HEAT, HABITAT, AND HABITABILITY:

Mapping the persistence of African wild dogs under environmental change



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DECLARATION

I declare that the work in this thesis is my own. Contributions by coauthors are stated at the start of each empirical chapter. None of the work has been submitted, in whole or in part, for any previous degree application.

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WIDER ACADEMIC CONTRIBUTIONS

Alongside my DPhil research, I have contributed to a number of collaborative papers and conservation assessments that fall outside the direct remit of this thesis, as detailed below.

PAPERS

1. Woodroffe, R., Fuller, A., Briner, J., Chaitezvi, C., Davies Mostert, H., du Plessis, C., Groom, R.J., Jumbam, K., Kapondo, P.K., **Linden, J.F.**, Rabaiotti, D., Roug, A., Watermeyer, J., Meyer, L. (2026) Refining the use of implanted biologgers in an endangered species. Journal of Applied Animal Ethics Research. doi.org/10.1163/25889567-bja10072

   Due to its relevance to Chapter 4 of this thesis, a copy of this manuscript is included in Appendix E (Page 153)

2. Madsen, E.K., Eckersley, L., **Linden, J.F.**, Hare, D., Lai, S., Macdonald, D.W., Kimaili, D., Kulunge, S., Mutinhuma, Y., Petracca, L., Rono, B.J., Sibanda, L., Sillero-Zubiri, C., Tacey, J., and Broekhuis, F. (2026) What's in a name? Not all mesopredators are mesocarnivores. Ecology and Evolution, 15. doi.org/10.1002/ece3.72768D
3. Willis Key, J., Nurbandi, W., González-Nava, B., Gomez, J., Alvarenga, G., Castera, F., Flottes de Pouzols, A., Lemaire, M., **Linden, J.**, Madsen, E.K., Coad, L., Hinsley, A., and Milner-Gulland, E.J. (2025) Gender dynamics of tropical wild meat systems: A systematic map of women's roles and influence. People and Nature. doi.org/10.1002/pan3.70133
4. Woodroffe, R.; Abrahms, B.; English, H.; Jumbam, K.; **Linden, J.**; Ngatia, D.; Rabaiotti, D.; McNutt, J.W. (2023) African wild dogs are hot and hungry: Response to Creel et al (2023). Biological Conservation, 284. doi.org/10.1016/j.biocon.2023.110198
5. Ngatia, D., Goheen, J., Fuller, A., Groom, R., Jumbam, K., Killian, H., **Linden, J.F.**, Meyer, L., Rabaiotti., R, Watermeyer, J., Woodroffe, R. (*in review*) Behavioral plasticity to rising temperatures across the range of African wild dogs: tests of the Heat Load Hypothesis and Climate Variability hypotheses. Journal of Zoology.
6. Ngatia, D., Woodroffe, R., Ferguson, A., Ford, A., Lamb, C., **Linden, J.F.**, Lentaam, S., Ngatia, S., Goheen, J. (*in review*) Rising temperatures increase risk of pathogen exposure for a globally endangered carnivore. Ecosphere.
7. Gomez, C.R., Machette-Downes, H., **Linden, J.F.**, Saror, C., Costa-Alvarenga, G., Pavey, T., Murray-Ramcharan, T., Steward, E., Burnham, D., Dickman, A. (*in review*) WildMAPS: A Global repository and visualisation tool for habitat suitability predictions. Ecological Informatics.

8. Woodroffe, R., **Linden, J.F.**, *et al* (*in prep*) Where the wild dogs are: measuring progress towards conservation visions in Africa

CONSERVATION ASSESSMENTS

1. Woodroffe, R., McNutt, T., Groom, R. & Ngatia, D. (2025). *Lycaon pictus*. The IUCN Red List of Threatened Species 2025. iucnredlist.org/fr/species/12436/221299510

   Contribution: edits and finalisation of the species' range map

2. IUCN/SSC (2024) Revised Regional Conservation Strategy for Cheetah and African Wild Dogs in Western, Central and Northern Africa. IUCN/SSC, Gland, Switzerland & Africa Range-Wide Cheetah Conservation Initiative. cheetahconservationinitiative.com/regional-strategies

   Contribution: participation at the workshop at which this strategy was designed; production of species range maps

3. Woodroffe, R., **Linden, J.F.**, *et al* (*in prep*) *Lycaon pictus* (Green Status assessment). The IUCN Red List of Threatened Species.

THESIS ABSTRACT

Heat, Habitat, and Habitability: mapping the persistence of African wild dogs under environmental change – **Jennifer F. Linden**

Human-driven environmental change is reshaping biodiversity through the combined effects of climate and land-use change, with consequences operating across spatial scales. In Africa, rising temperatures, continued land conversion, and expanding human populations are expected to intensify these pressures, placing particular strain on large carnivores with extensive space requirements and low population densities. The endangered African wild dog (*Lycaon pictus*) provides a valuable case study, as its persistence is likely shaped by both landscape-level habitat availability and sensitivity to environmental heat.

This thesis examines how heat and habitat jointly influence wild dog population persistence, from current habitat suitability to future demographic vulnerability. First, I use habitat suitability modelling (HSM) to assess whether suitable habitat may currently exist beyond the species' depleted known distribution. I estimate that approximately a quarter of its historical range may remain suitable, including understudied regions and potential reintroduction sites, which could be prioritised for local validation and targeted surveys. I then apply this framework to explore how projected climate and land-use change may alter habitat suitability across the continent. Results indicate likely declines across much of the current range, particularly under high-emissions and land-use scenarios, although some localised increases are projected at range margins. Next, I investigate the physiological basis of thermal constraints, finding that body temperature is highly labile and strongly influenced by both activity and air temperature. Elevated environmental temperatures appear to constrain behaviour, with reduced activity likely reflecting thermoregulatory responses that may carry consequences for fitness and reproductive success. Finally, I combine HSM projections with individual-based models incorporating temperature-dependent demographic processes. These results highlight strong contextual variation in climate sensitivity, with pronounced declines predicted in key strongholds such as the Kavango-Zambezi landscape, while populations in parts of East Africa may be comparatively less impacted.

Overall, my findings suggest that environmental change is likely to drive widespread but spatially variable declines in African wild dogs. Effective conservation will therefore require coordinated, multi-scale strategies that combine range-wide prioritisation of vulnerable and resilient populations with targeted local interventions to mitigate site-specific threats.

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CHAPTER 1 | INTRODUCTION



1.1. ENVIRONMENTAL CHANGE

Environmental change is driving rapid and accelerating biodiversity loss across the globe, with more species now threatened with extinction than ever recorded in modern times (IPBES, 2019). This large-scale disruption of the Earth's natural systems is primarily driven by human activities, which transform landscapes through land-use change, degrade seascapes through marine exploitation, and alter the atmosphere through climate change (IPBES, 2019).

Land-use change is one of the most pervasive drivers of contemporary environmental change. Over the last six decades it is estimated to have affected approximately one third of global land area (Winkler et al., 2021), including the conversion of natural habitats to agriculture and urban settlements in line with human population growth and economic development. In addition to reducing the total area of natural habitat available for species, associated habitat fragmentation also reduces connectivity and alters population-level processes. Land-use change is projected to continue throughout the 21st century, with ongoing implications for terrestrial ecosystems and biodiversity (Shukla et al., 2019). Climate change represents another major driver of environmental change. Global mean temperatures have already increased by approximately 1.1°C above pre-industrial levels (IPCC, 2023), altering climatic conditions across terrestrial ecosystems through shifts in temperature regimes, precipitation patterns, and the frequency and intensity of extreme weather events. These changes are expected to intensify over the coming decades, with widespread implications for ecological systems (IPCC, 2022).

Importantly, climate and land-use change do not operate independently. Instead, they can have interacting and reinforcing effects, whereby changes in one can induce changes in the other. Shifts in climatic conditions can influence land cover through natural processes such as desertification and vegetation change, as well as through human responses, for example as agricultural activity shifts to track climatic suitability. Land use can in turn influence climate through processes such as carbon sequestration, as well as greenhouse gas emissions associated with urbanisation and intensive agriculture (Barati et al., 2023).

1.1.1. Impacts of environmental change on biodiversity

The effects of environmental change on biodiversity ultimately depend on how species respond to altered environmental conditions. Climate change vulnerability is commonly conceptualised through three key components: exposure, sensitivity, and adaptive capacity (Foden et al., 2018). These components describe the degree of environmental change occurring within a species' range (exposure), the capability of the species to tolerate variation (sensitivity), and the ability of the

species to mitigate impacts by adjusting its behaviour, physiology, or distribution (adaptive capacity). Species responses to environmental change can broadly be grouped into three categories: changes in time, changes in space, and changes in self (Bellard et al., 2012). These changes include shifts in the timing of life-history events, geographic range shifts, and phenotypic plasticity or evolutionary adaptation. Such responses can mitigate the impacts of environmental change by allowing species to track suitable conditions or adjust to altered environments.

However, these responses are often constrained. Geographical range shifts, for example, may be limited by the availability of suitable habitat, or by barriers created by anthropogenic landscape modification. As a result, geographical range contractions have been observed among species in polar regions (Laidre et al., 2018), at high altitudes (Beever et al., 2011), and in areas surrounded by extensive habitat loss (Pomara et al., 2014). Similarly, behavioural responses to increased temperatures can reduce foraging success (Cunningham et al., 2015), with downstream consequences for fitness and offspring survival (van de Ven et al., 2020). Beyond affecting individual species, such responses can also propagate through ecological systems by altering trophic interactions, for example if shifts in breeding phenology lead to mismatches with the availability of key resources (Miller-Rushing et al., 2010).

Environmental change therefore influences species' persistence across multiple scales, from direct physiological constraints such as thermoregulation, to broader limitations on habitat availability. These pressures can generate demographic consequences that ultimately shape populations and wider ecosystems. Consequently, biodiversity conservation increasingly requires anticipating and mitigating future change, rather than addressing only current threats.

1.1.2. Environmental change in Africa

The continent of Africa is projected to experience more rapid and extreme climate change than the global average, with increased annual heatwave frequency already detected across the continent (Engdaw et al., 2021), and associated impacts on both people and biodiversity increasingly observed (IPCC, 2022). Across much of sub-Saharan Africa, mean temperatures, and the number of days experiencing extreme heat, are projected to increase, while mean precipitation is expected to decline and droughts to become more frequent (IPCC, 2022). In parallel, rapid land-use change across the continent could threaten global carbon dynamics (Sakala and Santos, 2025), with marked declines in forest cover over the last two decades largely attributed to conversion to cropland (Masolele et al., 2024). Continued expansion of cropland and urban areas, alongside further declines in forest cover, are forecast across the continent (Yahaya

et al., 2024). Meanwhile, the human population of sub-Saharan Africa is projected to increase by 79% over the coming three decades (United Nations, 2024), placing additional pressure on rangelands to provide sufficient food (Holechek et al., 2017).

This combination of anthropogenic pressures has contributed to substantial biodiversity loss across Africa in recent decades, with increasing extinction risk documented across assessed species (Brooks et al., 2016). Africa harbours globally important biodiversity, including diverse ecosystems, high levels of endemism, and the world's most intact assemblages of large terrestrial vertebrates (Ripple et al., 2015, Myers et al., 2000). With environmental change projected to intensify under continued human population growth, land-use expansion, and climate warming, Africa's unique biodiversity faces growing threats (Archer et al., 2018).

1.1.3. The vulnerability of large carnivores

Africa hosts a significant proportion of the world's remaining large carnivores, including some of the few regions where intact large carnivore guilds still coexist in sympatry (Ripple et al., 2014). Large carnivores play important and far-reaching roles in ecological communities, often acting as keystone species that regulate herbivore populations and behaviour, with cascading consequences for vegetation dynamics and ecosystem functioning (Estes et al., 2011). In addition, large carnivores can suppress or regulate populations of smaller predators, shaping community structure through competitive interactions with mesopredators (Ritchie and Johnson, 2009).

Despite their ecological importance, large carnivores are among the species most vulnerable to anthropogenic environmental change. Large carnivore species have experienced widespread declines in both abundance and geographical range over recent decades (Wolf and Ripple, 2017), largely driven by habitat loss and fragmentation, depletion of prey populations, and direct human persecution (Ripple et al., 2014). Such pressures disproportionately affect large carnivores because of their characteristic life-history traits, including large home ranges, low population densities, slow reproductive rates, and high energetic requirements. These traits limit their ability to persist in human-dominated landscapes, as large spatial requirements and energetic demands increase dependence on extensive, well-connected habitats and abundant prey populations (Ripple et al., 2014, Woodroffe and Ginsberg, 1998). Long generation times add susceptibility to change as they limit the possibility of rapid evolutionary adaptation, making large carnivores likely to be reliant on phenotypic plasticity to cope with environmental change (Hetem et al., 2014).

As a result, large carnivores are widely recognised as global conservation priorities, both because of their heightened extinction risk and their disproportionate ecological importance within

ecosystems (Wolf and Ripple, 2017, Ripple et al., 2014). Their large spatial requirements also mean they can act as umbrella species, with conservation efforts benefiting a broad suite of co-occurring taxa (Sergio et al., 2006). Understanding how environmental change influences their persistence is therefore critical not only for conserving these species themselves, but also for maintaining the ecological processes and trophic interactions they support.

1.2.THE AFRICAN WILD DOG (*LYCAON PICTUS*)

The African wild dog (*Lycaon pictus*, hereafter 'wild dog'), is a large carnivore species endemic to continental Africa. As the only extant member of its genus, the wild dog has a distinct evolutionary lineage thought to diverge from other canids approximately 1.7 million years ago (Chavez et al., 2019). Wild dogs are distinguished by their distinctive coat colouration, made up of irregular combinations of black, brown and white marks. Each wild dog's pelage is unique, allowing for individual identification (Maddock and Mills, 1994), and permitting long-term study that has generated extensive insight into their ecology and demography.

The wild dog is a highly social, cooperatively breeding species, with packs typically comprising a breeding dominant pair and a number of non-breeding subordinate individuals. Pack sizes generally range up to 30 adults, with each pack considered as a breeding unit (Woodroffe et al., 2025, Creel and Creel, 2002). Litters are born in dens, and are initially suckled by the mother, after which they are provisioned by regurgitation from other pack members. This period, termed the 'denning period', typically lasts for three months, throughout which at least one pack member typically remains at the den to guard the pups whilst the other pack members hunt (Malcolm and Marten, 1982). The denning period is recognised as being an energetically costly period for wild dogs (Woodroffe et al., 2017), with pack members travelling greater distances both searching for prey and returning to the den, and sharing food with both pups and babysitters (Malcolm and Marten, 1982). Breeding typically takes place seasonally every 12 months at latitudes above 2°, coinciding with the coolest time of the year (McNutt et al., 2019). At latitudes below 2°, breeding is aseasonal, and at one well-studied site occurred on average every 11 months (Woodroffe et al., 2017).

Wild dog packs hunt collectively, with captured prey shared amongst members. Hunting typically takes place following a bimodal pattern around dawn and dusk, with individuals otherwise largely inactive during the day (Estes and Goddard, 1967). Wild dogs are adapted for energetically-demanding cursorial hunting, with long slender limbs, and four digits on each foot (Girman et al., 1993). Their hunting strategy varies across habitat types – in open habitat they are known for long-

distance chases (Estes and Goddard, 1967), compared to short chases carried out by individuals in more closed vegetation (Hubel et al., 2016a). Diet composition similarly varies across sites, with impala (*Aepyceros melampus*) as the most important prey species across many, but with notable local specialism on considerably smaller species such as Kirk's dikdiks (*Madoqua kirkii*) (Woodroffe et al., 2007b) and larger species such as Burchell's zebra (Malcolm and Van Lawick, 1975). Other important prey species include comparatively larger greater kudu (*Tragelaphus strepsiceros*) and blue wildebeest (*Connochaetes taurinus*) (Fanshawe and Fitzgibbon, 1993, Mills and Gorman, 1997).

Wild dog packs occupy vast home ranges, averaging approximately 500km^2 (Woodroffe, 2011, Pomilia et al., 2015) but recorded as reaching over 2,000km^2 (Fuller et al., 1992). Across these extensive spaces, their population densities are contrastingly low, with an average of two individuals per 100km^2 (Mills and Gorman, 1997, Parsais et al., 2025) and sometimes much lower (Woodroffe et al., *in review*). New wild dog packs are formed via dispersal, usually with groups of same-sex siblings leaving their natal pack (McNutt, 1996) and at times travelling hundreds of kilometres in search of an opposite-sex dispersal group (Davies-Mostert et al., 2012, Sandoval-Serés et al., 2022). Dispersal is an important part of wild dog demography, and is essential for maintaining gene flow both within and between populations (Leigh et al., 2012). Wild dog movement and habitat selection notably differ between dispersal groups and resident packs, with dispersal often bringing individuals in closer proximity to humans (Cozzi et al., 2020, O'Neill et al., 2020).

Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) are wild dogs' dominant competitors, with lions as a significant cause of wild dog mortality (Creel and Creel, 1996), and hyaenas a common kleptoparasite of wild dog kills (Gorman et al., 1998). Both competitor species are hence thought to have a significant influence on both wild dog space use and activity (Jackson et al., 2014, Hayward and Slotow, 2009, van der Meer et al., 2013b, Sandoval-Serés et al., 2025). Wild dogs, in turn, influence the abundance of prey populations (Ford et al., 2015), with observed consequences for the distribution of tree species in savannas (Ford et al., 2014).

