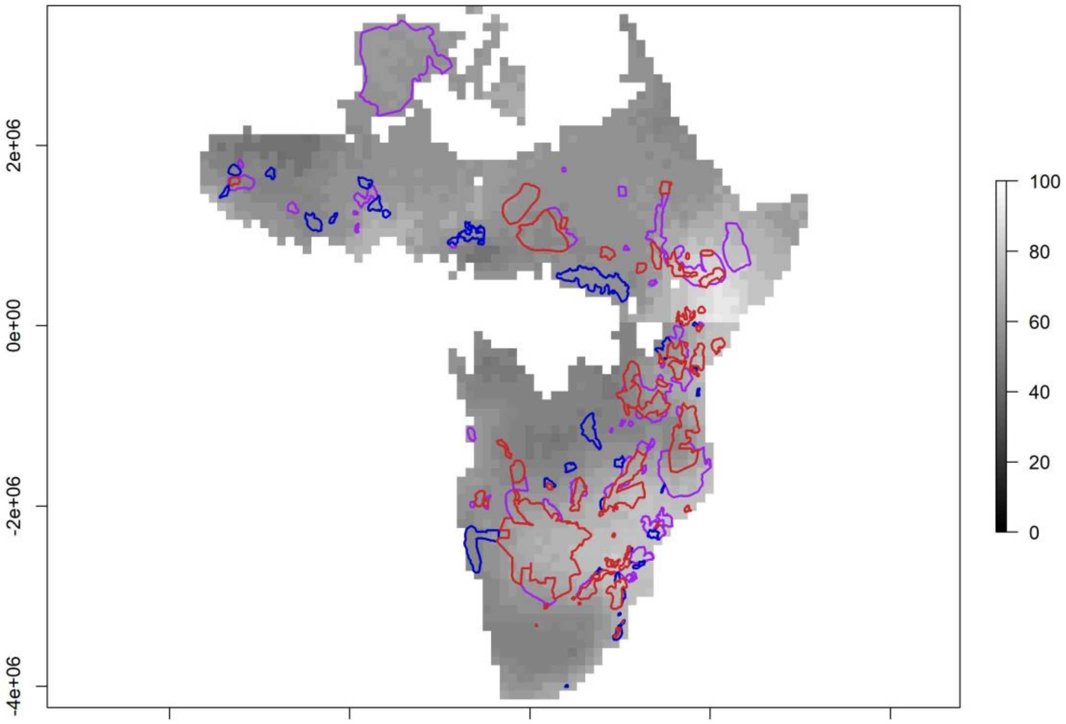
2.1.7 Demographic scenario 2 RCP 6.0



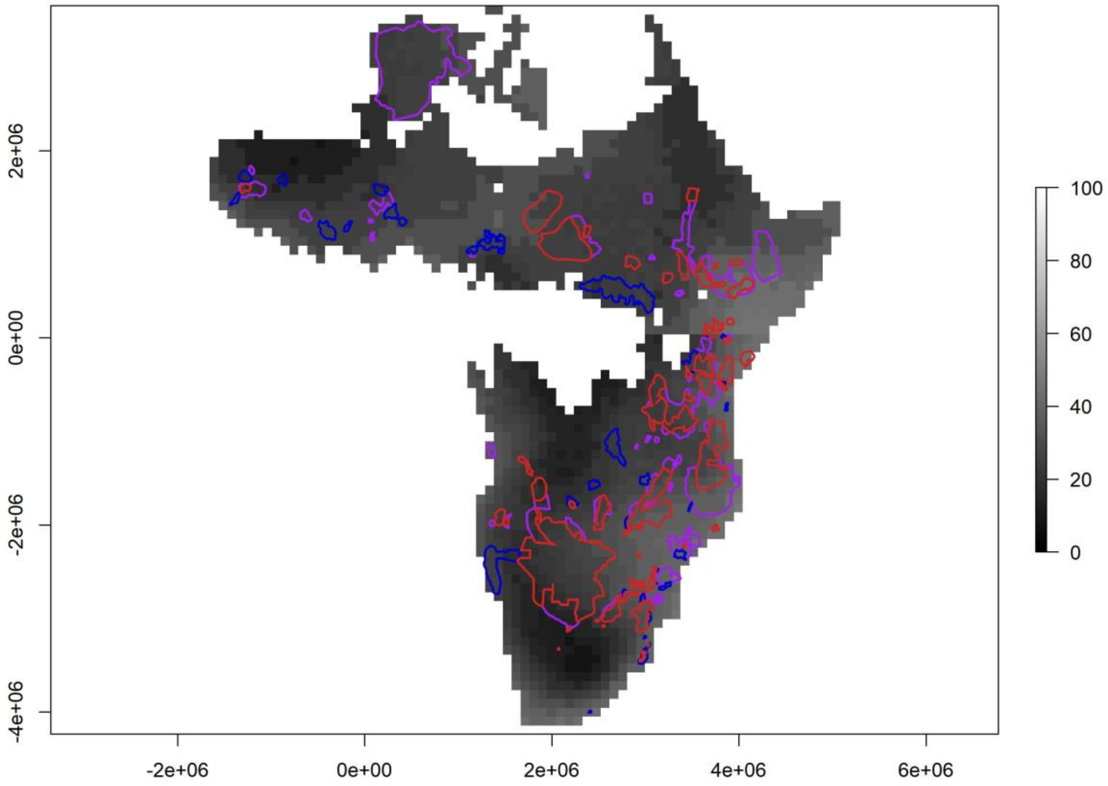
2.1.8 Demographic scenario 2 RCP 8.5



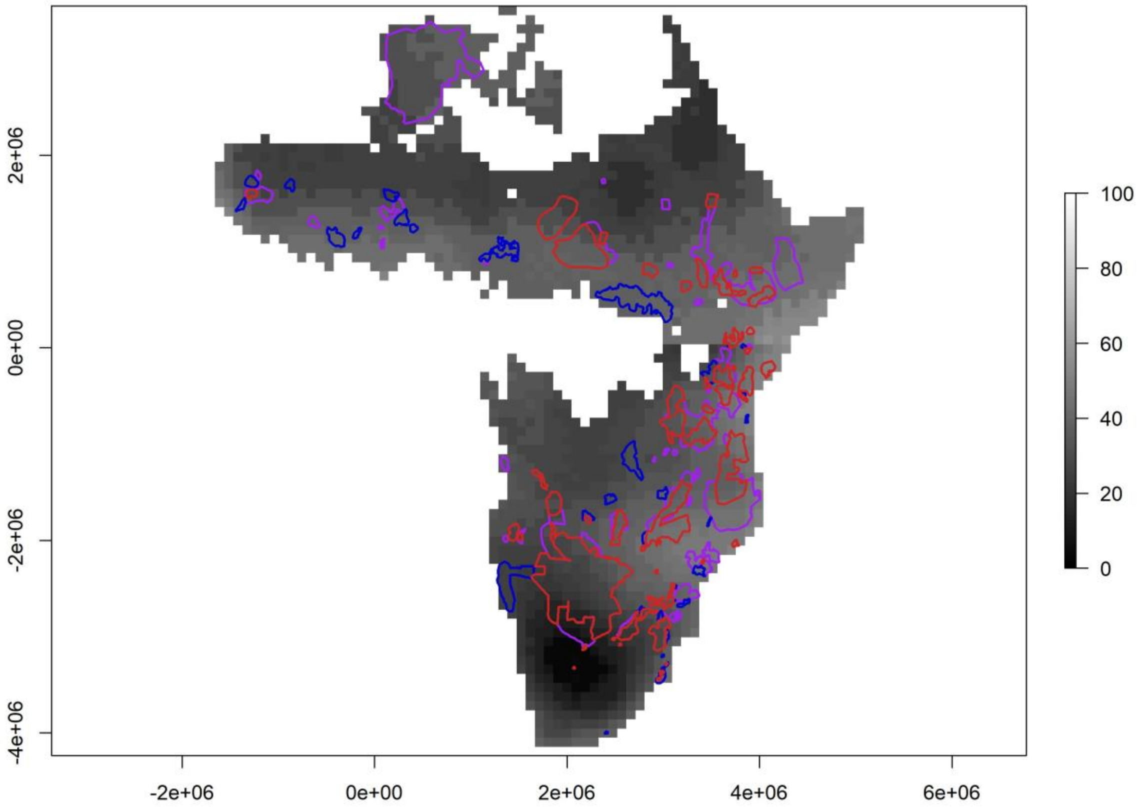
2.1.9 Demographic scenario 3 RCP 2.6