1.2.1. Current wild dog status

Wild dogs are globally endangered, with a population in global decline (Woodroffe et al., 2025). There are now estimated to be fewer than 700 packs remaining, each of which usually represents a single breeding pair (Woodroffe et al., 2025). Wild dogs were historically distributed across the

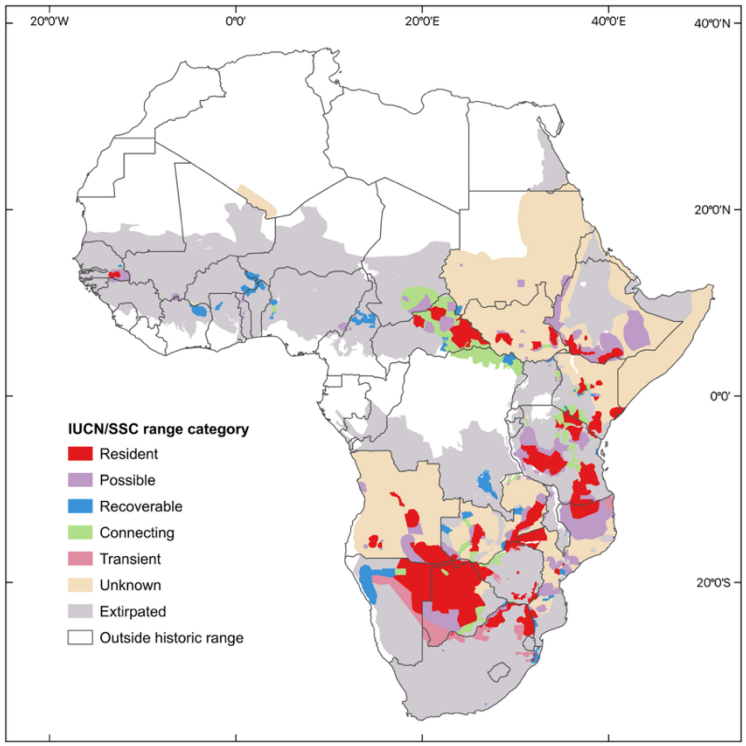


Figure 1.1. African wild dog historical range and current range categories, as defined and mapped by species experts participating in regional IUCN/SSC workshops (Woodroffe et al., 2025)

majority of sub-Saharan Africa, although avoiding the dense rainforest of the Congo basin (Figure 1.1). Today, their known resident range makes up just 8.5% of this historical range, and is fragmented across Southern, East, Central, and West Africa (Figure 1.1 – category '*resident'*). Notably, only a single wild dog population is known to remain in West Africa, found in Senegal's Niokolo-Koba National Park (Figure 1.1).

As a species known to require vast areas, both in which to live and through which to disperse, understanding and improving wild dog status requires transboundary efforts. To this end, the International Union for Conservation of Nature's (IUCN) Species Survival Commission (SSC) Canid Specialist Group (canids.org) hosts recurring workshops to chart wild dog status at both regional and national levels (IUCN/SSC, 2024, IUCN/SSC, *in prep-a,* IUCN/SSC, 2015). These workshops include extensive mapping of the species' range, recognising five categories in addition to resident or extirpated status (Figure 1.1) The resulting maps indicate that wild dog status remains uncertain in approximately 33% of historical range (Figure 1.1 – categories '*possible'* and '*unknown'*). This uncertain range represents a substantial portion of the continent, comprising near entire countries in some instances, such as Sudan and Somalia (Figure 1.1).

A number of successful reintroductions of wild dogs to former range have been carried out, and a further 1.7% of historical range has been identified as potentially suitable for further recovery efforts (Figure 1.1 – category '*recoverable*'). Due to extensive habitat loss in South Africa, and the

remaining natural habitat within the country predominantly consisting of small, fenced reserves, a managed metapopulation of wild dogs has been created via a series of reintroductions and translocations (Davies-Mostert et al., 2015). This population has seen successful population growth, and provided founder individuals for international reintroductions to Malawi (African Parks, 2023), Mozambique (Bouley et al., 2021) and Zambia (Zambian Carnivore Program, 2022).

Given the wild dog's depleted status across its once immense range, large-scale efforts will be essential for the species' restoration. These efforts could include further reintroductions to areas within recoverable range (Figure 1.1), which will require thorough local assessment of sites' suitability. Perhaps more pressing is the need to thoroughly understand the species' status within its uncertain range (Figure 1.1). Any remnant wild dog populations living undetected in these regions could add significantly to the species' known global population and range extent, and hence be of vital importance to its conservation. On both counts, quantitative evaluation of sites for either potential reintroduction, or surveying to determine presence, would be invaluable to permit spatial prioritisation across these vast landscapes.

1.2.2. Threats to wild dogs

The extirpation of wild dogs from much of their historical range has come alongside large-scale habitat destruction across the African continent, which has vastly reduced the space available to this wide-ranging and low-density species. Wild dogs do not persist in strongly human-dominated environments, instead occupying habitat characterised by natural land cover (O'Neill et al., 2020, Jackson et al., 2016, Pretorius et al., 2019) and low human population density (Woodroffe, 2000, Lindsey et al., 2004, van der Meer et al., 2013a). Wild dogs' large space requirements put populations at risk even within remaining intact habitat, as those closer to the edges are exposed to further anthropogenic threats (Woodroffe and Ginsberg, 1998). Ongoing habitat loss hence poses a dual threat to the species – both directly decreasing space and indirectly increasing risk.

Anthropogenic threats to wild dogs are numerous and vary in relative intensity across local contexts (Woodroffe et al., 2007a). Wild dogs commonly come into conflict with humans, due to actual or perceived instances of livestock depredation, which can result in retaliatory killing (Fraser-Celin et al., 2017, Gusset et al., 2009, Rasmussen, 1999). Infectious disease poses a substantial threat, which has led to the local extinction of past populations (Mutinda et al., 2017, Gascoyne et al., 1993, Ngatia et al., *in review-a*), and which can stem from spillover from domestic dogs (Woodroffe et al., 2012). Hunting of wild ungulates threatens wild dogs directly, when individuals are subject to bycatch in wire snares (Becker et al., 2013), and indirectly, by contributing

toward prey depletion (Reyes de Merkle et al., 2024). This combination of threats results in significant human-induced mortality for wild dogs (Woodroffe et al., 2007a), which is heightened outside of formally protected areas. Dispersal is especially dangerous, with elevated mortality rates correlating with traversing human-dominated landscapes in search of new pack-mates (Cozzi et al., 2020, Woodroffe et al., 2020).

1.2.3. Wild dogs under environmental change

With continued human population growth, land-use change, and climate change projected across continental Africa, wild dogs are likely to experience increasing environmental pressures in the coming decades. The magnitude of these changes will depend on future greenhouse gas emissions and socioeconomic development pathways, but rising air temperatures are projected across the species' current resident range under all possible scenarios (Figure 1.2). In parallel, land-cover change associated with agricultural expansion and urbanisation is expected to alter the availability and distribution of natural habitats across large areas of the continent (Figure 1.2). Together, these climatic and land-use changes have the potential to reshape the spatial distribution of suitable environments for wild dogs, further constraining populations that are already fragmented and depleted. Understanding how these drivers of environmental change will influence the distribution and availability of suitable habitat across the species' range is therefore critical for anticipating future conservation challenges for this endangered carnivore.

1.2.3.1. Wild dogs under climate change

Beyond its interaction with habitat availability, climate change may also directly threaten African wild dogs through potential thermal constraints on the species. Wild dogs are cursorial predators that rely on energetically demanding pursuit hunting, and have been described as operating under a delicate energetic balance supported by cooperative hunting strategies (Gorman et al., 1998, Hubel et al., 2016a). The high metabolic demands of sustained running generate substantial heat, the dissipation of which becomes increasingly challenging under elevated environmental temperatures (Fuller et al., 2026). As a result, wild dogs are thought to time their hunting activity to coincide with cooler periods of the day, typically around dawn and dusk, producing their characteristic crepuscular activity patterns (Hubel et al., 2016b). Consistent with this hypothesis, wild dog activity has been shown to decline with increasing air temperature (Pomilia et al., 2015, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017, Rafiq et al., 2023). Similarly, the energetically demanding denning period typically occurs during the coolest time of year across the species' seasonal range (McNutt et al., 2019), suggesting that reproduction may be timed to minimise thermal stress.

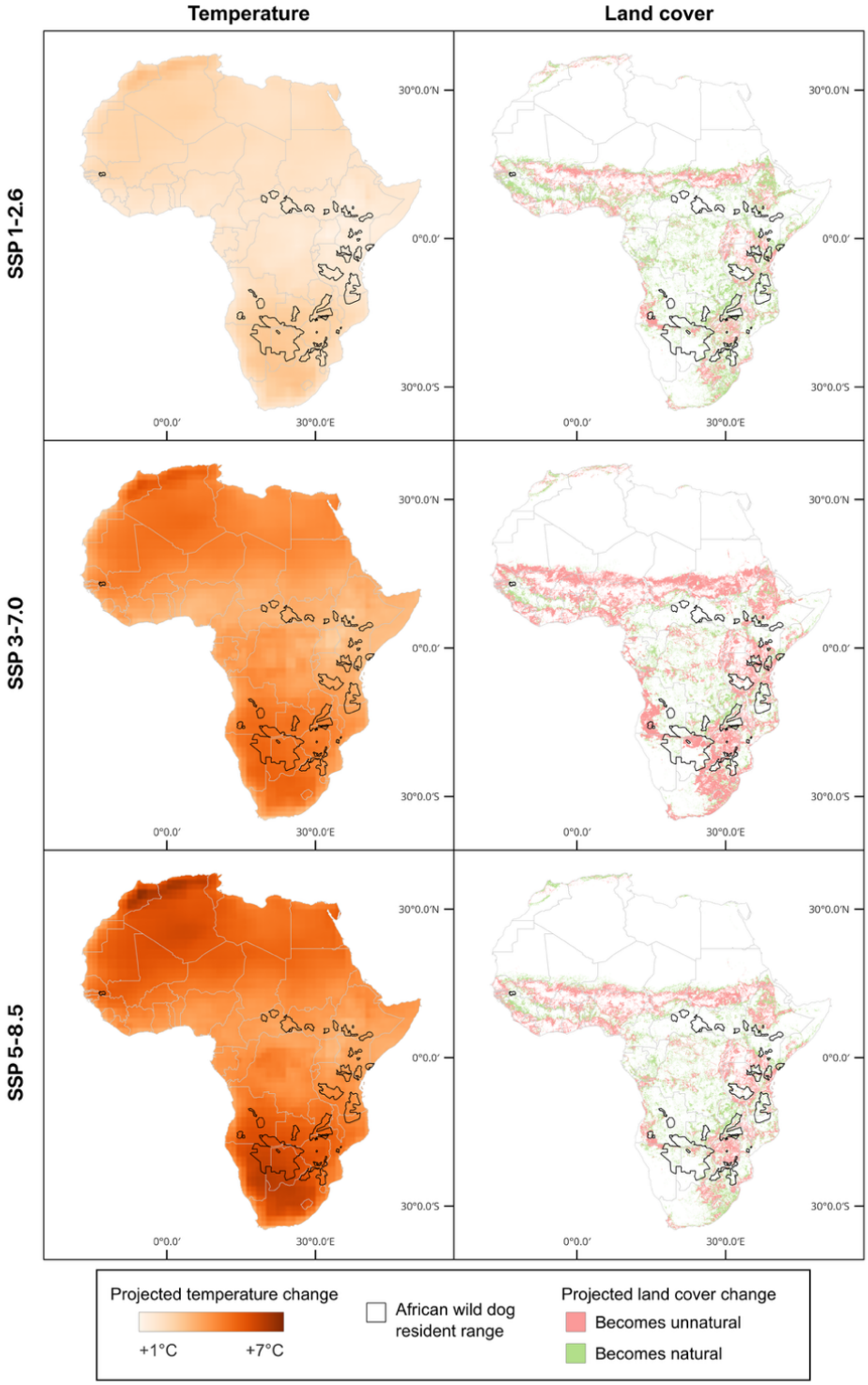


Figure 1.2. Projected changes in temperature and land cover across continental Africa under each of three available Shared Socioeconomic Pathways (SSPs). Temperature data are from CHELSA projections (Karger et al., 2017), land cover data from Chen et al. (2022). 'Becomes 'natural' and 'becomes unnatural' represent pixels that are projected to change from cropland or urban land cover to non-cropland or urban land cover, and vice versa. Current African wild dog resident range is outlined in black.

These behavioural patterns raise concern that increasing environmental temperatures may compromise wild dog hunting success and reproductive output under climate change. Indeed, higher ambient temperatures have been associated with reduced reproductive success (Woodroffe et al., 2017, Abrahms et al., 2022) and increased mortality in wild dog populations (Rabaiotti et al., 2021). However, the mechanistic basis of these demographic relationships remains poorly understood, and their interpretation has been subject to debate (Woodroffe et al., 2023, Creel et al., 2023).

Alternative hypotheses suggest that warmer conditions may benefit wild dogs by imposing greater thermal constraints on larger prey species and thereby improving hunting success (Creel et al., 2016). Although at one site higher kill rates were observed at elevated air temperatures, this was not accompanied by increased food intake and therefore did not confer an energetic advantage (Creel et al., 2016). It has also been argued that the persistence of wild dogs at relatively high population densities in some hot environments suggests that environmental temperature is not strongly limiting for the species (Creel et al., 2023). However, species operating close to their thermal limits may be particularly vulnerable to further warming (Hetem et al., 2014), and geographically widespread taxa may exhibit population-level variation in thermal tolerance (Atkins and Travis, 2010, DeMarche et al., 2019).

Resolving these contrasting perspectives on the role of climate in shaping wild dog ecology is critical for understanding their vulnerability under future environmental change. At present, this limitation is rooted in a lack of mechanistic understanding of wild dog thermophysiology, which remains poorly studied. Improving this understanding will be essential for disentangling the processes linking environmental temperature to behaviour, demography, and ultimately population persistence.

1.3.THESIS OVERVIEW

In this thesis, I aim to understand how environmental heat and habitat availability shape the persistence of the African wild dog under current and future environmental change. Specifically, I address the following knowledge gaps:

1. Uncertainty in the current distribution of suitable habitat across the species' historical range, as identified by expert-designated mapping processes (Chapter 2)
2. Limited understanding of how projected climate and land-use change will jointly influence future habitat suitability across the African continent (Chapter 3)
3. A lack of mechanistic understanding of the physiological vulnerability of wild dogs to environmental heat, particularly the factors influencing thermoregulation (Chapter 4)
4. Limited understanding of how differing observed relationships between environmental heat and demography translate into population-level impacts across space (Chapter 5)
5. A lack of combined forecasts of combined effects of environmental change across the species' vast historical range (Chapter 5)

Ultimately, this thesis aims to provide insights to inform conservation strategies for African wild dogs under environmental change, both at local and range-wide scales.

1.3.1. Thesis structure

Following this introductory chapter (Chapter 1), this thesis comprises five further chapters, four of which present empirical analyses (Chapters 2 to 5). Each of these chapters is formatted as an independent manuscript with a number of co-authors, and has been submitted or prepared for publication in a peer-reviewed scientific journal. In reflection of the collaborative nature of this work, I used the third person 'we' throughout these chapters. In the final chapter (Chapter 6) I synthesise the findings of these analyses, discuss the implications for conservation, and outline future research directions. Supplementary materials for each empirical chapter can be found in Appendices A-D. Below I provide an outline of each empirical chapter.

Chapter 2 – '*Modelling habitat suitability beyond known range to guide African wild dog recovery*' **Currently under review at Diversity and Distributions**

In this chapter, I evaluate habitat suitability for the African wild dog across its historical range, extending beyond the species' currently known resident distribution. I use points sampled from expert-derived range maps to build multi-scale Boosted Regression Tree models. The models incorporate both anthropogenic and ecological predictor variables, including climate, land cover,

protected area status, and human and livestock density, and I assess the relative importance of each variable in shaping predicted suitability. Focusing on the results within areas classified by experts as uncertain or recoverable, I aim to inform survey prioritisation and reintroduction planning, thereby improving understanding of the species' current and potential distribution.

Chapter 3 – '*Shifting habitat suitability for African wild dogs under future climate and land use change'*

Here, I apply the modelling framework developed in Chapter 2 to assess how habitat suitability for African wild dogs may be altered under projected environmental change across the continent. I project changes in habitat suitability under three emissions and socioeconomic scenarios, incorporating corresponding changes in temperature, precipitation, land cover, and human population density. I assess the relative roles of each predictor variable in driving forecast changes in suitability and identify areas of current resident and proposed recoverable range most at risk of future habitat degradation, whilst assessing the potential for spatial shifts in suitable habitat.

Chapter 4 – '*A Recipe for Hot Dogs: Physiological vulnerability to increasing air temperatures in a coursing predator*

In this chapter, I present the first dataset of body temperature from free-living African wild dogs. Collected from fourteen individuals across four sites in southern Africa over nearly 5,000 animal-days, these data provide novel insight into thermal variability in this species. Using concurrent activity data derived from accelerometer collars, I examine the relative influences of energy expenditure and environmental heat load on body temperature. This approach allows investigation of the mechanisms by which wild dogs may be thermally constrained, and how these constraints give rise to thermoregulatory behaviours.

Chapter 5 – '*Mapping risk and resilience: a multi-method modelling approach to forecasting vulnerability of an endangered carnivore'*

Finally, I adapt a published individual-based model to generate spatially explicit simulations of African wild dog population persistence under climate change across the continent. I parameterise the model according to two demographic scenarios, based on long-term life-history data from study populations in Kenya and Botswana. I then combine these outputs with the habitat suitability projections developed in Chapter 3, identifying areas of concordance and divergence between environmental and demographic predictions. Using this combined approach, I highlight spatial priorities for targeted conservation, with the aim of informing proactive strategies to enhance the species' long-term persistence under climate change.



CHAPTER 2 | Modelling habitat suitability beyond known range to guide African wild dog recovery

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Under review at *Diversity and Distributions*

AUTHOR CONTRIBUTIONS

JFL, DR, and RW conceived the study and developed the methodology. JFL curated the data, performed the analyses, and wrote the manuscript. DR and RW provided supervision and critically reviewed and edited the manuscript.

Modelling habitat suitability beyond known range to guide African wild dog recovery

ABSTRACT

Aim: To evaluate habitat suitability for the endangered African wild dog across its historical range, beyond today's known resident range of just 8.5%. Focussing on the 35% of historical range classified by experts as uncertain or potentially recoverable, we aim to guide survey prioritisation and reintroduction planning.

Location: African wild dog historical range (Sub-Saharan Africa, excluding the Congo Basin)

Methods: We used points sampled from expert-designated range maps to build multi-scale Boosted Regression Tree models to evaluate the distribution of suitable habitat across historical range. We considered anthropogenic and ecological variables, comprising climate, land cover, protected area status, human and livestock density. This approach builds directly on expert-derived range knowledge to provide a reproducible, data-efficient framework for other species of conservation concern, reducing reliance on extensive occurrence data.

Results: Our predictions indicate that up to 24.6% of the historical range could remain suitable for the species today, including 62.8% of expert-designated possible range, 25.8% of unknown range, and 49.8% of recoverable range. Model predictions identified extensive suitable habitat within historically occupied but under-studied regions, particularly in Angola, Ethiopia, Mozambique, and Somalia. Protected area status, rainfall, and human density emerged as the most important predictors, corroborating findings from several smaller-scale studies on drivers of wild dog habitat suitability.

Main conclusions: Knowledge of species' distributions is essential for effective conservation planning, yet comprehensive assessments are often limited for rare or elusive species. This study provides a quantitative next step from expert range mapping, helping to translate expert knowledge into actionable conservation tools. While not a realised distribution, our results can guide targeted local assessments, prioritising survey and reintroduction efforts. Populations discovered or re-established through such actions could markedly improve the species' depleted range and conservation status.

KEYWORDS

Lycaon pictus, African wild dog, habitat suitability modelling, expert range mapping, survey prioritisation, reintroduction planning

2.1. INTRODUCTION

Knowledge of a species' distribution is fundamental to effective conservation planning, underpinning assessments of formal protection coverage and the implementation of targeted management strategies (Marcer et al., 2013, Richardson and Whittaker, 2010, Syfert et al., 2014). Accurate information on geographic ranges is also critical for evaluating extinction risk; under the IUCN Red List criteria, for instance, a species may be classified as Endangered solely on the basis of a small or declining range (IUCN, 2012). Widespread habitat loss and fragmentation has rendered large, wide-ranging carnivores a particular focus of conservation concern (Sollmann et al., 2011). However, their elusive behaviour and naturally low population densities make them difficult to monitor, complicating efforts to obtain reliable estimates of abundance and distribution (Guisan et al., 2006, Lomba et al., 2010).

The African wild dog (*Lycaon pictus*, hereafter 'wild dog') is a highly social, cooperatively breeding carnivore species, which is classified as endangered by the IUCN Red List (Woodroffe et al., 2025). Once distributed throughout most of Sub-Saharan Africa, the species is now known to persist in just 8.5% of its historical range, with a declining population of fewer than 700 packs, equivalent to 700 breeding pairs (Woodroffe et al., 2025). Key threats to the species, which have driven these declines, include habitat loss, infectious disease, and human-wildlife conflict (Woodroffe and Ginsberg, 1999). Wild dogs are extremely wide-ranging and live at very low densities (Fuller et al., 1992, Creel and Creel, 2002). Home ranges average approximately 500km^2 (Woodroffe, 2011, Pomilia et al., 2015) but can reach over 2,000km^2 (Fuller et al., 1992), whilst population densities average two individuals per 100km^2 (Mills and Gorman, 1997, Parsais et al., 2025).

Distribution maps generated in the course of participatory workshops hosted by the IUCN/SSC Cat and Canid Specialist Groups have indicated that, whilst the species is known to persist in 8.5% of its historical range, its status remains uncertain in approximately 33%; i.e. neither residence nor absence has been confirmed (IUCN/SSC, *in prep-a,* IUCN/SSC, 2024, IUCN/SSC, 2015) (Figure 2.1, Table 2.1 – categories '*possible'* and '*unknown'*). Wild dogs are likely to have been extirpated across much of this uncertain range, but any populations which do remain would be of conservation importance, due to the species' depleted status and declining population (Woodroffe et al., 2025). However, extensive surveying of such vast areas across continental Africa (almost 6,000,000km^2) is infeasible, with respect to both time and cost, particularly as wild dogs are rarely seen even in areas where they persist at relatively high densities, and aerial surveys are unlikely to detect them (Woodroffe et al., 2025). Recent and ongoing political instability in countries with the largest expanses of uncertain wild dog range, such as Somalia and Sudan, adds to these difficulties by

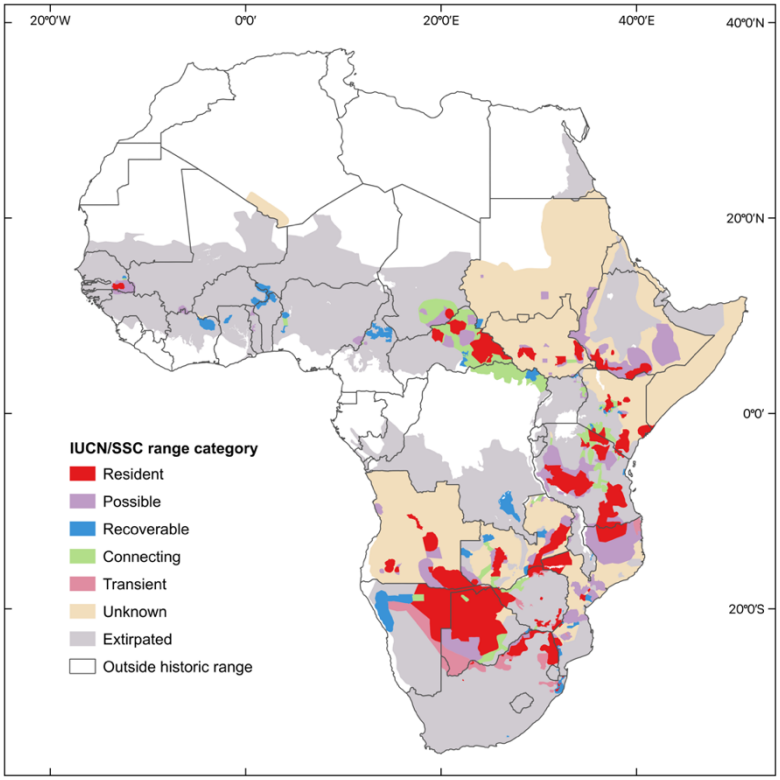


Figure 2.1. African wild dog historical range and current range categories, as defined and mapped by species experts participating in regional IUCN/SSC workshops (Woodroffe et al., 2025). See Table 2.1 for definitions and characteristics of each category.

Table 2. 1. African wild dog current range categories, as defined by the IUCN/SSC range mapping process (Woodroffe et al., 2025).

Range category	Definition	Characteristics
Resident	Wild dogs are known to be resident	Wild dogs regularly detected over several years
		Evidence of breeding (e.g. pups or dens recorded)
		Sightings of complete packs (groups containing members of both sexes, usually more than three animals)
Possible	Wild dogs may be resident, but residency hasn't been confirmed in the last ten years	Usually areas with suitable habitat and prey, but little/no ground-based surveying in recent years
		Some areas with unconfirmed reports, or sparse/irregular sightings
		Includes one-off surveys that have detected presence but not breeding behaviour
Recoverable	Either natural or assisted recovery of wild dogs might be possible	Habitat and prey remain over sufficiently large area
		Recovery feasible within the next tean years if reasonable conservation action were to be taken
Connecting	Wild dogs not thought to be resident, but dispersing animals may move through between occupied areas	Might take the form of 'corridors' of continuous habitat or 'stepping stones' of habitat fragments
		Could also be used to recolonise extirpated range
Transient	Intermittent use by wild dogs, but they are not known to be resident, and there is no connection to resident range	Unlikely to be suitable for use by resident populations through any reasonable form of management
		Likely to be natural habitats that are only marginally suitable, or heavily modified/human impacted areas
		Includes areas which have been used sporadically by dispersing animals
Unknown	Wild dog status is currently unknown	Status cannot be inferred using knowledge of the local status of habitat and prey
Extirpated	Wild dogs have been extirpated	Habitat has been so heavily modified (e.g. by cultivation/urbanisation) or fragmented as to be uninhabitable by resident animals for the foreseeable future

further reducing accessibility for surveys. It would therefore be valuable for wild dog conservation to prioritise survey locations within these range categories. One means by which to achieve this is by quantitatively identifying areas that continue to contain suitable habitat for the species today, and hence are more likely to have retained remnant populations.

In addition to protecting current populations, the reintroduction of wild dogs to former range has been recommended to boost population size and recover areas of former range (Woodroffe et al., 2025, PWF, 2023), with a number of successful reintroductions having taken place in recent years (Bouley et al., 2021, African Parks, 2023, Zambian Carnivore Program, 2022). The IUCN/SSC mapping process additionally identifies areas deemed potentially appropriate for such reintroductions or natural recolonisation. This range currently represents 1.7% of historical range, comprised of 42 sites across the continent (IUCN/SSC, *in prep-a,* IUCN/SSC, 2024, IUCN/SSC, 2015) (Figure 2.1, Table 2.1 – category *'recoverable'*). These sites have mostly not been formally assessed for their reintroduction potential, having instead been identified primarily through local knowledge and recurring inclusion in national and regional workshops, though without subsequent implementation. Empirical guidance on habitat suitability for wild dogs within this *recoverable* range would hence be beneficial to stimulate targeted localised reintroduction assessments.

Habitat Suitability Modelling (HSM, sometimes referred to as Species Distribution Modelling) is a technique used in an array of ecological applications to understand the relationship between species occurrence and the environment (Guisan and Thuiller, 2005), and to consequently predict suitability of habitats for given species across space. HSM can be used to estimate a species' distribution in un-surveyed or unsampled areas, on the assumption that the known distribution of the species reflects its environmental preferences and constraints (Gogol-Prokurat, 2011, Lagos et al., 2020, Marini et al., 2010, Watts et al., 2019). Previous studies have tested such HSM predictions with field surveys, and in some cases successfully confirmed species' occurrence (Fois et al., 2015, Elith et al., 2006, Rebelo and Jones, 2010, Stirling et al., 2016). HSM can also be used to aid in identifying the most appropriate areas for reintroduction (Adhikari et al., 2012, Maes et al., 2019, Miranda et al., 2019, Westwood et al., 2019), with the aim of ensuring that selected sites match the species' environmental preferences, hence increasing the likelihood of persistence of translocated individuals.

Whilst a number of previous studies have investigated wild dog habitat suitability or selection on national and sub-national scales (O'Neill et al., 2020, Pretorius et al., 2019, Strampelli et al., 2022, Broekhuis et al., 2022), to our knowledge only one peer-reviewed study has modelled these

associations on a continental scale (Jones et al., 2016). This paper focussed on future predictions of habitat suitability, with a focus on interspecific competition with lions, rather than on elucidating suitability in the present (Jones et al., 2016).

Here, we use HSM methods to identify suitable habitat within wild dog historical range. We propose that these predictions be used as a guide in the targeting of surveys to such areas within uncertain range to ascertain presence, as well as in the local evaluation of sites previously identified for potential reintroductions within recoverable range. We additionally use these models to assess which predictors are most strongly associated with wild dog habitat suitability on this continental scale to aid in understanding drivers of site-specific suitability.

2.2. METHODS

All analyses were carried out in R version 4.4.0 (R Core Team, 2024), with spatial analyses using the package *terra* (Hijmans, 2024), and in QGIS version 3.34.14 (QGIS.org, 2024).

2.2.1. Study area

The historical range of the African wild dog (circa 1900), as defined by local experts participating in IUCN/SSC regional and national workshops (IUCN/SSC, *in prep-a,* IUCN/SSC, 2015, IUCN/SSC, 2024), serves as the study area (Figure 2.1) (Woodroffe et al., 2025). This historical distribution map was agreed upon using a combination of evidence of wild dog sightings and habitat distribution prior to wide-spread human caused extirpations.

In the same mapping workshops, point data of recent confirmed records of wild dogs' breeding presence were additionally collated and used to estimate polygons of current *resident* range (Figure 2.1, Table 2.1). The mapping process recognises six additional categories of current geographical range: *possible, recoverable, connecting, transient, unknown, and extirpated* (Table 2.1, Figure 2.1). These range categories will hereafter be referred to as 'expert-designated'. Maps were further refined and updated at national action planning workshops (e.g. Tanzania Wildlife Research Institute, 2016, Department of Wildlife & National Parks Botswana, 2019) . Shapefiles for the historical range and each range category are available in the species' latest IUCN Red List assessment (Woodroffe et al., 2025).

2.2.2. Species presence and absence data

This study requires range-wide presence data in order to capture wild dogs' habitat preferences across their current known range, which includes substantial variation between regions and sites

(Woodroffe et al., 2025). Whilst there are extensive records of wild dog occurrence at well-studied sites, predominantly in East and Southern Africa, with several long-term projects responsible for monitoring the species, there is a paucity of data available from Central, West, and the Horn of Africa (IUCN/SSC, *in prep-a,* IUCN/SSC, 2024, IUCN/SSC, 2015). This pattern is reflected in online biodiversity databases such as the Global Biodiversity Information Facility (gbif.org) and iNaturalist (inaturalist.org). Excluding these areas would very likely result in an inaccurate range-wide model, particularly as wild dogs in these regions inhabit markedly different habitats to their southern and eastern counterparts (Woodroffe et al., 2025). In addition, the majority of occurrence records do not differentiate between resident and dispersing individuals, but habitat use varies markedly between these groups. Dispersing wild dogs travel long distances and often traverse areas of low suitability – such as human-modified landscapes or fragmented habitats – while searching for suitable areas to settle (Cozzi et al., 2020, Woodroffe et al., 2020, O'Neill et al., 2020). As such, including these records in habitat suitability analyses without distinguishing behavioural context may lead to misrepresentations of preferred habitat.

In reflection of these factors, we instead used "pseudo-presence" points sampled from across expert-designated *resident* range polygons, which are delineated expressly to encompass resident breeding populations (Figure 2.1, Table 2.1). Whilst this likely results in the inclusion of some false positive presence data, comparison of species' environmental use between range polygons and occurrence data has been shown to be closely correlated (Alhajeri and Fourcade, 2019). We hence deemed this to be an appropriate choice when working at this continental scale and in the interest of avoiding the use of biased occurrence data (Fourcade, 2016). Likewise, we used "pseudo-absence" points sampled from across expert-designated extirpated range polygons (Figure 2.1, Table 2.1). Our study can hence be framed as identifying areas of wild dog historical range that are most similar to *resident* range, and most dissimilar to *extirpated* range.

We rasterised the IUCN/SSC wild dog distribution shapefile (Figure 2.1) onto a grid of the target resolution of 10km to algin with predictor variables. Any grid cells that intersected the *resident* range polygons were considered to be occupied and their centroids hence treated as presence points; any grid cells that intersected the *extirpated* range polygons were considered to be unoccupied and their centroids hence treated as absence points. Cells that intersected both *resident* and *extirpated* range were excluded. *Resident* range polygons representing the managed metapopulation of wild dogs in South Africa were not included due to the intensive degree of management required to sustain packs in these small (<1,000km^2) reserves. This process resulted in 18,966 pseudo-presence points and 116,051 pseudo-absence points.

Table 2.2. Raster layers included as candidate predictor variables in Boosted Regression Tree models. * = raster layers were created from an available dataset.

Predictor name	Source dataset	Timestamp	Description	Citation
Tmax_annual	Extracted from: CHELSA	1979 - 2013	Mean of the monthly mean maximum daily temperature	Karger *et al*., 2017, chelsa-climate.org
Tmin_annual	CHELSA*	1979 - 2013	Mean of the monthly mean minimum daily temperature	Karger *et al*., 2017, chelsa-climate.org
Tmax_range	CHELSA*	1979 - 2013	The range in temperature between the months with the highest and lowest mean daily maximum temperature	Karger *et al*., 2017, chelsa-climate.org
Tmax_cold	CHELSA*	1979 - 2013	Mean maximum daily temperature of the coldest three consecutive months (denning season)	Karger *et al*., 2017, chelsa-climate.org
Annual_precip	CHELSA	1979 - 2013	Accumulated precipitation amount over one year	Karger *et al*., 2017, chelsa-climate.org
Precip_seasonality	CHELSA	1979 - 2013	The standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates	Karger *et al*., 2017, chelsa-climate.org
PA_strictness	World Database on Protected Areas*	2023	Strictness of Protection: 2 = IUCN Protected Area Management Category I-IV, 1 = other protected area, 0 = not protected)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
PA_area	World Database on Protected Areas*	2023	Area (m^2) of contiguous strict protected areas (IUCN category I-IV)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
PA_distance	World Database on Protected Areas*	2023	Distance (m) from non-protected areas and non-strict protected areas to the nearest strict protected area (IUCN category I-IV)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
Cropland	Copernicus Global Land Cover*	2019	Binary - cropland (1) or not cropland (0), from remote sensing data	Buchhorn *et al*., 2020, land.copernicus.eu
Forest	Copernicus Global Land Cover*	2019	Binary - forest (1) or not forest (0), from remote sensing data	Buchhorn *et al*., 2020, land.copernicus.eu
Grassland	Copernicus Global Land Cover*	2019	Binary - grassland (1) or not grassland (0), from remote sensing data	Buchhorn *et al*., 2020, land.copernicus.eu
Shrubland	Copernicus Global Land Cover*	2019	Binary - shrubland (1) or not shrubland (0), from remote sensing data	Buchhorn *et al*., 2020, land.copernicus.eu
Urban	Copernicus Global Land Cover*	2019	Binary - urban (1) or not urban (0), from remote sensing data	Buchhorn *et al*., 2020, land.copernicus.eu
Humans	LandScan	2021	Human population distribution, determined using remote sensing and census data	Sims *et al*., 2022, landscan.ornl.gov
Cattle	Gridded Livestock of the World (v3)	2015	Distribution of cattle, determined using spatial covariates and census data	Gilbert *et al*., 2018, fao.org
Shoats	Gridded Livestock of the World (v3)	2015	Distribution of sheep & goats, determined using spatial covariates and census data	Gilbert *et al*., 2018, fao.org

2.2.3. Predictor variables

Table 2.2 summarises the GIS layers considered as candidate predictor variables to model wild dog habitat suitability. We chose a combination of environmental and anthropogenic variables, which have documented biological relevance to the species. These comprised variables describing climate (Pomilia et al., 2015, Rabaiotti et al., 2021, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017, Buettner et al., 2007), Protected Area status (Woodroffe and Ginsberg, 1998, van der Meer et al., 2013a, Pacifici et al., 2020), land cover (O'Neill et al., 2020, Jackson et al., 2016, Pretorius et al., 2019), human population density (Woodroffe, 2000, Lindsey et al., 2004, van der Meer et al., 2013a), and livestock population density (Woodroffe et al., 2005, Gusset et al., 2009, Lyamuya et al., 2014).

2.2.4. Data preparation

All raster layers were first resampled to a 10km resolution to match the resolution of the coarsest variables, then centred and scaled to have a mean of 0 and standard deviation of 1. It is increasingly

recognised that animals (particularly those of wide-ranging species) respond to different landscape features at different scales (McGarigal et al., 2016). To account for this, we followed a multiscale approach (Khosravi et al., 2019, Sun et al., 2022, Rezaei et al., 2022), wherein we first identified the most influential scale for each predictor variable for inclusion in the final model. We chose three scales in addition to the 10km ($100km^2$) resolution, with biological relevance ranging from local selection to population level, within the confines of our chosen 10km resolution. These scales were: $275km^2$ (9km radius), $1000km^2$ (18km radius), $3000km^2$ (31km radius). We calculated per-pixel focal values for each resampled raster layer at each of these scales, obtaining the mean value for continuous and count data, and the proportion of land cover variables.

Protected Area shapefiles were obtained from the World Database on Protected Areas (WDPA) (UNEP-WCMC and IUCN, 2023). Only polygon data were retained, and these were filtered to remove non-designated Protected Areas, along with those which did not meet the IUCN definition of a Protected Area (UNEP-WCMC and IUCN, 2023). As National Parks in South Africa were not assigned an IUCN Protected Area Management Category within this database, we assigned these Protected Areas to Category II, consistent with National Parks in other African countries. The Protected Area raster layers, described in Table 2.2, were then created from the resulting shapefile at a 10km resolution. These layers were retained at this single scale, and not included in scale selection, as the inclusion of area and distance metrics already accounted for scale (Table 2.2).