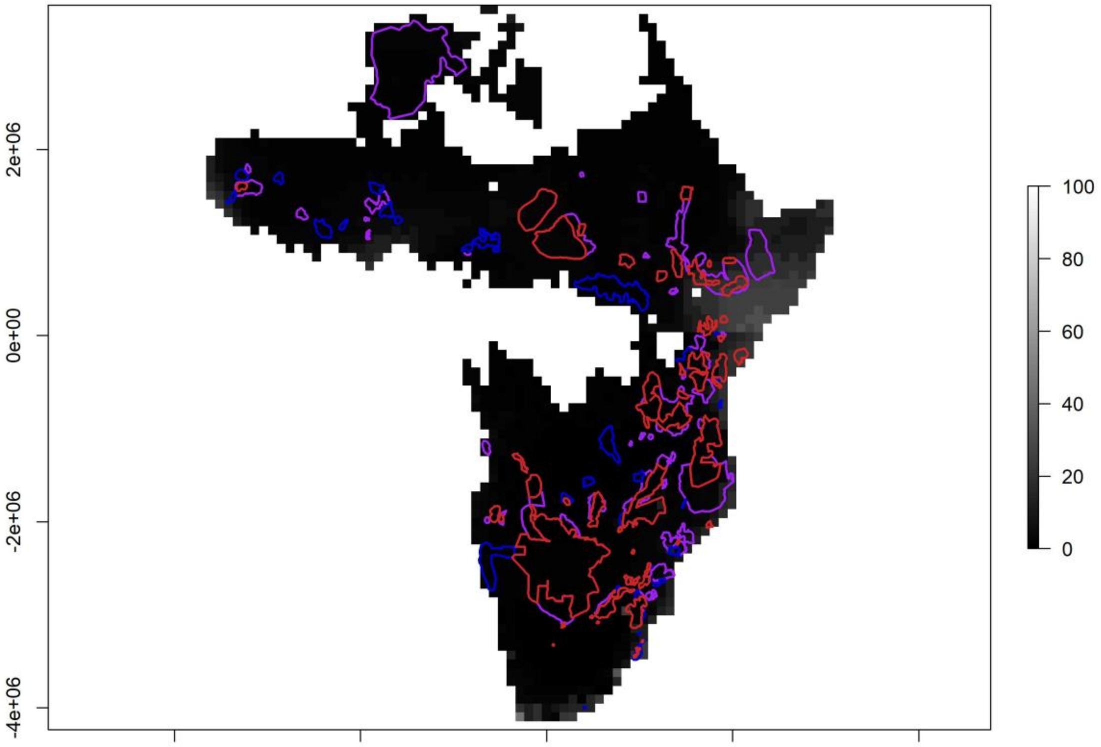
2.1.10 Demographic scenario 3 RCP 4.5



2.1.11 Demographic scenario 3 RCP 6.0



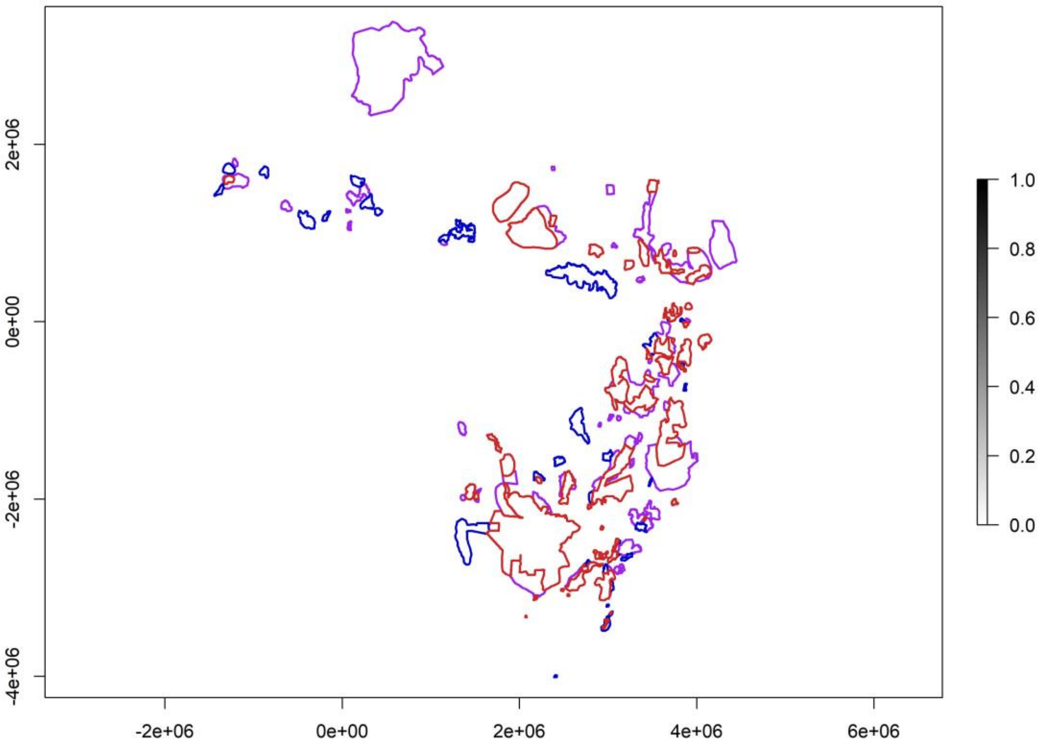
2.1.12 Demographic scenario 3 RCP 8.5