2.2.5. Modelling methods

We used Boosted Regression Tree (BRT) modelling in this study (Elith et al., 2008). This method is capable of handling different types of predictors, accounting for missing data and outliers, fitting complex nonlinear relationships, controlling for overfitting, and including interactions between predictors by default (Elith et al., 2008). BRTs have performed favourably in previous comparisons against other methods in HSM (Valavi et al., 2022, Aguirre-Gutierrez et al., 2013).

We tuned the BRT models by estimating the optimal number of trees and learning rate using a forward stepwise cross-validation approach, using the *R* packages *dismo* (Hijmans et al., 2023) and *gbm* (Greenwell et al., 2024), stipulating a minimum number of 1,000 trees (Elith et al., 2008). We first conducted univariate analyses for each predictor at each spatial scale, selecting the most influential scale for inclusion in the full model based on the resulting cross-validated Area Under the Curve (AUC) statistic (Hallman and Robinson, 2020). We then assessed pairwise correlations and collinearity among the selected predictors using Pearson correlation coefficients and Variance

Inflation Factors (VIF), excluding variables exceeding accepted thresholds (|r| > 0.7, VIF > 5) (Valavi et al., 2022). This led to the exclusion of the *Tmax_cold* variable.

The remaining predictor variables (at their optimum scales) were then included in the final multi-scale model. Due to a lack of an independent test data set, we instead allowed for evaluation of model performance through five-fold cross validation (Yates et al., 2023). The data were partitioned via spatial blocking using the *R* package *blockCV* (Valavi et al., 2019) to minimise spatial autocorrelation between training and testing datasets (Figure S2.1). We did not carry out variable selection because BRT models ignore non-informative predictors when fitting trees (Elith et al., 2008). We assessed model performance through calculation of AUC, Kappa Statistics, and True Skills Statistics (TSS) using the *R* packages *dismo* (Hijmans et al., 2023) and *SDMTools* (VanDerWal et al., 2014).

2.2.6. Predictor influence

We used the relative influence of each predictor variable from the *gbm* output (Greenwell et al., 2024) to interpret the variables most strongly associated with the modelled wild dog habitat suitability.

2.2.7. Model predictions

We projected the five resulting cross-validated predictions across wild dog historical range, then calculated a consensus prediction by taking the mean value at each pixel across the five maps. As a means of identifying the most favourable sites within expert-designated *possible, unknown,* and *recoverable* range, we reclassified the maps into 'moderately suitable' and 'highly suitable' pixels, by taking the 75^{th} and 90^{th} percentiles of pixels respectively. The remaining pixels were classed as 'unsuitable'. We calculated the area (in km^2) of any contiguous suitable (moderate or high) pixels across this map. We retained only pixel patches covering at least 3,000km^2 as these can be considered as potentially viable range due to wild dogs' large range requirements (IUCN/SSC, *in prep-a,* IUCN/SSC, 2024, IUCN/SSC, 2015). We then calculated predicted suitable (moderate, high, and total) areas within each *possible* and *recoverable* range polygon (Figure 2.1). *Unknown* range polygons are mostly extremely large, often covering almost entire countries (Figure 2.1), and hence do not represent meaningful units within which to consider conservation action. We therefore defined new polygons within the *unknown* range categories based on contiguous pixels of predicted suitable area.

We calculated additional suitable area within *resident* range polygons (Figure 2.1) and defined new polygons within the *extirpated* range category (Figure 2.1) as with the *unknown*, to assess prediction performance across pixels which were themselves used as input data.

Each polygon within these five range categories was classed as either a) containing sufficient suitable area (>3,000km^2 of suitable area within the polygon's boundaries), b) intersecting sufficient suitable area (1,000km^2 - 3,000km^2 of suitable area within the polygon itself, but part of a >3,000km^2 patch extending beyond the polygon's boundary), or c) insufficient or no suitable area within or beyond the polygon. To highlight the most suitable areas predicted, we lastly identified polygons within each range category that contained sufficient (>3,000km^2) highly suitable area.

To aid in interpreting which variables drive their respective suitability or unsuitability, we extracted mean values of each predictor within each polygon of these five range categories (*possible, recoverable, unknown, resident, extirpated* – Figure 2.1, Table 2.1).

2.3. RESULTS

2.3.1. Scale selection

A range of spatial scales were selected following univariate modelling, from the native 100km^2 to the largest scale of 3,000km^2 (Table 2.3). The 3,000km^2 scale was the most commonly selected, comprising eight of the 13 predictors for which scale selection was carried out (Table 2.3).

2.3.2. Multi-scale model performance

The multi-scale, cross-validated models performed well by all metrics, with a mean AUC value across the five model folds of 0.976 (SD = 0.015), mean TSS of 0.782 (SD = 0.100), and mean Kappa Statistic of 0.785 (SD = 0.104).

2.3.3. Predictor influence

All the included predictors influenced the model and were hence retained and accounted for when fitting trees (Table 2.3). Protected Area strictness had the largest mean relative influence (15.83% ± 5.68 SD, Table 2.3), with higher suitability within Protected Areas than unprotected areas, and marginally higher suitability in non-strict Protected Areas (those not classed as IUCN Protected Area category I-IV, Table 2.2, Figure S2.2). This was followed by annual precipitation (14.09%, Table 2.3), with highest suitability at mid-range precipitation levels (Figure S2.2), and human population (12.12%, Table 2.3), with highest suitability at lowest human population densities (Figure S2.2). Response curves for all predictors across all model folds can be found in Figure S2.2.

Table 2.3. Scale selected for each predictor variable from univariate models, and mean relative influence of each of these variables from resulting five-fold cross-validated multi-scale Boosted Regression Tree models, with standard deviation (SD). Protected Area (PA) layers were not included in scale selection, and were retained at their native 100 km² scale.

Variable	Scale selected (km²)	Mean relative influence	SD
PA strictness	-	15.83	5.68
Precipitation annual	3,000	14.09	2.27
Humans	1,500	12.12	1.49
Shoats	500	11.92	7.30
Precipitation seasonality	100	10.39	2.76
Shrub	3,000	7.98	3.58
Tmax annual	3,000	5.84	2.50
Tmax range	500	4.69	0.62
Tmin annual	3,000	4.47	1.34
PA area	-	4.13	2.06
Forest	3,000	2.57	0.82
PA distance	-	1.96	0.90
Crop	3,000	1.32	0.59
Grass	3,000	1.29	0.44
Cattle	100	1.27	0.32
Urban	3,000	0.14	0.05

Table 2.4. Total area (km²) and percentage of expert-defined wild dog range categories (historical, resident, extirpated, possible, recoverable, and unknown) (Woodroffe et al., 2025) predicted as suitable by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable.

Range category	Metric	Moderately suitable	Highly suitable	Total suitable
Historical	Area (km²)	2,599,263	1,796,048	4,395,311
	% of category	14.5	10.1	24.6
Resident	Area (km²)	449,334	962,088	1,411,422
	% of category	29.4	62.9	92.3
Possible	Area (km²)	356,779	320,642	677,421
	% of category	33.1	29.7	62.8
Recoverable	Area (km²)	90,301	64,064	154,365
	% of category	29.1	20.7	49.8
Unknown	Area (km²)	1,032,188	227,765	1,259,954
	% of category	21.1	4.8	25.8
Extirpated	Area (km²)	472,030	80,000	552,030
	% of category	5.1	0.9	5.9

2.3.4. Model predictions

A total of over 4 million km² was predicted as potentially suitable, representing 24.6% of historical range, of which 10.1% (1.8 million km²) was classified as highly suitable (Table 2.4). Of the 63 existing expert-designated *possible* range polygons, 27 were identified as containing sufficient

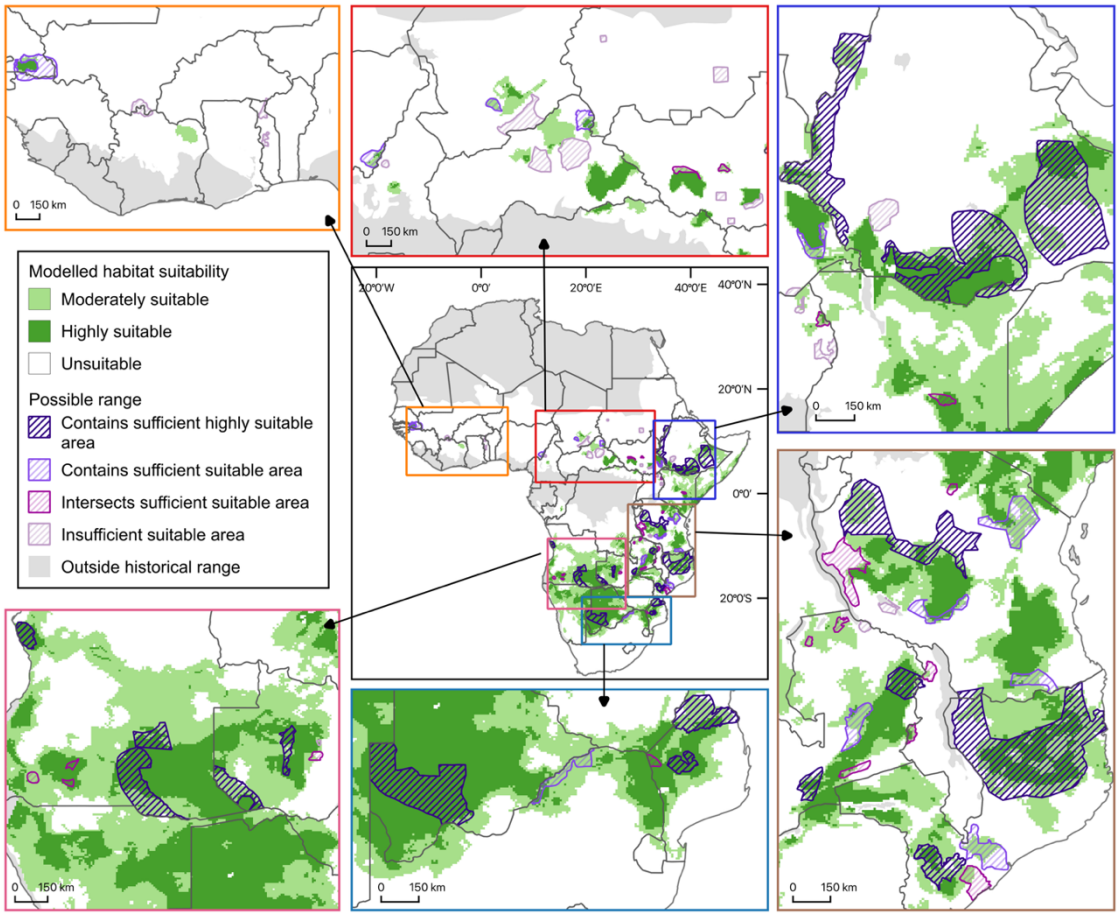


Figure 2.2. Modelled wild dog habitat suitability within expert-defined *possible* range polygons (Woodroffe et al., 2025) as predicted by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable. Sufficient suitable area defined as at least 3,000 km^2 of moderate or high suitability.

suitable area, of which 16 contained sufficient highly suitable area, along with 13 intersecting sufficient suitable area (Figure 2.2, Table S2.1). Among the 42 existing expert-designated *recoverable* range polygons, 11 were identified as containing sufficient suitable area, of which 6 contained sufficient highly suitable area, with a further 6 identified as intersecting sufficient suitable area (Figure 2.3, Table S2.2). Within the expert-designated *unknown* range, we defined 28 polygons containing sufficient suitable area, of which 11 contained sufficient highly suitable area. We defined a further 15 polygons within *unknown* range which intersected sufficient suitable area (Figure 2.4, Table S3).

Predicted suitable area within expert-designated *resident* range totalled 92.3% of the category (Table 2.4), with four of the existing 37 polygons predicted to contain no or insufficient suitable habitat (Figure S2.4, Table S2.4). Predicted suitable area within expert-designated *extirpated* range totalled 5.9% of the category, with 43 polygons defined containing or intersecting sufficient suitable habitat (Figure S2.5, Table S2.5).

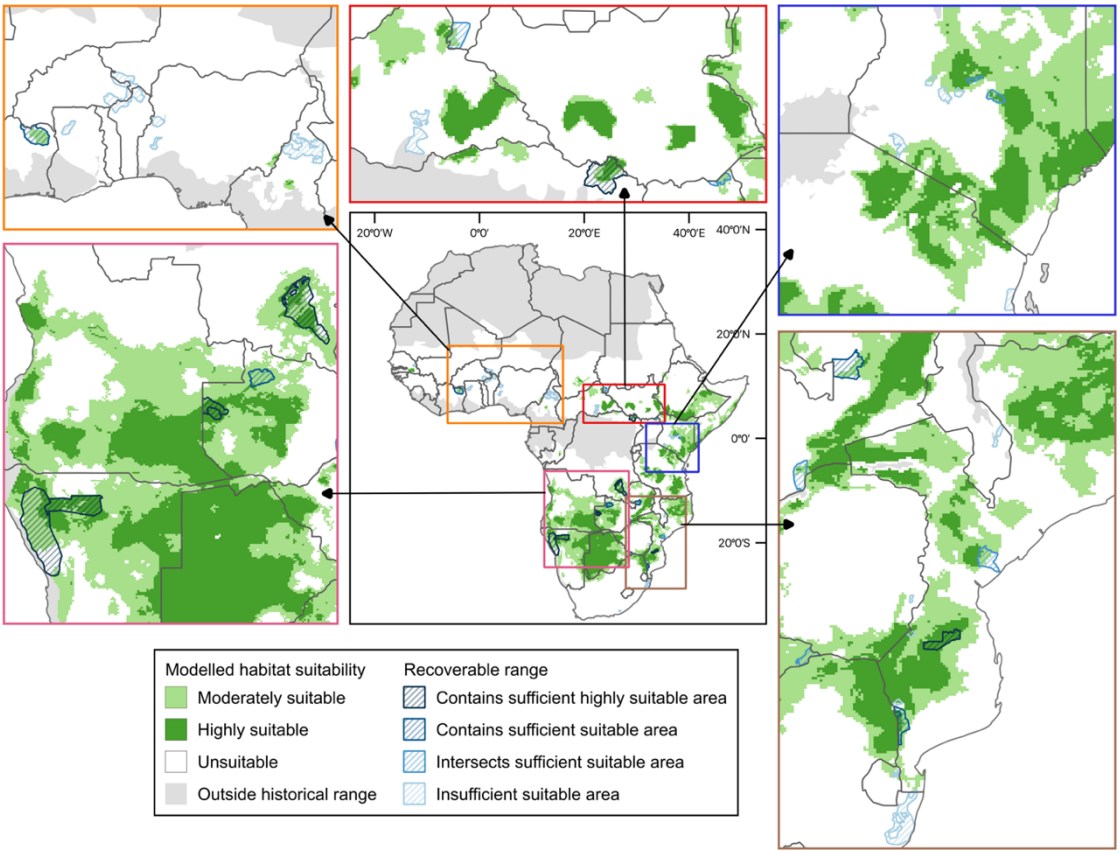


Figure 2.3. Modelled wild dog habitat suitability within expert-defined *recoverable* range polygons (Woodroffe et al., 2025) as predicted by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable. Sufficient suitable area defined as at least 3,000 km² of moderate or high suitability.

Continuous predictions for each model fold are in Figure S2.3; predictions for each constituent range polygon, along with associated mean predictor values, are in Tables S2.1-S2.5.

2.4. DISCUSSION

Our findings suggest that substantial suitable habitat for wild dogs may remain outside the areas where residence has been confirmed empirically. Some of these lands may still support resident packs; others may prove suitable for natural or assisted recolonisation. These results hence represent a useful guide for further local evaluation of conservation action.

2.4.1. Predictors of wild dog distribution

The most important predictor of habitat suitability in our models was Protected Area status, with lower suitability predicted in unprotected areas (Figure S2.2). There was little difference in suitability between strict (IUCN Category I-IV) and non-strict Protected Areas, with non-strict

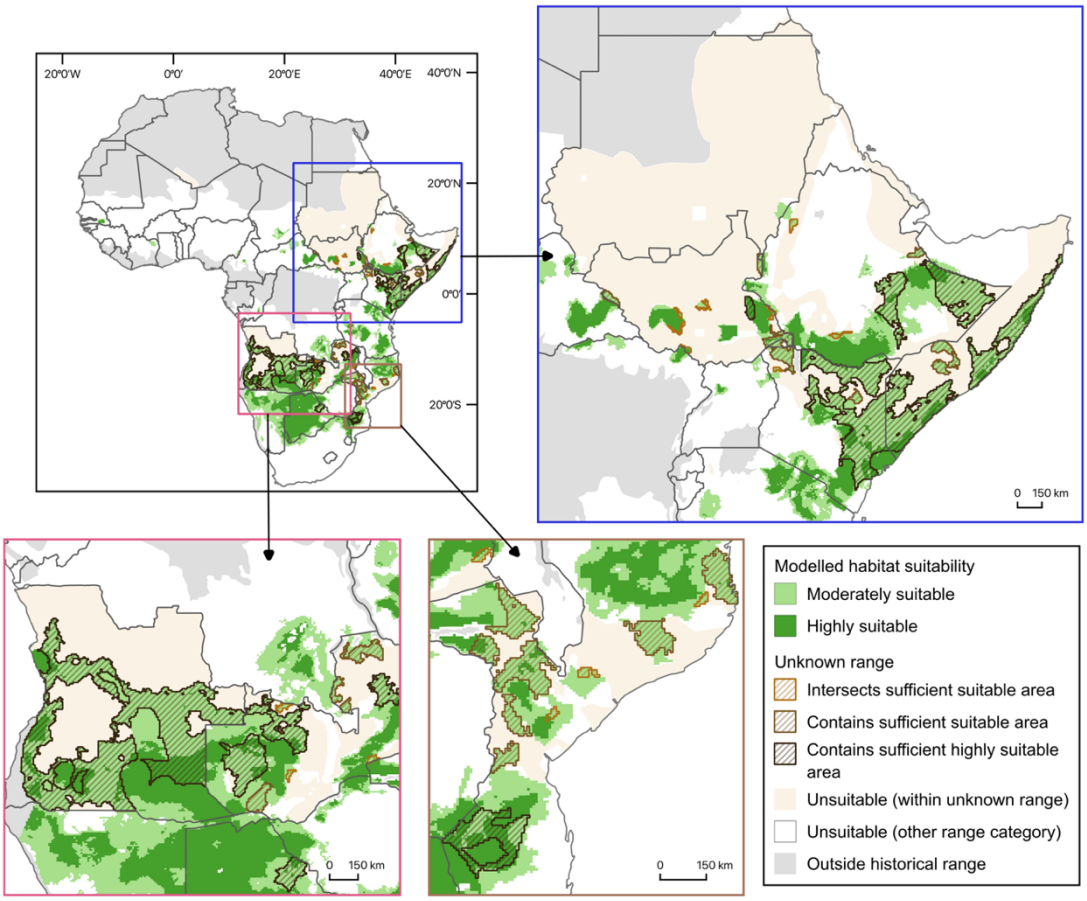


Figure 2.4. Modelled wild dog habitat suitability within expert-defined *unknown* range polygons (Woodroffe et al., 2025) as predicted by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable. Sufficient suitable area defined as at least 3,000 km^2 of moderate or high suitability.

Protected Areas having marginally higher suitability (Figure S2.2). This association could be linked to the sustainable use of resources, including hunting, which are permitted in non-strict Protected Areas (Dudley 2008). Densities of ungulate prey and lions might thus be lower in these areas (Croes et al., 2011), when compared to, for example, National Parks (typically IUCN Category II), where high lion densities have been linked to wild dogs moving out of Protected Areas (van der Meer et al., 2013a, van der Meer et al., 2011). We emphasise that not all known wild dog populations live within Protected Areas (Woodroffe, 2011), and that many of the areas predicted as suitable here fall outside any formal protection. However, outside Protected Areas, wild dogs face more human-dominated landscapes, with associated conflict with livestock and game farmers, and disease infection from domestic dogs (Woodroffe and Ginsberg, 1997). Given these threats, Protected Areas are likely to be important in sustaining wild dog populations (Pacifici et al., 2020). This corresponds with observations made about other species, including the cheetah (*Acinonyx jubatus*) (Durant et al., 2017), which has a similar geographical distribution in Africa and faces comparable threats. We note, however, that this result may reflect a bias towards detected

occurrences within Protected Areas potentially introduced during the *resident* range mapping process (Martin et al., 2012).

Annual rainfall was the second most important predictor of habitat suitability for wild dogs, with rainfall seasonality also in the top five predictors. The strongest suitability was predicted at mid-level rainfall and seasonality (Figure S2.2), echoing a pattern seen in their historical distribution, wherein species occurrence has not been recorded in very dry (such as the Sahara) or very wet conditions (such as the Congo basin) (Figure 2.1). Within this historical range, rainfall can be considered a proxy for prey carrying capacity (McNutt et al., 2019), as high rainfall increases abundance of ungulates in tropical savanna ecosystems (Ogutu et al., 2008, Owen-Smith and Mills, 2006). Rainfall can, however, improve prey species' body condition, making them more difficult to catch (Bourgarel et al., 2002), and rendering drier climatic conditions potentially more favourable (Buettner et al., 2007, Mills, 1995). With high rainfall, savanna ultimately gives way to forest (Hopcraft et al., 2010) and the habitat becomes unsuitable for wild dogs. Rainfall is additionally positively correlated with lion (*Panthera leo*) distribution and density (Abade et al., 2014, Celesia et al., 2009), a species which wild dogs are thought to avoid at high densities due to the threat of predation (Creel and Creel, 1996, Mills and Gorman, 1997).

Human and small livestock densities made up the remainder of the top five most influential variables in our models, each showing negative relationships with wild dog habitat suitability (Table 2.3, Figure S2.2). These effects likely reflect the multiple impacts of people (habitat conversion, prey loss, deliberate killing, road accidents) (Woodroffe, 2000), as well as human-wildlife conflict over livestock depredation (Fraser-Celin et al., 2018), and disease transmission from domestic dogs (Woodroffe et al., 2012). Interestingly, cattle densities played only a very small role, consistent with wild dogs tending to kill sheep and goats more frequently than cattle (Lyamuya et al., 2014, Woodroffe et al., 2005). These top five predictors together accounted for 64% of variation in wild dog habitat suitability (Table 2.3), whilst other variables (including temperature and land cover) played much smaller roles (each <8%; Table 2.3).

A range of scales was selected as a result of the univariate modelling (Table 2.3), supporting growing evidence that different variables influence habitat preferences at different scales. The most commonly selected scale was the largest (3,000km^2), which is reflective of population-level habitat requirements. However, it is important to note that the global environmental layers used in this study – some of which are themselves derived from models – may not accurately represent conditions at finer, local scales. This limitation may contribute to spatial inconsistencies in the predictions; for example, international borders are visible in the results, suggesting discrepancies

in variable measurement between countries. We therefore advise local practitioners and researchers to consult Tables S2.1-S2.5 to evaluate the reliability of these predictors in their specific context.

Several critical variables – including competitor density, prey density, human attitudes, and disease risk – could not be included in our models as the required data are not available on a continental scale. The predictors included in this study can be considered proxies for these variables, but imperfectly so. Wild dogs typically avoid areas with high densities of lions and spotted hyaenas (*Crocuta crocuta*) due to threats of mortality and kleptoparasitism (Mills and Gorman, 1997, Creel and Creel, 1996). In some areas, hunting of wild prey by people has led to drastic reductions or absence of prey species (El Khidir and Ali, 2018, Henschel et al., 2014, Goodheart et al., 2021), potentially leaving an insufficient prey base for wild dog persistence. Human attitudes toward wild dogs themselves have historically included shooting individuals even within Protected Areas (Bere, 1955), and still influence wild dogs' ability to persist in specific areas (Lindsey et al., 2005). Infectious disease can cause rapid population crashes or local extinction entirely without change in local habitat or prey (Gascoyne et al., 1993, Mutinda et al., 2017). These factors have significant impacts on wild dog distribution, which means that our modelled suitability must not be interpreted as equivalent to empirical confirmation of residence. Rather, our predictions should be taken as evidence of where wild dogs might persist, or be able to persist, which can be used to guide further investigation.

2.4.2. Model predictions

2.4.2.1. Uncertain range

Within uncertain range, sufficient highly suitable area was predicted within only 16 of 63 expert-designated *possible* range polygons (Figure 2.2, Table S2.1), and 11 newly defined *unknown* range polygons (Figure 2.4, Table S2.3). This result hence serves as a considerable refinement to the vast areas currently mapped as uncertain, aiding in prioritisation of surveys across these regions. Substantial areas of suitable habitat were predicted in southern and eastern Ethiopia, along the coast of Somalia, the extreme west of Mozambique, and southern Angola (Figures 2.2 & 2.4). Civil unrest in Somalia has meant that surveying has not been possible in the past, resulting in the country consisting entirely of *unknown* range. Likewise, residency of wild dogs in Angola was confirmed only within the last decade, prior to which knowledge of the species' distribution was extremely limited (Kosmas et al., 2023). Surveys targeting these areas would be warranted to elucidate vast regions of uncertainty and establish possible residency.

West and Central Africa represent the most depleted portions of the wild dog's historical range, with known breeding individuals now restricted to Niokolo-Koba National Park in Senegal and three sites in the Central African Republic (CAR) (Figure 2.1) (Brugière et al., 2015). Any additional individuals persisting elsewhere would therefore constitute a substantial proportion of the regions' remaining population and genetic diversity. Within these regions, three areas were predicted to contain sufficiently suitable habitat: Gashaka-Gumti National Park in Nigeria, Siniaka-Minia in Chad, and André Félix National Park in the CAR (Figure 2.2; Table S2.1). Targeted surveys in these sites are therefore recommended to determine current occupancy status and to clarify whether these regions still support additional remnant wild dog populations.

2.4.2.2. Recoverable range

Our models also predict the potential suitability of certain areas for restoration or reintroduction efforts, with the largest suitable patches located in Etosha National Park, Namibia, and Upemba National Park, southern Democratic Republic of Congo (Figure 2.3, Table S2.2). However, we note that wild dogs have historically encountered difficulties in some migratory systems, including past reintroductions to Etosha (Scheepers and Venzke, 1995), as well as in the Serengeti National Park (Tanzania), and Liuwa Plain National Park (Zambia). Although formal studies are lacking, field observations indicate that wild dogs may struggle to obtain sufficient prey during the energetically costly pup-reading ("denning") period (Woodroffe et al., 2017) in these migratory systems, when wild dog movement is limited to centre around den sites (Alting et al., 2021, Comley et al., 2023), whilst prey densities shift seasonally. This factor should therefore be carefully evaluated before any reintroduction attempts into such systems.

Expert-designated *recoverable* range in West Africa is largely categorised as unsuitable in our results (Figure 2.3, Table S2.2). This prediction could be influenced by the small proportion of pseudo-presence points from the region used to parameterise the models, resulting from the single known population (Figure 2.1). Only one expert-designated *recoverable* range polygon in the region was identified as containing moderately sufficient area: Comoé National Park in Côte d'Ivoire (Figure 2.3, Table S2.2). Given its potential significance as the only suitable *recoverable* area in the most depleted region of the species' historical range, this warrants consideration for a reintroduction attempt.

A full, formal evaluation of the capacity of such places to hold wild dogs is essential prior to any reintroduction attempt. Critically, such evaluations should include assessment of local threats, such as snaring pressure (Becker et al., 2013), prey depletion (Reyes de Merkle et al., 2024), and

disease risk (Woodroffe et al., 2012). Careful consideration should also be given to the choice of source populations for any such reintroductions, considering genetic diversity and the potential for local adaptation (IUCN/SSC, 2013).

2.4.2.3. Resident and extirpated range

Our models predict that some areas designated as *resident* range are, counterintuitively, unsuitable (Figure S2.4, Table S2.4). This pattern may reflect the at-times imprecise mapping of range, which could include drawing approximate polygons to encompass an area of known residency, or the inclusion of an entire Protected Area, of which part is not actually used (Merow et al., 2016). Four of the five *resident* range polygons for which insufficient suitability was predicted do not themselves meet the 3,000km^2 area threshold used to classify sufficiently large areas for population persistence (Table S2.4). The fifth, in the Aouk region of Chad, was later revised to *possible* range during the IUCN/SSC mapping review process (IUCN/SSC, 2024).

Similarly, a number of polygons was defined as suitable within expert-designated *extirpated* range (Figure S2.5). The majority of these polygons bordered further suitable range within other categories, with the exception of Mbam et Djerem National Park in Cameroon, Léfini and Lessio-Louna sanctuaries in Congo, Murchison Falls National Park in Uganda, and a number of conservancies and parks in Namibia (Figure 2.5, Table S2.5). Given these locations' isolation amidst predicted unsuitability, they could be worthy of evaluation to potentially reassess their categorisation as *extirpated* range.

The presence of these counterintuitive predictions – unsuitability within resident range and suitability within extirpated range – suggests that sampling pseudo-presence and pseudo-absence points from these polygons did not produce an overfitted model, underscoring the robustness of the spatially blocked cross-validation approach used here.

2.4.3. Conservation implications

Correlative habitat suitability models only allow for the prediction of habitat suitability based on identified associations between selected environmental variables and occurrence records. Even models with high predictive ability may not fully capture the breadth of a species' suitable habitat (Pearson et al., 2006). It is therefore important that wild dogs are not assumed to be absent from all areas predicted as unsuitable here. The aim of this study was instead to identify areas most similar to known *resident* range, narrowing the vast regions of uncertain status to prioritise surveys and refine potential reintroduction sites. Our study thus provides a decision-support tool for

conservation action, though it should be interpreted with caution and not as a realised distribution.

By providing a quantitative next step from expert range mapping, this approach strengthens the value of expert knowledge and encourages its systematic use across taxa. The framework can be applied to other species for which comparable expert-designated range maps exist, such as the cheetah (Durant, 2024), reducing reliance on extensive occurrence data and promoting consistent, data-informed conservation assessment. We emphasise, however, that this methodology would not be suitable for more localised habitat suitability modelling, or for studies which aim to estimate a realised distribution.

For an endangered species in population decline with a vastly reduced resident range (Woodroffe et al., 2025), the extensive areas of potentially suitable habitat identified here could be of great value to wild dog conservation. We encourage wildlife managers to consult these maps, with appropriate local validation, to guide future surveys and reintroduction assessments for the species. Extending this research to project wild dogs' future distribution under different development, human population growth, and climate scenarios would further target conservation action toward areas with the greatest likelihood of long-term persistence.



CHAPTER 3 | Shifting habitat suitability for African wild dogs under future climate and land use change

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AUTHOR CONTRIBUTIONS

JFL and RW conceived the study and developed the methodology. JFL curated the data, performed the analyses, and wrote the manuscript. AD and RW provided supervision and critically reviewed and edited the manuscript.

Shifting habitat suitability for African wild dogs under future climate and land use change

ABSTRACT

Aim: To evaluate how projected climate and land-use change may alter habitat suitability for the endangered African wild dog across its current and potential future range, and to identify areas of conservation priority under different emissions and socioeconomic scenarios.

Location: Continental Africa

Methods: We used multi-scale Boosted Regression Tree models, parameterised with pseudo-presence and absence points derived from expert-designated range maps to model current habitat suitability. Predictor variables included climate, land cover, protected area status, and human population density. Models were projected under three Shared Socioeconomic Pathways (SSP1-2.6, SSP3-7.0, SSP5-8.5) across two future periods (2041-2070 and 2071-2100), and changes in suitability were quantified across the continent and within resident and recoverable ranges.

Results: Model performance was high, and projections indicated widespread spatial variation in future suitability. Under higher-emissions scenarios, a greater area was predicted to decline rather than increase in suitability, with substantial decreases identified in key current strongholds, including the Kavango-Zambezi Transfrontier Conservation Area and parts of central Africa. Up to 32.1% of current resident range was projected to decrease in suitability by the late century. In contrast, changes within recoverable range were generally limited. Decreases in suitability were frequently associated with increasing temperatures, expansion of cropland, and loss of shrubland. Notably, the greatest declines were predicted under the high land conversion scenario, SSP3-7.0, highlighting the importance of land-use change alongside climate warming.

Main conclusions: Climate and land-use change are likely to impose increasing constraints on African wild dog populations, particularly within core conservation areas. These findings emphasise the need to integrate future environmental change into conservation planning, including safeguarding key populations, maintaining landscape connectivity, and informing reintroduction strategies.

KEYWORDS

Lycaon pictus, African wild dog, habitat suitability modelling, climate change, land-use change, conservation planning

3.1. INTRODUCTION

Climate change has been established as a prominent threat to biodiversity, with observed impacts including alterations to species' distributions, phenology, and demography (Wernberg et al., 2011, Vittoz et al., 2013, Williams et al., 2019, Spooner et al., 2018), and future impacts predicted to cause large scale species extinctions (Bellard et al., 2012). Africa is projected to experience more extreme and rapid climate change than the global average, with increased annual heatwave frequency already detected across the continent (Engdaw et al., 2021) and associated impacts on both people and biodiversity increasingly observed (IPCC, 2022). Across the majority of sub-Saharan Africa, it is predicted that average temperatures and number of days subject to extreme temperatures will increase, average precipitation will decrease, and drought will increase in frequency (IPCC, 2022). In parallel, it is predicted that land cover change across Africa will include increases in cropland and urban areas, and decreases in forest cover (Yahaya et al., 2024).

Climatic changes within a species' range can cause habitat to become inhospitable, driving range shifts to track suitable conditions. However, such range shifts are often prohibited by availability of suitable habitat, with contractions in habitat observed in polar regions (Laidre et al., 2018), at high altitudes (Beever et al., 2011), and in areas subjected to surrounding anthropogenic habitat loss (Pomara et al., 2014). Human-induced habitat loss and fragmentation can therefore act to limit the ability of species to adapt to changes in climate. These impacts could be further exacerbated by the interaction between climate and land use change (Williams et al., 2019), as climate change is predicted to lead to further conversion of natural to human-dominated land cover, for example by people shifting croplands and settlements to track climatic suitability and avoid desertification (Jia et al., 2019).

The African wild dog (*Lycaon pictus* – hereafter wild dog), is an endangered carnivore species, whose extremely wide-ranging behaviour leaves it particularly vulnerable to habitat loss (Woodroffe, 2011, Pomilia et al., 2015). Home ranges average approximately 500km^2 (Woodroffe, 2011, Pomilia et al., 2015) but can reach over 2,000km^2 (Fuller et al., 1992), whilst population densities average two individuals per 100 km^2, but can be considerably lower (Mills and Gorman, 1997, Parsais et al., 2025). Wild dog historical range is limited by the sand deserts of the Sahara to the north, where there is a lack of water and prey species (Lhote, 1946). Today, the species' known resident range is limited to the south by anthropogenic land use, where former habitat has been converted to agriculture and urban areas in South Africa. Throughout the remainder of its historical range, vast areas of habitat have become unsuitable due to human pressures, leaving the remaining global wild dog population in several isolated pockets representing 8.5% of historical

range (Figure S3.1) (Woodroffe et al., 2025). This vast range reduction, along with the species' ecology, makes it a candidate for concern for ongoing habitat loss under future climate and land use change. Forecasting whether parts of remaining wild dog resident range will become unsuitable for the species in the near future, and whether there is scope for any shifts in range to track suitable habitat, will be important for the species' conservation.

Reintroductions of wild dogs are being considered in parts of former range in an effort to increase the global population size and restore historical ecosystems (Woodroffe et al., 2025, PWF, 2023), and have already been conducted to former range states (Bouley et al., 2021, African Parks, 2023). Participatory mapping workshops held in range states have identified an additional 1.7% of historical range as potentially appropriate for further reintroduction attempts (IUCN/SSC, 2024, IUCN/SSC, *in prep-a,* IUCN/SSC, 2015). Considering how habitat suitability within these sites may be altered by predicted climate and land use change will be a key factor in determining the feasibility and prudence of any reintroduction attempts.

Habitat Suitability Modelling (HSM, sometimes referred to as Species Distribution Modelling) is a method to understand the relationship between a given species' occurrence and environmental conditions, enabling predictions of habitat suitability for the species across space. Such predictions can also be projected in time to forecast how habitat suitability may change under given environmental conditions – this is commonly carried out to estimate impacts arising from future climate (Dale et al., 2022, Mancino et al., 2022, Mota et al., 2022, Zamora-Gutierrez et al., 2018, Lawson et al., 2023, Ngila et al., 2023, Rather et al., 2020, Dejene et al., 2021) and land use (Zamora-Gutierrez et al., 2018, Dejene et al., 2021, Newbold, 2018) change.

Here, we use HSM methods to predict future habitat suitability for African wild dogs across Africa under projected climate and land use change, considering a number of emissions and socioeconomic scenarios. From these predictions, we quantify potential changes in suitability over time, identifying priority areas where conservation efforts could be directed. This includes evaluation of whether sites currently identified as recoverable via reintroduction are likely to remain viable in the future.