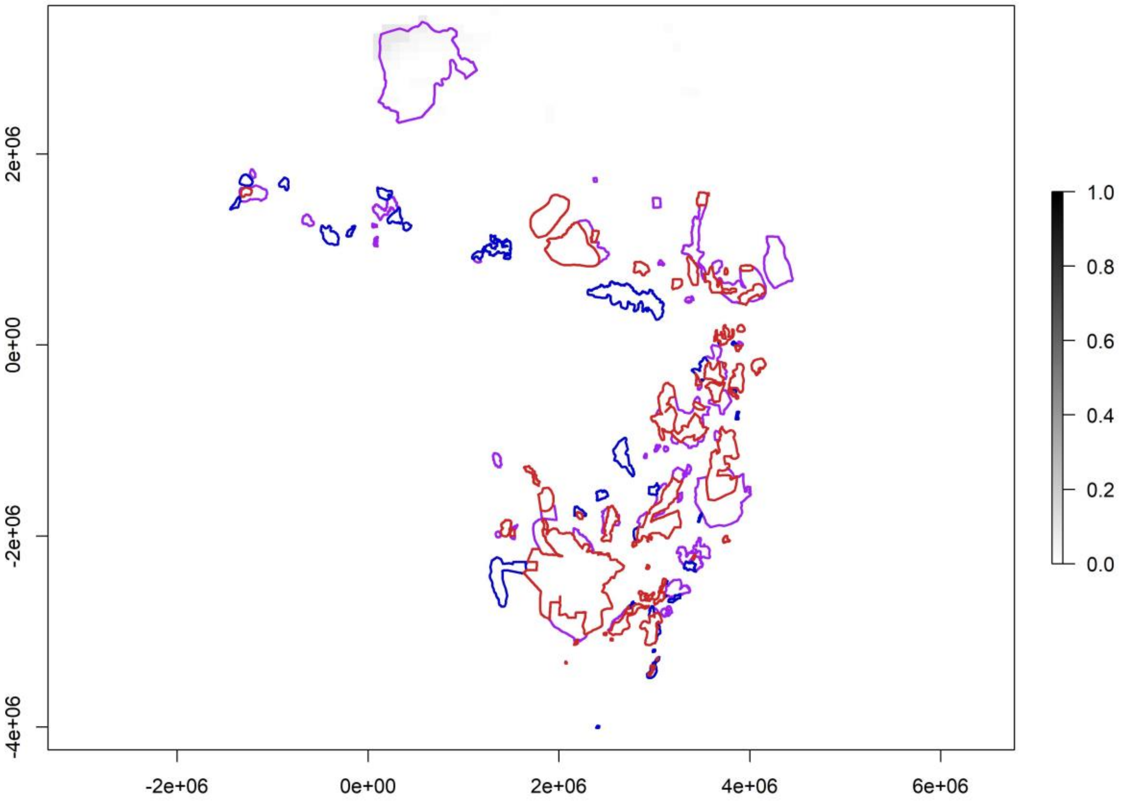
Appendix 2.2 Maps of extinction risk

On all maps current range is denoted by a red outline, recoverable range by a purple outline and possible range by a blue outline. Scale denotes probability of extinction.