3.2. METHODS

All analyses were carried out in R version 4.4.0 (R Core Team, 2024), using the package terra (Hijmans, 2024) and in QGIS version 3.4.05 (QGIS.org, 2024). HSM methods broadly followed those described in Chapter 2.

3.2.1. Study area

The area considered in this study was continental Africa. We chose not to restrict predictions of future habitat suitability to the species' established historical range (Woodroffe et al., 2025) as changes in climate and land cover could feasibly cause shifts beyond these limits. Within this area, we focused predominantly on predictions within expert-designated 'resident' and 'recoverable' range (Figure S3.1). Expert-designated 'extirpated' range was additionally used for point sampling (see below). These range polygons were mapped by local experts participating in IUCN/SSC regional and national workshops with the following definitions (IUCN/SSC, 2024, IUCN/SSC, *in prep-a,* IUCN/SSC, 2015):

- Resident range: where wild dogs are known to be resident, with regular detection over several years of complete packs and evidence of breeding.
- Recoverable range: where wild dogs are known to be absent, but where habitat and prey remain over sufficiently large areas, meaning either natural or assisted recovery of wild dogs might be possible within the next ten years with reasonable conservation action.
- Extirpated range: where wild dogs are known to be extirpated, and habitat has been so heavily modified (e.g. by cultivation/urbanisation) or fragmented as to be uninhabitable by resident animals for the foreseeable future.

3.2.2. Species presence and absence data

As in Chapter 2, pseudo-presence points were sampled from expert-designated resident range polygons. In addition to the expert-designated extirpated range polygons used to sample pseudo-absence points in Chapter 2, historically absent polygons (i.e. those beyond historical range, but within continental Africa) were also used in order to capture and characterise additional unoccupied habitat. We rasterised the IUCN/SSC wild dog distribution shapefile (Woodroffe et al., 2025) (Figure S3.1) onto a grid of a target resolution of 10km – any grid cells that intersected the resident range polygons were considered to be occupied and their centroids treated as presence points; any grid cells that intersected the extirpated range polygons or those beyond historical range were considered to be unoccupied and their centroids treated as absence points. Cells that intersected both resident and extirpated or historically absent range were excluded. Resident range polygons representing the managed metapopulation of wild dogs in South Africa were not included due to the intensive degree of management required to sustain packs in these small (<1,000km^2) reserves.

Table 3.1. Raster layers included as predictor variables, and associated projected future layers. * = raster layers were created from an available dataset.

Predictor name	Time period	Source dataset	Description	Citation
Tmax_annual	Current & Future	CHELSA v2.1*	Mean of the monthly mean maximum daily temperature	Karger *et al*., 2017, chelsa-climate.org
Tmin_annual	Current & Future	CHELSA v2.1*	Mean of the monthly mean minimum daily temperature	Karger *et al*., 2017, chelsa-climate.org
Tmax_range	Current & Future	CHELSA v2.1*	The range in temperature between the months with the highest and lowest mean daily maximum temperature	Karger *et al*., 2017, chelsa-climate.org
Tmax_cold	Current & Future	CHELSA v2.1*	Mean maximum daily temperature of the coldest three consecutive months (denning season)	Karger *et al*., 2017, chelsa-climate.org
Annual_precip	Current & Future	CHELSA v2.1*	Accumulated precipitation amount over one year	Karger *et al*., 2017, chelsa-climate.org
Precip_seasonality	Current & Future	CHELSA v2.1*	The standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates	Karger *et al*., 2017, chelsa-climate.org
PA_strictness	Current	World Database on Protected Areas*	Strictness of Protection: 2 = IUCN Protected Area Management Category I-IV, 1 = other protected area, 0 = not protected)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
PA_area	Current	World Database on Protected Areas*	Area (m^2) of contiguous strict protected areas (IUCN category I-IV)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
PA_distance	Current	World Database on Protected Areas*	Distance (m) from non-protected areas and non-strict protected areas to the nearest strict protected area (IUCN category I-IV)	UNEP-WCMC & IUCN, 2023, protectedplanet.net
Cropland	Current	ICDR Land Cover*	Binary - cropland (1) or not cropland (0), from remote sensing data	Copernicus Climate Change Service cds.climate.copernicus.eu Chen *et al*., 2022 10.5281/zenodo.4584774
	Future	Global PFT-based land projection*		
Forest	Current	ICDR Land Cover*	Binary - forest (1) or not forest (0), from remote sensing data	Copernicus Climate Change Service cds.climate.copernicus.eu Chen *et al*., 2022 10.5281/zenodo.4584774
	Future	Global PFT-based land projection*		
Grassland	Current	ICDR Land Cover*	Binary - grassland (1) or not grassland (0), from remote sensing data	Copernicus Climate Change Service cds.climate.copernicus.eu Chen *et al*., 2022 10.5281/zenodo.4584774
	Future	Global PFT-based land projection*		
Shrubland	Current	ICDR Land Cover*	Binary - shrubland (1) or not shrubland (0), from remote sensing data	Copernicus Climate Change Service cds.climate.copernicus.eu Chen *et al*., 2022 10.5281/zenodo.4584774
	Future	Global PFT-based land projection*		
Urban	Current	ICDR Land Cover*	Binary - urban (1) or not urban (0), from remote sensing data	Copernicus Climate Change Service cds.climate.copernicus.eu Chen *et al*., 2022 10.5281/zenodo.4584774
	Future	Global PFT-based land projection*		
Humans	Current	WorldPop	Human population distribution, determined using remote sensing and census data	WorldPop & CIESIN, 2018 wordlpop.org Wang *et al*., 2022 10.6084/m9.figshare.19608594.v3
	Future	Projecting 1 km-grid population distributions		

3.2.3. Predictor variables

Table 3.1 summarises the GIS layers included as predictor variables to model current wild dog habitat suitability, along with the associated projected future layers. These predictors align with those described in Chapter 2, although different datasets were used where necessary to ensure that input data for modelling present and future suitability were based on consistent methodology. We chose a combination of environmental and anthropogenic variables, which have documented biological relevance to the species. These comprised variables describing climate (Pomilia et al., 2015, Rabaiotti et al., 2021, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017), protected area status (Woodroffe and Ginsberg, 1998, van der Meer et al., 2013a, Pacifici et al., 2020), land cover (O'Neill et al., 2020, Jackson et al., 2016, Pretorius et al., 2019), and human population density (Woodroffe, 2000, Lindsey et al., 2004, van der Meer et al., 2013a). Unlike in Chapter 2, livestock densities were not included here due to the unavailability of future projections of these predictors. The current protected area layers were held constant for use in the future predictions

as, in the absence of existing predictions, we assumed protected area status would remain unchanged.

3.2.4. Data preparation and modelling methods

The data preparation and modelling procedures followed those described in Chapter 2. In brief, raster layers were resampled to 10 km resolution and standardised, and a multiscale approach was applied to identify the most relevant spatial scale for each predictor of the following scales: 275km^2 (9km radius), 1000km^2 (18km radius), 3000km^2 (31km radius). Protected area data were processed from the World Database on Protected Areas (WDPA) (UNEP-WCMC and IUCN, 2023) and incorporated at the single native scale of 100 km^2. Habitat suitability models were fitted using Boosted Regression Trees (BRTs) (Elith et al., 2008), with model tuning conducted via forward stepwise cross-validation to optimise parameters using the *R* packages *dismo* (Hijmans et al., 2023) and *gbm* (Greenwell et al., 2024, Hijmans et al., 2023). Predictor variables were screened for collinearity, resulting in the exclusion of the *Tmax_cold* variable, and the most informative variables (at their optimal scales) were retained. Model performance was evaluated using spatially structured five-fold cross-validation with the *R* package *blockCV* (Valavi et al., 2019) and by calculating of Area Under the Curve (AUC), Kappa Statistics, and True Skills Statistics (TSS) using the *R* packages *dismo* (Hijmans et al., 2023) and *SDMTools* (VanDerWal et al., 2014).

3.2.5. Future scenarios

Projected future climatologies were downloaded from the CHELSA CMIP6 ISIMIP3 database (Karger, 2021) for all available global circulation models (GCMs): GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0 and at all available Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs): SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5, hereafter referred to as SSPs 1-2.6, 3-7.0, and 5-8.5, respectively.

SSP 1-2.6 (“Taking the Green Road”) is a sustainability-focused, low-emissions scenario, featuring global cooperation and land conservation, with the increase in global mean temperature limited to approximately 2°C by 2100 (IPCC, 2021). SSP 3.7-0 (“A Rocky Road”) is a high-emissions, high-population scenario, with regional conflict and extensive land-use change, leading to warming above 3°C by 2100 (IPCC, 2021). SSP 5-8.5 (“Taking the Highway”) is a fossil-fuel driven, high-emissions scenario with more limited population growth, characterised by technological growth and extreme warming of over 4°C by 2100 (IPCC, 2021).

The climatologies used were for the periods 2041-2070 and 2071-2100. A consensus climate layer was created for each climate variable (Table 3.1), SSP, and period by taking the mean of all available

GCM predictions for each pixel. Corresponding future predictions of land cover and human population size were also obtained for each SSP and period (Table 3.1). The resulting six combinations of SSP and period will hereafter be referred to as future scenarios.

3.2.6. Model predictions

We first projected the model predictions across continental Africa for the current period (1981-2010), to establish a baseline for comparison with future suitability projections. This projection generated one map from each of the five cross-validated folds, each representing the probability of suitability (ranging from 0 to 1) for the species in each pixel. A consensus prediction was then generated by averaging the values from the five maps at each pixel. This process was repeated for each future scenario, producing six corresponding maps. To assess changes over time, the value at each pixel in the current consensus map was subtracted from that in each of the future scenario maps, yielding six maps which represented the predicted change in suitability between the current and each future scenario, on a scale from -1 to 1. These maps were then reclassified into the following categories: extreme decrease (-1 to <-0.75), strong decrease (-0.75 to <-0.5), moderate decrease (-0.5 to <-0.25), negligible change (-0.25 to <0.25), moderate increase (0.25 to <0.5), strong increase (0.5 to <0.75), and extreme increase (0.75 to 1). We then calculated the total area (km^2) falling into each of the reclassified categories for each scenario, excluding negligible change in order to focus on areas predicted to undergo substantial changes in suitability. This was carried out both across the continent and specifically within expert-designated resident and recoverable ranges (Figure S3.1).

We created consensus change maps for each future period by summing the reclassified suitability change maps across the three SSPs. This resulted in maps for 2041-2070 and 2071-2100 with values ranging from -6 to 6, where -6 indicates a strong decrease in suitability agreed across SSPs, and 6 indicates a strong increase in suitability agreed across SSPs. This approach enabled the identification of areas where suitability decrease or increase is consistently predicted across emissions and socioeconomic scenarios, so can be considered conservation priorities with reduced scenario-related uncertainty.

We refrained from applying thresholds to model predictions to delineate suitable and unsuitable categories, thereby avoiding uncertainties associated with transforming continuous model outputs into binary predictions (Zamora-Gutierrez et al., 2018). By focusing on areas predicted to experience suitability changes of at least ±0.25, we capture substantial shifts indicative of altered

habitat quality, which may, for example, correspond to reduced carrying capacity and lower population density (Weber et al., 2016).

3.2.7. Changes in predictors

To assess how changes in suitability were associated with specific predictors, we generated, for each applicable predictor variable (Table 3.1), layers of predictor change for each of the six future scenarios, by subtracting the current predictor layer from its corresponding future layer. We then overlaid the predictor change layers with the reclassified suitability change layers (grouping all decreases together, and all increases together) to extract the change in each predictor associated with corresponding changes in suitability in each pixel. We additionally identified 'patches' of at least 500km2 of contiguous pixels for which increase or decrease was predicted within resident and recoverable range polygons. We then extracted the mean values of change in each predictor within each patch to aid in interpreting local drivers of predicted increases and decreases in suitability.

3.3. RESULTS

3.3.1. Multi-scale model performance

The multi-scale, cross-validated BRT models performed well by all metrics, with a mean AUC value across the five models of 0.984 (SD = 0.007), mean TSS of 0.763 (SD = 0.072), and mean Kappa Statistic of 0.762 (SD = 0.060).

3.3.2. Model predictions

Compared to the current projection (Figure S3.2), both increases and decreases in suitability were predicted for all six future scenarios, both across continental Africa and within resident and recoverable African wild dog range (Figures 3.1-3.4). Overall, a greater area was predicted to become less, rather than more, suitable across continental Africa under SSPs 3-7.0 and 5-8.5, but not under SSP 1-2.6 (Figure 3.2). Substantial decreases in suitability were predicted in central Africa in four out of six future scenarios, and in southern Africa across all six scenarios (Figure 3.1). SSP 1-2.6 was associated with the largest area of increase in suitability and smallest decreased in both the 2041-2070 and 2071-2100 periods (Figure 3.2). The scenario associated with the largest area of decrease in suitability and smallest increase was SSP 3-7.0, particularly in the 2071-2100 period (Figure 3.2).

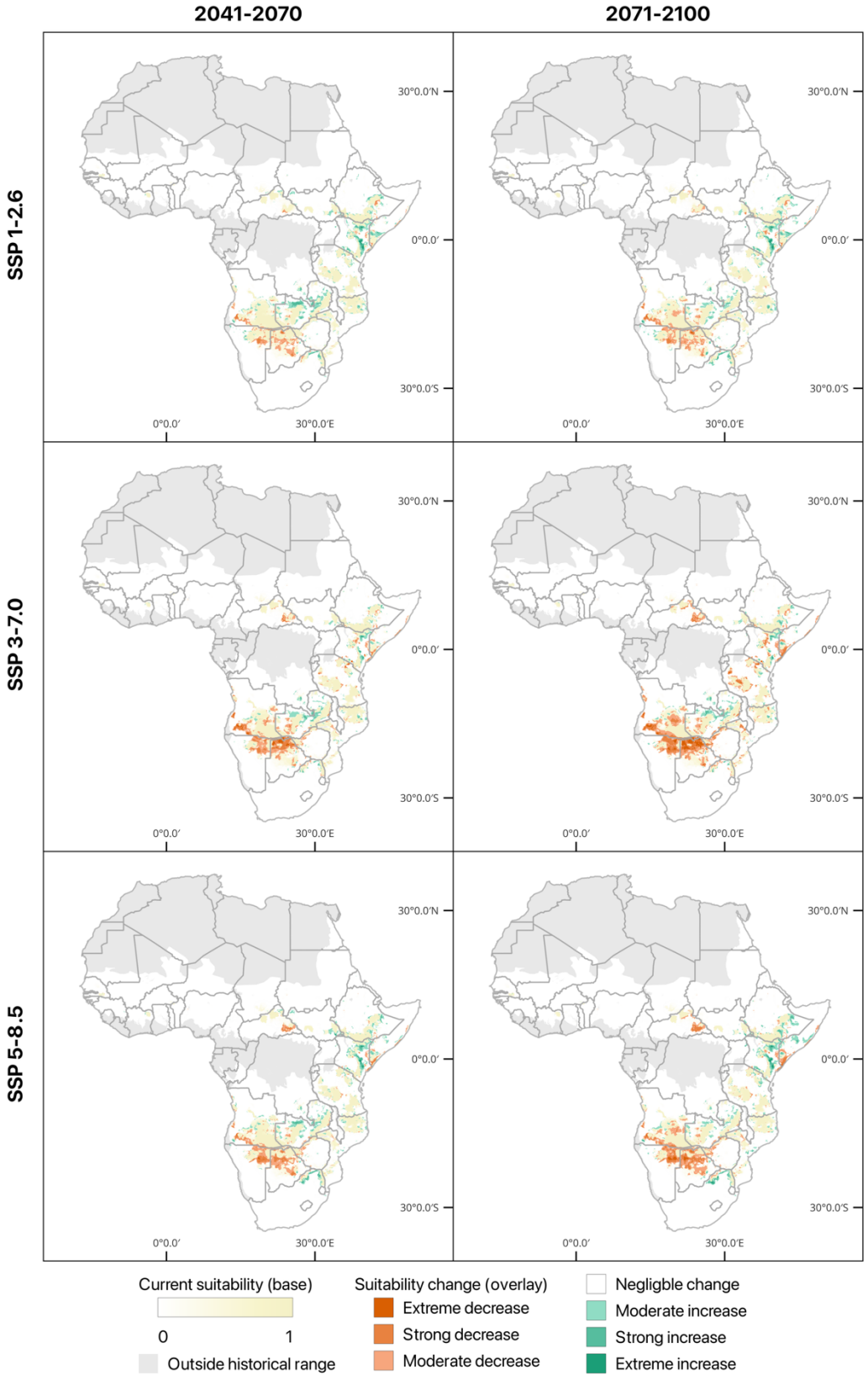


Figure 3.1. Predicted change in habitat suitability for wild dogs under six future scenarios compared to current suitability, as predicted by multi-scale Boosted Regression Tree models. Suitability change is on a scale of -1 to 1. Thresholds for extreme, strong, and moderate increase or decrease are ±0.75, ±0.5, and ±0.25 respectively.

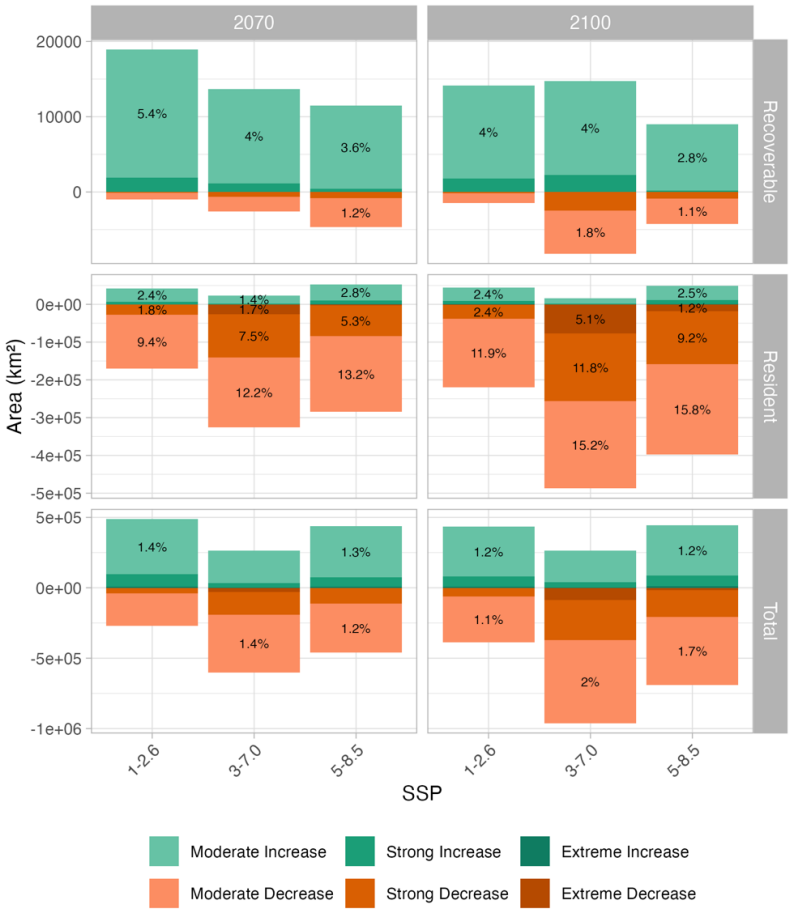


Figure 3.2. Area (km²) predicted to change in habitat suitability for African wild dogs under six future scenarios, relative to current suitability, as modelled using five cross-validated multi-scale Boosted Regression Tree models. Suitability change ranges from -1 to 1, with thresholds for extreme, strong, and moderate increase or decrease are ±0.75, ±0.5, and ±0.25 respectively. Results are shown within expert-defined *recoverable* and *resident* range categories (IUCN/SSC, *in prep-a,* IUCN/SSC, 2015, IUCN/SSC, 2024), as well as for the total study area of continental Africa. Labels indicate the percentage of total area within each category, displayed only where values exceed 1%.

Substantial areas of resident range were predicted to become less suitable across scenarios, with 32.1% of currently defined resident range predicted to decrease in suitability by 2071-2100 under SSP 3-7.0, including 5.1% predicted to undergo an extreme decrease (Figure 3.2). Across scenarios within modern-day recoverable range, a greater area was predicted to increase in suitability than decrease; however, both increases and decreases made up small percentages of total recoverable range across scenarios, indicating a majority of pixels are forecast to experience negligible change (Figure 3.2).

The 2041-2070 consensus maps indicated predicted decreases in suitability across scenarios within resident range in the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA) at the nexus of Angola, Botswana, Namibia, Zambia, and Zimbabwe, along with the Chinko area of the Central African Republic (CAR), Ijara and Isolo in Kenya, Bicuar and Mupa National Parks in Angola, and northern Tanzania (Figures 3.3 & 3.4). These decreases grew in spread and strength in the 2071-2100 period, and include additional decreases in Tanzania's Rungwa-Ruaha landscape, and the surroundings of Zimbabwe's Mana Pools National Park, extending into Zambia (Figure 3.4).

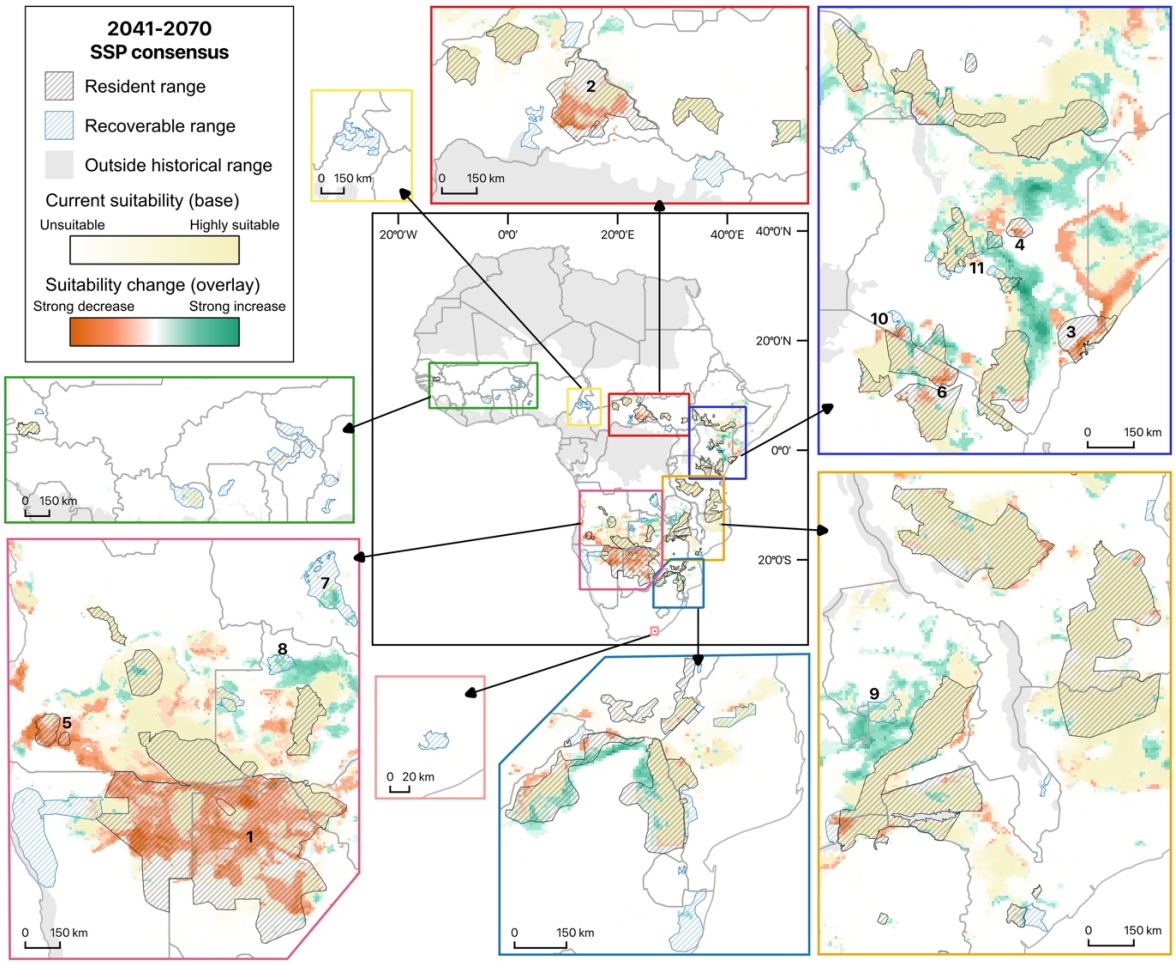


Figure 3.3. Predicted change in habitat suitability for wild dogs in the period 2041-2070 compared to current suitability, with a focus on expert-defined resident and recoverable range polygons (IUCN/SSC, *in prep-a,* IUCN/SSC, 2015, IUCN/SSC, 2024), as modelled by five cross-validated multi-scale Boosted Regression Tree models. Suitability change is on a scale of -1 to 1; thresholds for extreme, strong, and moderate increase or decrease are ±0.75, ±0.5, and ±0.25 respectively for each SSP, with change summed across three SSPs to give the SSP consensus. Strong increase/decrease indicates where strong increase/decrease in a given pixel is predicted under all three SSPs. Numbers indicate locations discussed in the text: 1 – Kavango-Zambezi Transfrontier Conservation Area; 2 – Chinko; 3 – Ijara; 4 – Isiolo; 5 – Bicuar and Mupa National Parks; 6 – northern Tanzania; 7 – Kundelungu National Park; 8 – West Lunga National Park; 9 – Bangweulu National Park; 10 – Maasai Mara border; 11 – west Laikipia.

Predicted changes in suitability within recoverable range were minimal (Figure 3.2), with low suitability predicted in the current timestep in most polygons (Figure S3.2). The consensus maps, however, show predicted increases in suitability in Kundelungu National Park in the Democratic Republic of the Congo (DRC) at both periods (Figures 3.3 & 3.4), and the West Lunga and Bangweulu National Parks in Zambia in the 2041-2070 period, but notably these increases aren't predicted in the 2071-2100 period (Figure 3.3 & 3.4). Decreases in suitability were predicted in the recoverable range bordering the Maasai Mara ecosystem, and west Laikipia in Kenya under both time periods, and in Mozambique's Zinave National Park in the 2071-2100 period (Figure 3.3 & 3.4).

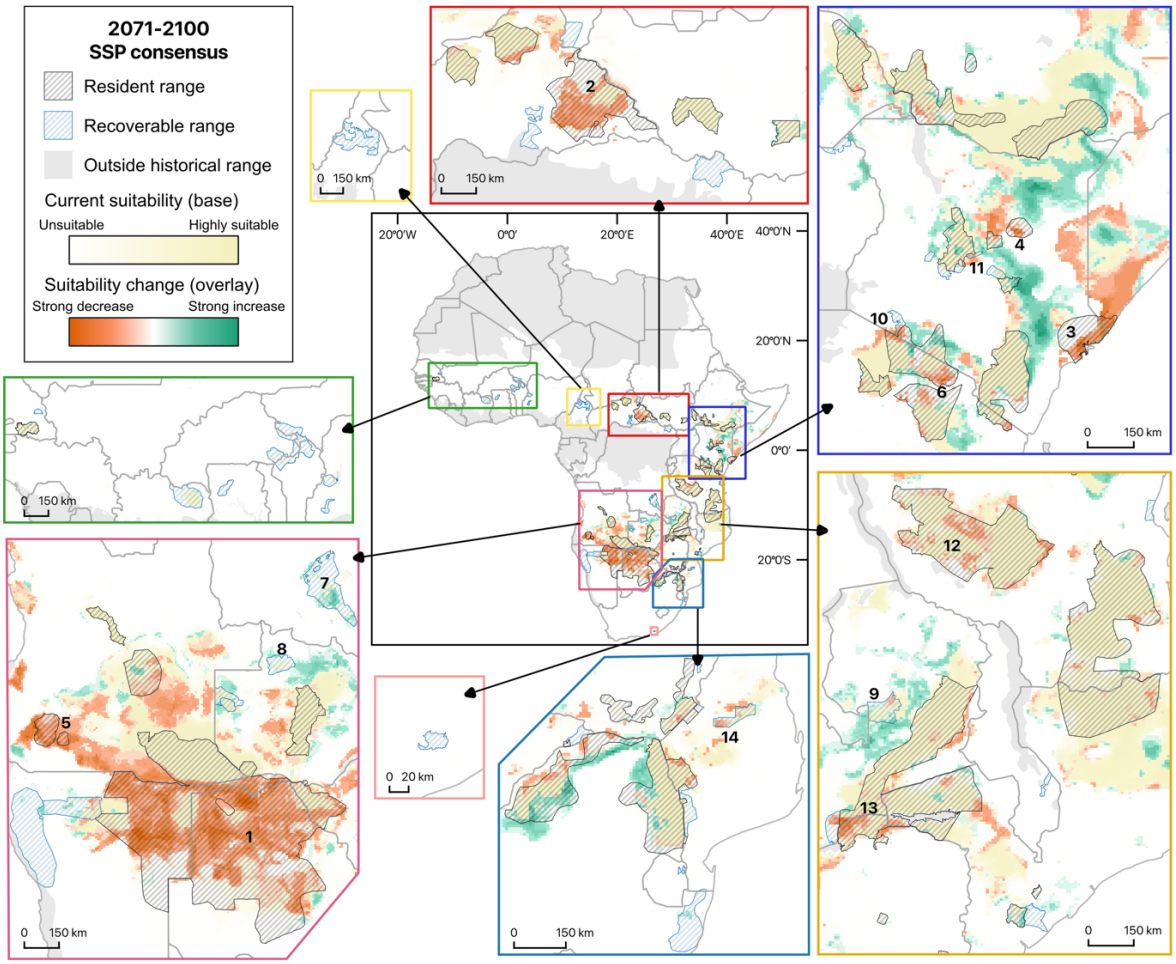


Figure 3.4. Predicted change in habitat suitability for wild dogs in the period 2071-2100 compared to current suitability, with a focus on expert-defined resident and recoverable range polygons (IUCN/SSC, *in prep-a,* IUCN/SSC, 2015, IUCN/SSC, 2024), as modelled by five cross-validated multi-scale Boosted Regression Tree models. Suitability change is on a scale of -1 to 1; thresholds for extreme, strong, and moderate increase or decrease are ±0.75, ±0.5, and ±0.25 respectively for each SSP, with change summed across three SSPs to give the SSP consensus. Strong increase/decrease indicates where strong increase/decrease in a given pixel is predicted under all three SSPs. Numbers indicate locations discussed in the text: 1 – Kavango-Zambezi Transfrontier Conservation Area; 2 – Chinko; 3 – Ijara; 4 – Isiolo; 5 – Bicuar and Mupa National Parks; 6 – northern Tanzania; 7 – Kundelungu National Park; 8 – West Lunga National Park; 9 – Bangweulu National Park; 10 – Maasai Mara border; 11 – west Laikipia; 12 – Rungwa-Ruaha; 13 – Mana Pools surrounds; 14 – Zinave National Park.

3.3.3. Predictor importance and changes over time

All the included predictors influenced the model and were hence retained and accounted for when fitting trees (Table 3.2). The most influential predictors were human population density, annual precipitation, and shrubland cover (Table 3.2). However, decreases in habitat suitability between the current and future time periods were often associated with greater temperature increases in Tmax range, Tmax annual, and Tmin annual, along with increases in cropland cover and decreases in shrubland cover (Figure S3.3). These relationships were more pronounced for some scenarios than others, for example a strong skew towards loss of shrubland in pixels for which habitat

Table 3.2. Scale selected for each predictor variable from univariate models, and mean relative influence of each of these variables from resulting five-fold cross-validated multi-scale Boosted Regression Tree models, with standard deviation (SD). Protected Area (PA) layers were not included in scale selection, and were retained at their native 100 km^2 scale.

Variable	Scale selected (km^2)	Mean relative influence	SD
Humans	3,000	18.01	3.27
Precipitation annual	3,000	16.68	3.44
Shrub	3,000	15.91	4.49
PA strictness	-	9.79	5.21
Precipitation seasonality	100	9.22	3.01
PA area	-	8.82	5.33
Tmax range	1,500	7.92	3.34
Tmax annual	3,000	3.55	0.59
Tmin annual	3,000	3.28	0.81
Forest	3,000	2.91	0.70
PA distance	-	1.57	0.32
Crop	3,000	1.51	0.34
Grass	3,000	0.74	0.47
Urban	3,000	0.10	0.04

suitability decreased under SSP 3-7.0 in the 2071-2100 period (Figure S3.3), and a high proportion of pixels which lost suitability associated with extreme increases in Tmax annual in SSP 5-8.5 in the 2071-2100 period (Figure S3.3). Changes in predictor values within patches of increased and decreased suitability in resident and recoverable range polygons are reported in Tables S3.1-S3.6.

3.4. DISCUSSION

Our findings indicate that the combined effects of climate and land-use change are projected to reduce habitat suitability for African wild dogs across the continent under high-emissions scenarios relative to present-day conditions, and within their current resident range under all emissions scenarios. In our model outputs, suitability is a continuous metric, with higher values indicating more favourable habitat, rather than a binary prediction of realised presence/absence (Guillera‐Arroita et al., 2015). Accordingly, projected declines in suitability should not be interpreted as range contractions, but rather as reductions in the relative quality of environmental conditions. Evidence suggests that environmental suitability can correlate with demographic parameters such as abundance, carrying capacity, or population density (Weber et al., 2016, VanDerWal et al., 2009), although this relationship is not universal (Dallas and Hastings, 2018). Therefore, the predicted decreases in suitability identified here are most appropriately interpreted as potential constraints on population persistence, rather than explicitly forecast local extirpations.

3.4.1. Predictors of change

We identified patterns of change in climate, human pressure, and land cover associated with shifts in wild dog habitat suitability. Human population density, rainfall, and shrubland cover were the three most influential predictors of habitat suitability overall (Table 3.2), although their importance in explaining current suitability did not always translate directly into a consistent association with projected changes in suitability. In particular, greater increases in maximum and minimum temperatures were linked to declines in suitability, as were increases in cropland cover and reductions in shrubland cover (Figure S3.3, Tables S3.1-S3.6). This pattern reinforces the importance of considering multiple aspects of environmental change when predicting future habitat suitability for a given species (Williams et al., 2019). The influence of land cover change on habitat suitability is evident in the SSP 3-7.0 predictions resulting in greater net decreases than under the higher emissions of SSP 5-8.5 (Figure 3.2). SSP3-7.0 represents larger human population growth, more extensive land conversion, and weak international cooperation (IPCC, 2021); the impacts of these factors appear to outweigh those of the more severe warming projected under SSP5-8.5.

Human population density was the most influential predictor in the models (Table 3.2), consistent with evidence that wild dogs are particularly sensitive to anthropogenic pressure through habitat degradatopm, persecution, and disruption of movement across human-dominated landscapes (Woodroffe et al., 2007, Cozzi et al., 2020). However, projected changes in human population density were not consistently associated with changes in habitat suitability (Figure S3.3). This may reflect the concentration of future population growth in pixels surrounding existing urban and densely settled areas (United Nations, 2025), many of which are already unsuitable for wild dogs, such that further increases in human population size result in relatively little additional change in predicted suitability for wild dogs. Therefore, whilst human density is important in determining the current spatial distribution of suitable habitat, changes in climate and land cover appear to be more influential in driving future suitability shifts.

Pixels predicted to experience decreased habitat suitability for wild dogs were often characterised by marked rises in both mean daily minimum and maximum ambient temperatures, particularly under SSPs 3-7.0 and 5-8.5 (Figure S3.3), suggesting that some parts of the continent may become prohibitively hot for wild dogs. High ambient temperatures have been linked to reduced activity, increased mortality, and reduced reproductive success in the species across multiple sites (Pomilia et al., 2015, Rabaiotti et al., 2021, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017, Abrahms et al., 2022). Although wild dogs historically occupied a broad climatic range, this does not

guarantee that the species is resilient to extreme conditions. Rather, the breadth of their distribution could reflect local adaptation by different populations (Atkins and Travis, 2010, DeMarche et al., 2019), with populations inhabiting the hottest regions potentially already living close to their thermal limits, leaving little scope for further acclimatisation and rendering them particularly vulnerable to future climate change (Hetem et al., 2014). A deeper understanding of the mechanism by which high temperatures limit wild dogs across their current range would be beneficial to mitigate the impact of climate change on a local scale.

Shrubland cover was the predictor with the third-highest mean relative influence in our models (Table 3.2), and declines in habitat suitability were frequently associated with reductions in shrubland within surrounding pixels (Figure S3.3). However, the opposite pattern – apparent increases in suitability coinciding with expansions of shrubland cover, often alongside declines in cropland – should be interpreted with caution. The future land-cover layers used here do not incorporate the ecological processes underlying landscape recovery (Chen, 2022), and as a result, pixels projected to transition out of cropland are often automatically reclassified as shrubland, without accounting for the timescales required for such recovery to occur. We therefore suggest that increases in habitat suitability are potentially overpredicted here.