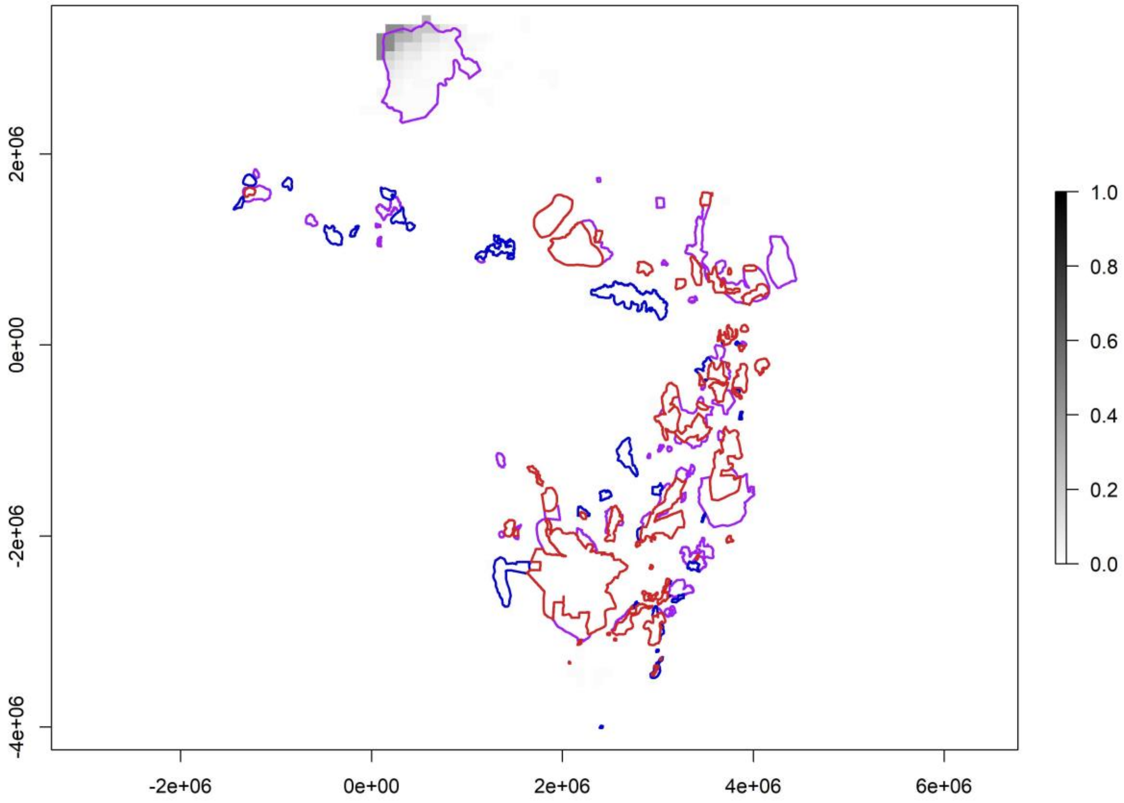
2.2.1 Demographic scenario 1 RCP 2.6



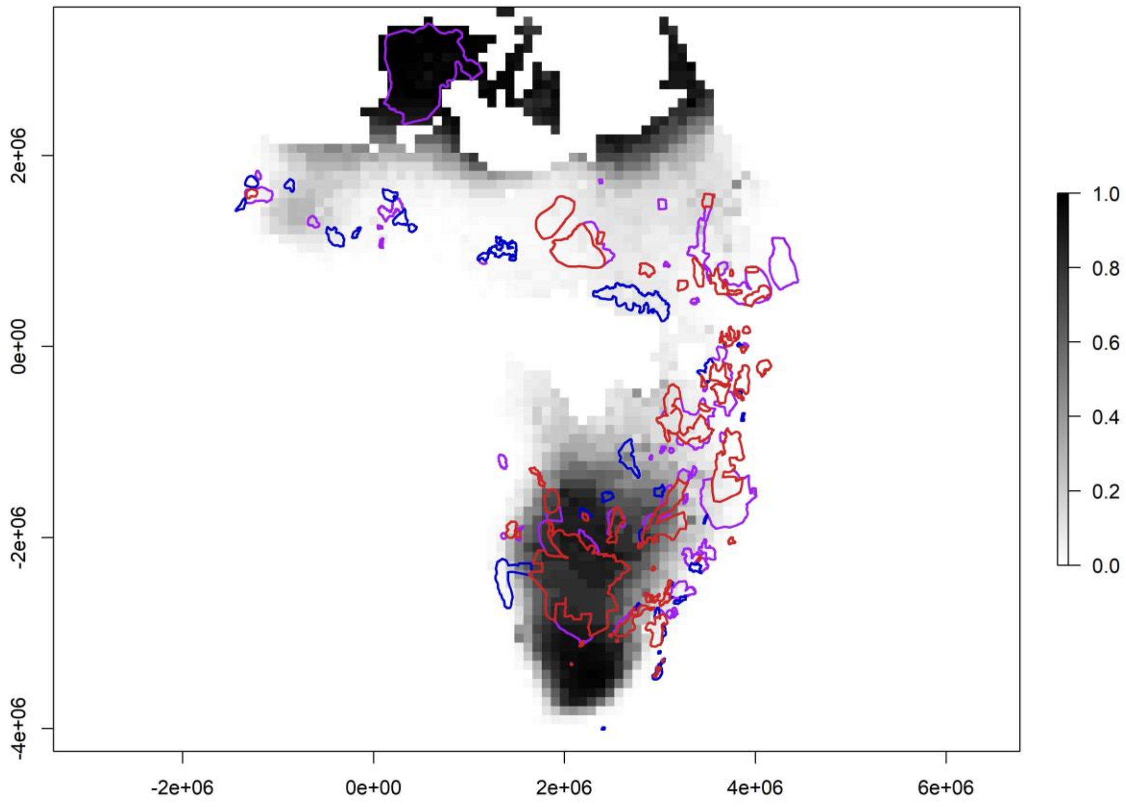
2.2.2 Demographic scenario 1 RCP 4.5



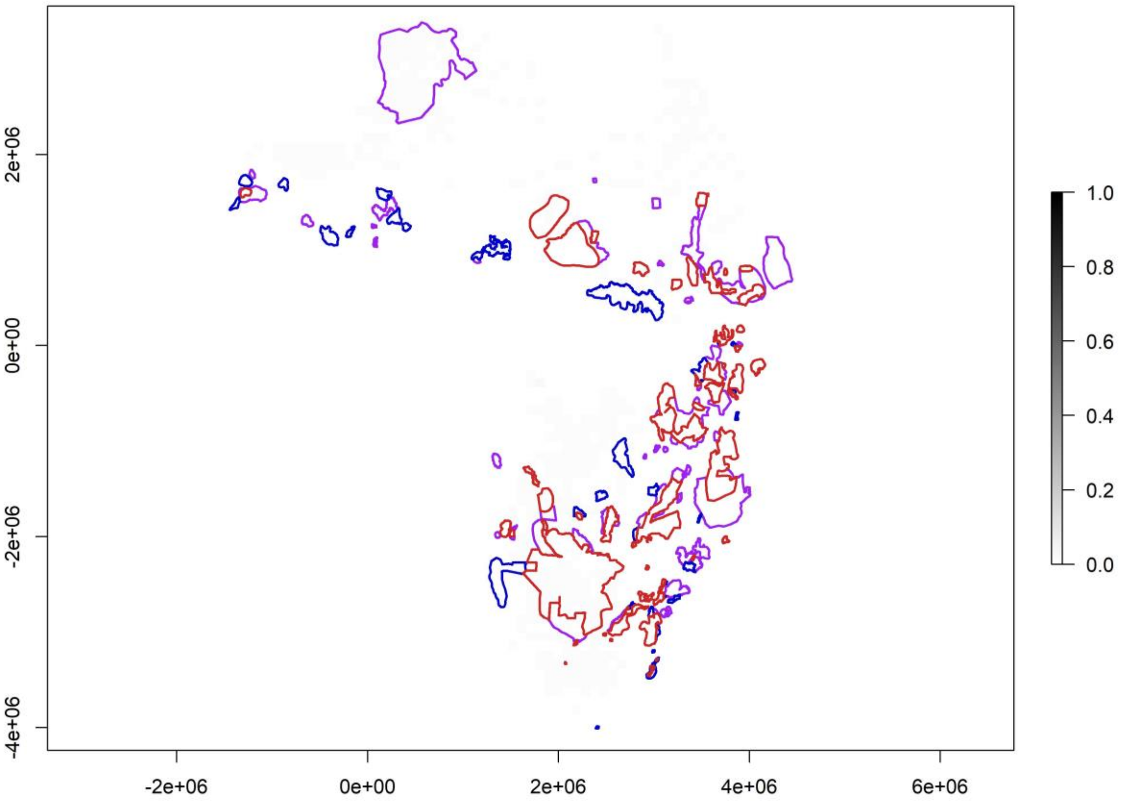
2.2.3 Demographic scenario 1 RCP 6.0



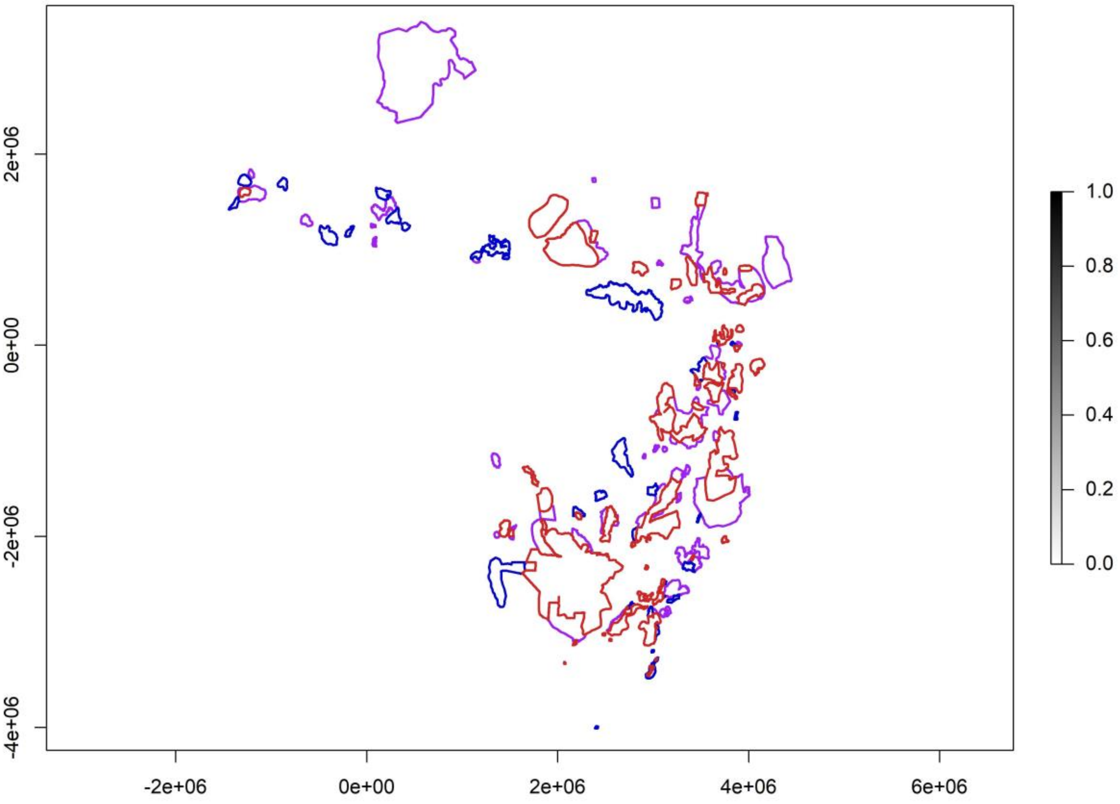
2.2.4 Demographic scenario 1 RCP 8.5



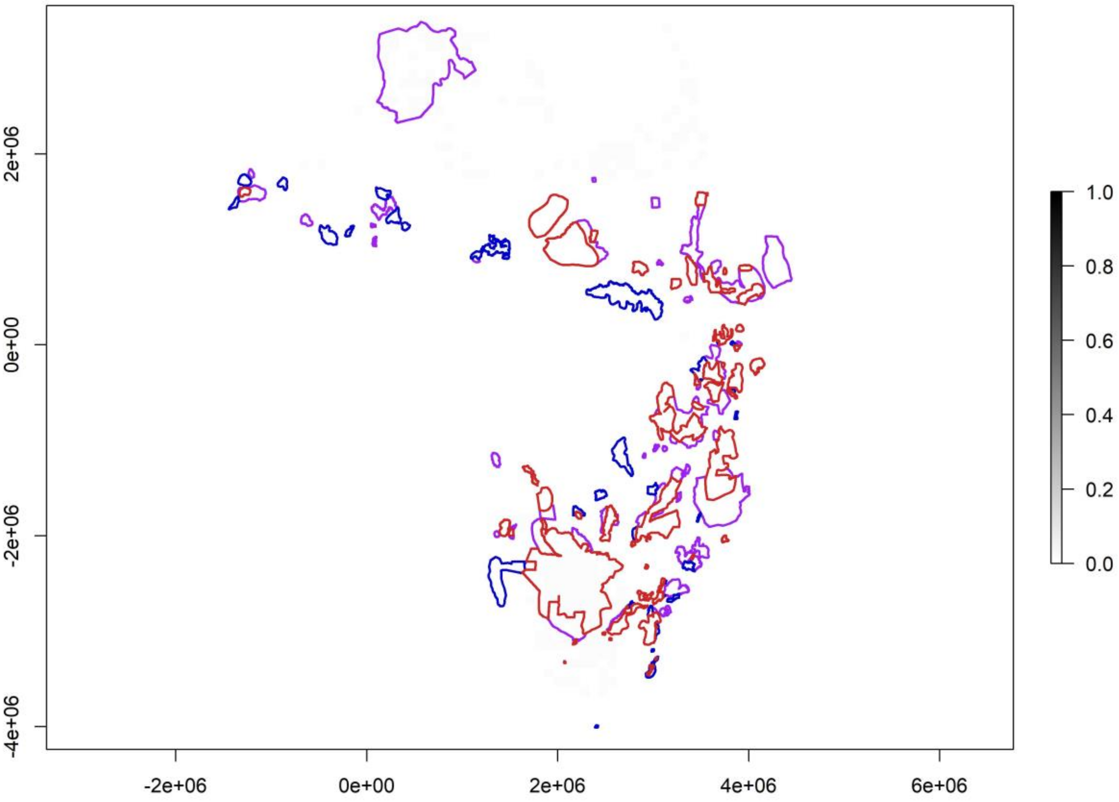
2.2.5 Demographic scenario 2 RCP 2.6



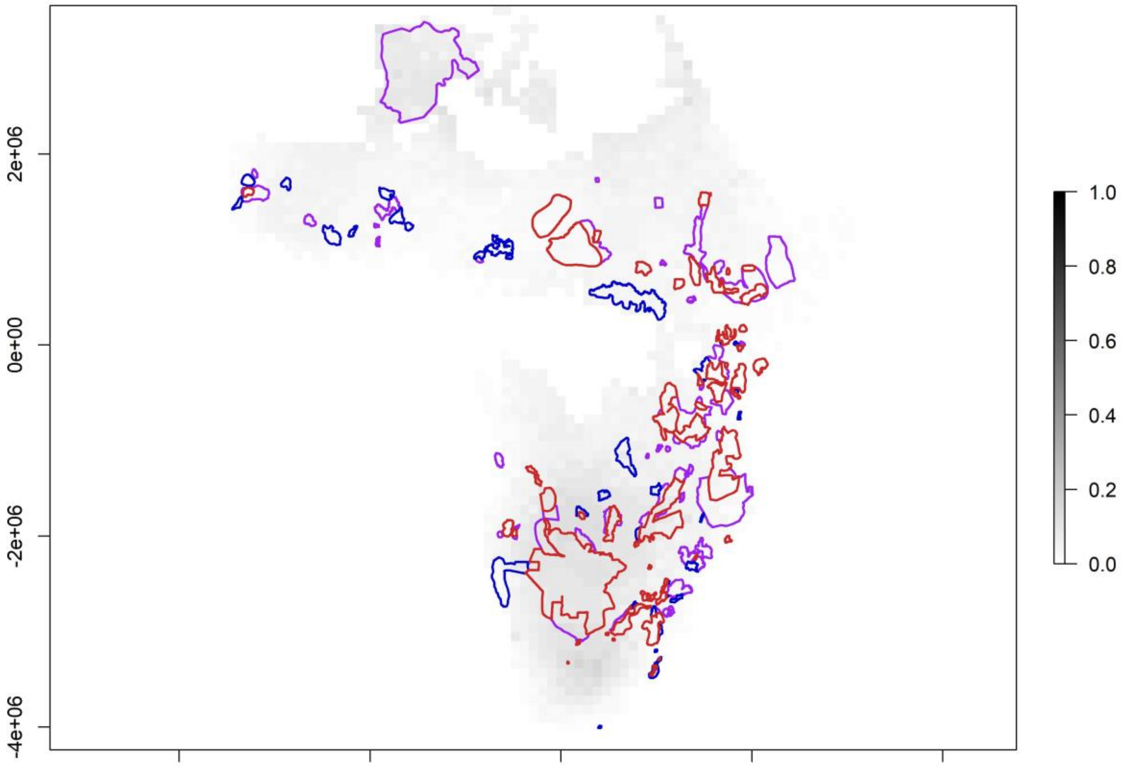
2.2.6 Demographic scenario 2 RCP 4.5



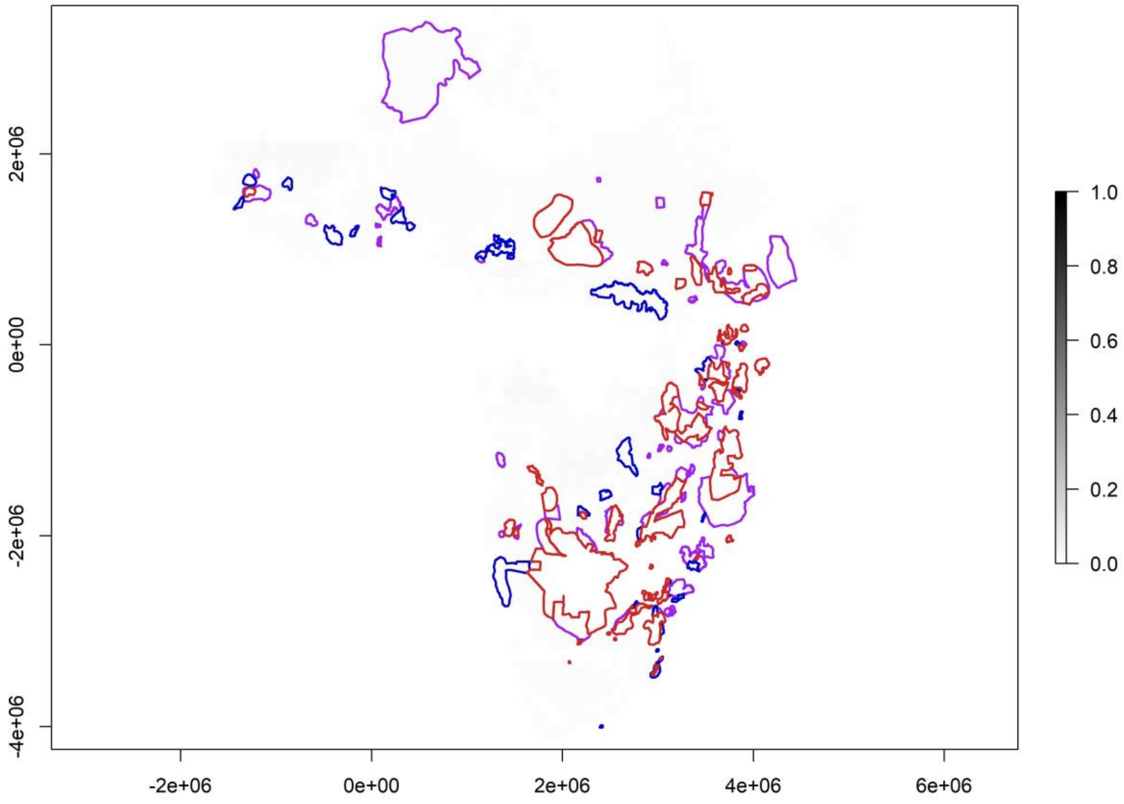
2.2.7 Demographic scenario 2 RCP 6.0



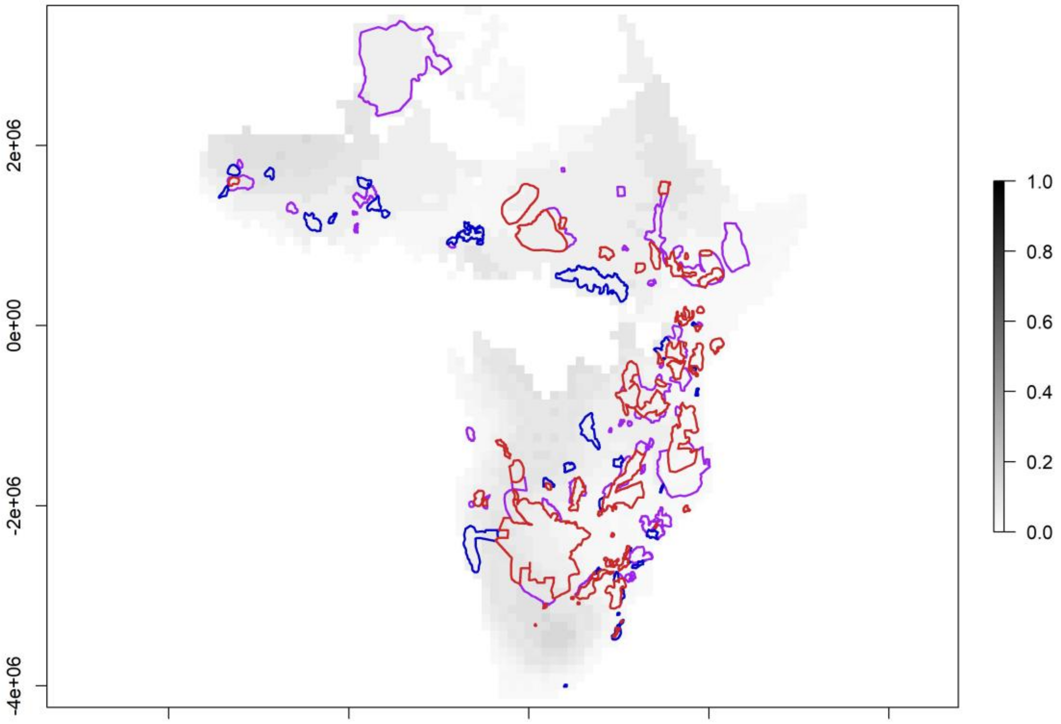
2.2.8 Demographic scenario 2 RCP 8.5



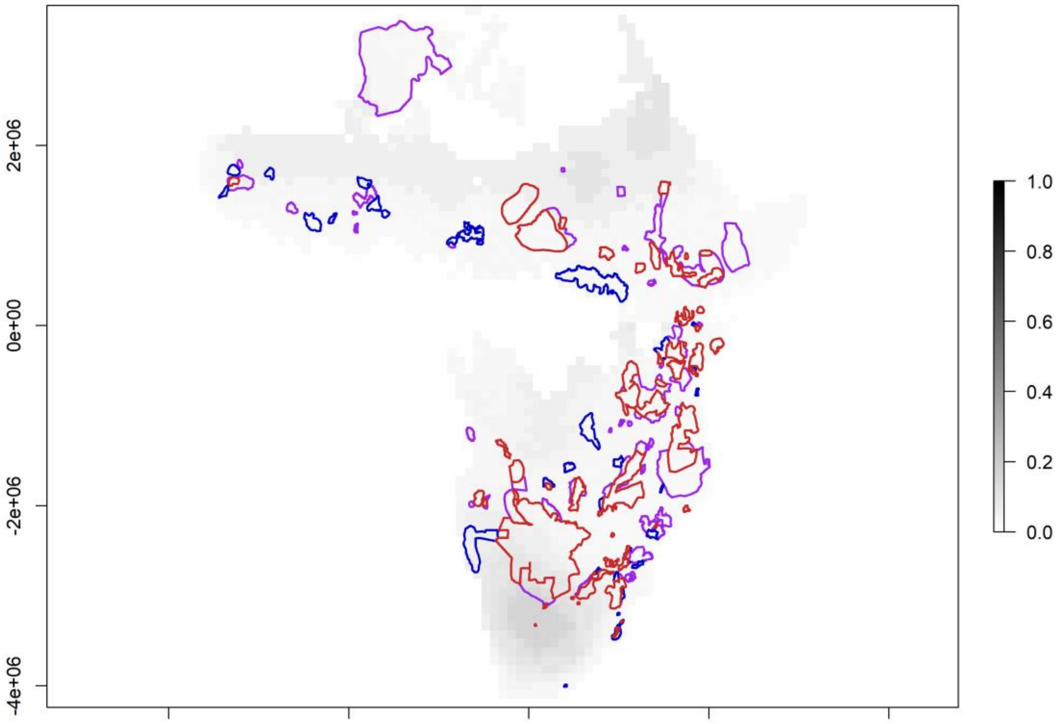
2.2.9 Demographic scenario 3 RCP 2.6



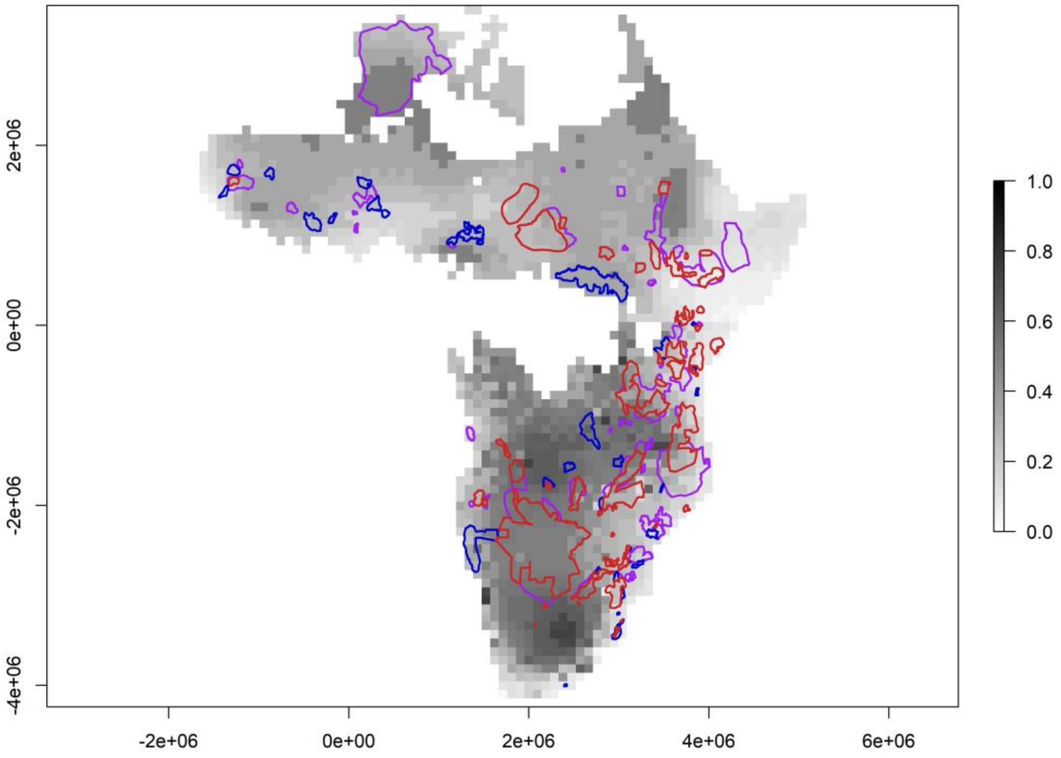
2.2.10 Demographic scenario 3 RCP 4.5



2.2.11 Demographic scenario 3 RCP 6.0



2.2.12 Demographic scenario 3 RCP 8.5



Appendix 2.3 Tables of means and standard deviations of remaining population and extinction risks

2.3.1 Table of means of remaining population

Demographic scenario	RCP	Mean population remaining (%)	Standard deviation (%)
1	2.6	68	6
	4.5	26	8
	6.0	31	11
	8.5	2	4
2	2.6	75	3
	4.5	53	4
	6.0	56	5
	8.5	29	10
3	2.6	64	5
	4.5	27	8
	6.0	33	11
	8.5	3	4

2.3.2 Table of means of extinction risk

Demographic scenario	RCP	Mean extinction risk (%)	Standard deviation
1	2.6	0	0
	4.5	0	0
	6.0	0	0
	8.5	6	4
2	2.6	0	0
	4.5	0	0
	6.0	0	0
	8.5	39	38
3	2.6	0	0
	4.5	5	6
	6.0	3	4
	8.5	36	14

References

Adahl, E., Lundberg, P. and Jonzen, N. 2006. From climate change to population change: the need to consider annual life cycles. *Global Change Biology*. **12**(9), pp.1627–1633.

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