Two additional limitations may mean that future declines in habitat suitability are underestimated. First, due to a lack of data, prey availability was not explicitly represented in the models, despite evidence that anthropogenic prey depletion can constrain population persistence (Goodheart et al., 2021, Reyes de Merkle et al., 2024). Areas projected to retain favourable climatic and land cover conditions may therefore be less able to support wild dogs if prey populations decline under increasing hunting or other anthropogenic pressures. Second, protected area status was held constant across future scenarios. However, legal protection may be downgraded or removed in the future, while human population growth and land conversion may also erode habitat quality and management effectiveness even within areas that remain formally protected (Chiaka et al., 2024, Li et al., 2026). In not accounting for these processes, the models may overestimate the suitability of future habitat, making the projected declines comparatively conservative.

3.4.2. Predictions within *resident* range

Our models predicted a decrease in suitability (of at least -0.25) in at least 11.2% of present-day resident wild dog range (Figure 3.2 – scenario 2041-2070 SSP 1-2.6), and up to 32.1%, including strong or extreme decrease in approximately 17% (Figure 3.2 – scenario 2071-2100 SSP 3-7.0), indicating that wild dog habitat quality is forecast to decline regardless of climate change scenario.

Of particular concern is the widespread decrease in suitability in the KAZA region of Southern Africa, which is forecast under all scenarios, and worsens in severity between the two periods considered (2041-2070 and 2071-2100) (Figure 3.1, 4-5). Already characterised by a hot climate, predicted decreases in suitability within this area were associated with substantial increases in temperature and decreases in rainfall under all scenarios (Tables S3.1-S3.6), rendering it an increasingly challenging environment to inhabit. This area is the largest remaining stronghold of wild dogs today, with an estimated population of approximately 220 packs (almost a third of the global total), spanning international borders of five countries (Woodroffe et al., 2025). As such, a significant reduction in the size of this population could influence the species' global status. The largest portion of KAZA forecast to remain suitable in the future is located in Angola (Figure 3.3 & 4), a country for which wild dog residency was confirmed only within the last decade (Nieman, 2023, Overton et al., 2020) and where rapid land use change already threatens population persistence (IUCN/SSC, *in prep-b*). Prior to these recent efforts, knowledge of the species' distribution in Angola was very limited, as is the case for wider biodiversity nationwide, following decades of civil war (Huntley et al., 2019). Anthropogenic impacts on wildlife in Angolan KAZA (Luengue-Luiana and Mavinga National Parks) remain high (Petracca et al., 2019, Nieman and Botha, 2023), making their mitigation a potential global conservation priority for wild dogs to secure the future of the species' largest remaining population.

Central Africa's remaining African wild dog population is confined to the CAR (Figure S3.1), with its primary stronghold in and around Chinko National Park in the south-east. Our models predict progressively severe declines in habitat suitability across scenarios in this region (Figures 3.1, 3.3-3.4), associated with substantial projected increases in temperature and rainfall (Tables S3.1-S3.6). This population was only recently reconfirmed following prolonged armed conflict (Hickisch and Aebischer, 2013), and subsequent monitoring has already documented marked declines associated with increasing human pressure (Aebischer et al., 2020). Given the geographic isolation of this population, further climate- and land-use-mediated reductions in habitat suitability may compound existing anthropogenic threats, increasing the risk of local extirpation. Loss of this population would represent an irreversible erosion of regional biodiversity and the disappearance of a unique and potentially irreplaceable component of the species' genetic diversity (Ramage, *in review*).

Predicted change in habitat suitability remained negligible in several wild dog *resident* range polygons, including South Africa's Kruger National Park, Kenya's Tsavo National Parks, and Zambia's Kafue and Luangwa National Parks (Figures 3.3-3.4), which together support approximately 20%

of the global population (Woodroffe et al., 2025). Notably, the wild dogs at these sites are primarily threatened by snaring, causing both direct mortalities and prey depletion (Goodheart et al., 2021, IUCN/SSC, *in prep-a,* IUCN/SSC, *in prep-b*). Similarly, predicted change in suitability was negligible within Senegal's Niokolo-Koba National Park (Figure S3.1), which is promising for west Africa's last known wild dog population. This population is, however, small (estimated at 30 individuals), and threatened by road traffic collisions (IUCN/SSC, 2024). The stability of these areas as safeholds for wild dog populations should be ensured by continued conservation efforts to understand and mitigate these threats. In addition, notable areas bordering *resident* range that were predicted to experience a strong increase in suitability were located in Kenya and Zambia (Figures 3.3-3.4). These areas could represent the potential for localised range shifts and expansions, offering some further promise for the species under an increasingly extreme future climate.

3.4.3. Predictions within *recoverable* range

Habitat suitability within *recoverable* range was predicted to remain predominantly unchanged in future scenarios (Figures 3.2-3.4), which is reflective of the current low suitability of much of this range in the current prediction (Figure S3.2). Increases in suitability are predicted to cover larger areas than decreases across scenarios, however these predicted increases are almost entirely moderate changes rather than strong or extreme (Figure 3.2).

As the most depleted region of wild dog historical range, West Africa could be considered a priority region for potential reintroduction efforts, with several *recoverable* polygons identified by regional experts (Figure S3.1). Of these, suitability was largely predicted to be unchanged across scenarios, reflecting mostly low suitability in the current projection (Figure S3.2). We note that low predicted suitability of the region might, however, be biased by the small proportion of pseudo-presence points from west Africa used to parameterise the models, resulting from the species' limited known extent at present. The most promising potential reintroduction site within the region these appears to be Côte d'Ivoire's Comoé National Park, where suitability was predicted to be sustained under all scenarios (Figures 3.1, 3.3-3.4). This park is among the largest protected areas in west Africa, and wildlife recovery has been promising following years of civil war (Scholte et al., 2025). Comoé is also under consideration for possible reintroductions of the lion (*Panthera leo*), regarding which local perceptions appear positive (Janvier et al., 2023) – further study of attitudes towards potential wild dog reintroductions would be beneficial to aid in determining viability.

Elsewhere, Kundelungu National Park in DRC was predicted to increase in suitability across scenarios (Figures 3.1, 3.3-3.4). There is very little published literature available considering

Kundelungu, making inferences about its potential for reintroductions challenging. A 2008 report, however, details critical wildlife depletion (Vanleeuwe et al., 2009), which likely indicates a lack of a sufficient prey base for wild dogs. Extensive anthropogenic impacts, including bushfires, associated deforestation, and agricultural development, are additionally documented over more recent years (Sikuzani et al., 2023). A full evaluation of the capacity of any proposed reintroduction site to sustain wild dogs should be undertaken prior to any reintroduction attempt. Careful consideration should also be given to possible source populations for any such reintroductions, considering genetic diversity and potential local adaptation (IUCN/SSC, 2013, Ramage, *in review*).

3.4.4. Conservation implications

Our results indicate that climate and land-use change are likely to reshape the environmental landscape for African wild dogs over the coming century, with net declines in habitat suitability projected across much of the species' current resident range. Although these changes do not imply inevitable range collapse, they signal increasing constraints on populations within several of the species' most important strongholds. Notably, the high land conversion scenario (SSP 3-7.0) was associated with the most extensive predicted declines in suitability, underscoring the importance of considering land-use change alongside climate change and highlighting local governance as a critical determinant of wild dog persistence.

We therefore suggest that wild dog conservation planning should begin to integrate forward-looking projections of habitat suitability to enable proactive safeguarding of populations. Reducing anthropogenic mortality, maintaining or restoring landscape connectivity, and strengthening transboundary cooperation may prove essential for securing populations both in regions projected to face substantial decreases in suitability (e.g. KAZA and Chinko), and in areas expected to function as relative refugia (e.g. Kruger, Tsavo, and Luangwa). Integrating climate-informed planning into ongoing conservation efforts will be key to enhancing the species' long-term resilience under accelerating environmental change.



CHAPTER 4 | A Recipe for Hot Dogs: physiological vulnerability to increasing air temperatures in a coursing predator

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AUTHOR CONTRIBUTIONS

AF, LM, RH, LB, and RW conceived the study and developed the methodology. CP, DR, DN, JR, JW, KJ, LM, and RG collected the data. JFL curated the data, performed the analyses, and wrote the manuscript. CD and CM assisted with analysis. RW and CD provided supervision. AF, CM, CD, RH, and RW critically reviewed and edited the manuscript. This author list is currently unconfirmed and will be finalised for publication.

A Recipe for Hot Dogs: physiological vulnerability to increasing air temperatures in a coursing predator

ABSTRACT

Large terrestrial carnivores are declining globally and may be especially vulnerable to climate change due to their high energetic demands, large home ranges, and low population densities. The endangered African wild dog (*Lycaon pictus*) has been identified as sensitive to rising air temperatures, yet the physiological mechanisms underlying this vulnerability remain unclear. As cursorial predators, wild dogs experience substantial heat loads during hunting, which may constrain activity under high environmental temperatures. We measured body temperature in 13 free-living wild dogs across four sites in southern Africa using implanted temperature-sensitive loggers, alongside concurrent activity data from eight individuals collected via accelerometer collars. Body temperature was recorded for 8-15 months per individual, and activity for 2-9 months. Wild dogs exhibited marked inter-individual variation in body temperature, with diel profiles atypical of large mammals. In half of the individuals, body temperature closely tracked activity patterns. Generalised additive mixed-effects models revealed a rapid increase in body temperature with activity, with effects persisting for up to 30 minutes and intensifying at higher air temperatures. Under conditions of high activity and high air temperature, predicted body temperatures approached levels associated with heat illness in domestic dogs. When two individuals were temporarily held in enclosures, mean, maximum, and diel range of body temperature were all lower than under free-living conditions. As high activity levels are indicative of hunting behaviour, these findings suggest that wild dogs likely limit hunting at high air temperatures to avoid hyperthermia. Under increasing thermal extremes, such constraints may reduce time available for hunting, potentially limiting food intake and leading to negative demographic consequences for this endangered species.

4.1. INTRODUCTION

Large terrestrial carnivores are essential for maintaining biodiversity and ecosystem function, yet 77% of their populations are in global decline (Ripple et al., 2014). Their high energetic demands, large home ranges, slow life histories, and low population densities increase large carnivores' extinction risk (Hilbers et al., 2016) and may make them particularly vulnerable to climate change (Fuller et al., 2016). While many studies focus on indirect, climate-mediated impacts – such as shifts in habitat suitability and geographic range (Jones and Harris, 2025, Mitchell et al., 2024, Zhang et al., 2025, Rezaei et al., 2023, Mohammadi et al., 2022) – climate can also exert direct physiological stress through increasing air temperatures and reduced water availability, independent of habitat change (Fuller et al., 2026).

Such direct impacts of climate on animals arise through weather-driven effects on physiology and behaviour, which in turn influence reproduction and survival. Understanding these physiological responses is therefore essential for predicting climate change impacts at species, population, and ecosystem levels (Helmuth et al., 2005, Seebacher and Franklin, 2012, Hetem et al., 2014, Mitchell et al., 2018). To reduce heat exposure, increase heat loss, or reduce metabolic heat gain, endotherms frequently thermoregulate behaviourally, including reducing activity levels or seeking shade during the heat of the day (Beever et al., 2017). These responses can, however, incur opportunity costs by limiting investment in essential behaviours such as foraging, mating, or offspring care (Cunningham et al., 2021), potentially compromising energetically demanding but essential activities (Hetem et al., 2014).

Hunting represents one of the most energetically taxing behaviours performed across taxa (Williams et al., 2020), generating heat and therefore requiring significant evaporative cooling reliant on adequate water balance. Cursorial hunting, in particular, requires both sustained locomotion and high-intensity chases, requiring substantial energetic expenditure and imposing measurable constraints on energy balance (Gorman et al., 1998). High-resolution movement studies show that even short, opportunistic chases can entail considerable energetic costs, shaping the trade-off between energy gain and expenditure (Hubel et al., 2016b). Understanding how thermophysiological constraints interact with the energetic costs of hunting is therefore central to predicting climate change impacts on cursorial predators.

The African wild dog (*Lycaon pictus*, hereafter "wild dog") is a highly social and endangered cursorial predator (Woodroffe et al., 2025). Once widespread across sub-Saharan Africa, the species now persists in only 8.5% of its historical range, with fewer than 700 packs remaining

(Woodroffe et al., 2025). Wild dogs hunt through long-distance searching followed by high-speed chases (Creel and Creel, 2002), and activity is largely restricted to cooler periods around dawn and dusk, declining at higher air temperature (Pomilia et al., 2015, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017, Rafiq et al., 2023). Although increased nocturnality has been observed following days with high air temperature, this behavioural shift does not fully compensate for reduced daytime activity (Rabaiotti and Woodroffe, 2019), likely due to constraints imposed by moonlight availability (Cozzi et al., 2012, Ngatia et al., *in review-b*).

Elevated air temperature has also been linked to demographic consequences in wild dogs. Across the majority of the species' range, the energetically costly denning period coincides with the coolest time of year (McNutt et al., 2019), and higher air temperature during this period is consistently associated with reduced pup survival (Woodroffe et al., 2017). Increasingly warm denning conditions over the last three decades in Botswana have coincided with reduced reproductive success (Abrahms et al., 2022). High air temperature has also been linked to longer inter-birth intervals (Woodroffe et al., 2017) and increased adult mortality (Rabaiotti et al., 2021). Accordingly, climate change is projected to pose substantial risks to wild dog population persistence (Rabaiotti et al., 2023).

The mechanisms underlying the relationships between air temperature and wild dog demography remain unresolved. It has been hypothesised that high air temperature constrains hunting activity (Woodroffe et al., 2017), with wild dogs capitalising on hunting windows around dawn and dusk that are sufficiently cool, whilst also sufficiently light (Hubel et al., 2016b). Reduced hunting time, or hunting under hotter conditions with higher thermoregulatory costs, could decrease net energy gain and limit investment in reproduction, including pup provisioning and lactation. Other research has proposed that warmer conditions may, conversely, enhance wild dog hunting outcomes by imposing greater heat constraints on large prey species (Creel et al., 2016). However, greater kill rates observed at higher air temperature in the Selous Game Reserve of Tanzania were not accompanied by increased food intake (Creel et al., 2016) and thus did not translate into greater energetic returns.

As coursing, predominantly diurnal predators (Frame et al., 1979), wild dogs experience substantial heat loads during exercise that must be dissipated or stored (Taylor et al., 1971). For endurance hunters, undergoing hyperthermia due to reducing evaporative cooling may conserve body water and make it possible to extend chase duration (Taylor et al., 1971). A treadmill study using one tame, juvenile wild dog found that rectal temperature did indeed increase under high air temperature (>35°C) during exercise, suggesting reliance on heat storage (Taylor et al., 1971).

Similarly, cheetah (*Acinonyx jubatus*) displayed low evaporative water loss and high rectal temperature in a comparable treadmill study (Taylor and Rowntree, 1973). However, free-living cheetah showed no comparable increase in body temperature during their high-speed chases (Hetem et al., 2013), indicating that these experiments did not reflect natural hunts accurately. To our knowledge, body temperature has not been reported to date in any free-living coursing predator. An improved understanding of the influence of combined exercise and environmental heat loads on wild dog body temperature and hyperthermia is therefore fundamental to reconcile contrasting perspectives surrounding how climate change may impact the species, along with other coursing predators.

In this study, we measured body temperature and activity in free-living wild dogs across four sites in southern Africa, using implanted temperature-sensitive loggers and accelerometer collars. Our objectives were to (i) describe body temperature profiles in free-living wild dogs for the first time, and (ii) examine how activity and air temperature influence body temperature. More broadly, we aimed to improve understanding of wild dog thermophysiology and to elucidate the mechanistic pathways through which climate change may impact this endangered species.

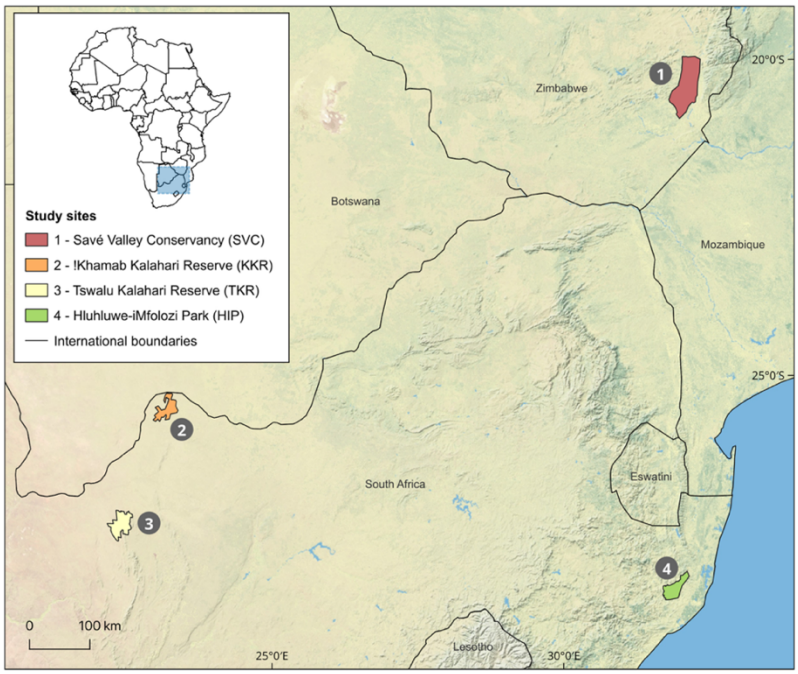


Figure 4.1. Locations of the four study sites in Southern Africa at which African wild dogs were fitted with temperature-sensitive data loggers and Daily Diary accelerometer collars between 2021 and 2022.

4.2. METHODS

4.2.1. Study sites

Data were collected in 2021 and 2022 at four sites in southern Africa: Savé Valley Conservancy in Zimbabwe (32°00'E, 20°05'S - SVC), and !Khamab Kalahari Reserve (23°12'E, 25°31'S - KRR), Tswalu

Kalahari Reserve (22°28'E, 27°12'S - TKR), and Hluhluwe-iMfolozi Park (31°56'E, 28°13'S - HIP) in South Africa (Figure 4.1). SVC lies in the semi-arid lowveld, KKR and TKR in the semi-arid Kalahari, and HIP in more mesic, humid savanna. All four sites share the hot wet summers and cool dry winters typical of southern Africa, but differ in their air temperature and rainfall profiles, as observed during our study period. KKR and TKR showed the greatest seasonality, with marked daily air temperature ranges (Figure 4.2). SVC and HIP were more thermally stable across the year but differed in rainfall regime: SVC experienced the highest total rainfall, concentrated between December and March, while HIP received relatively low and less seasonally concentrated rainfall (Figure 4.2).

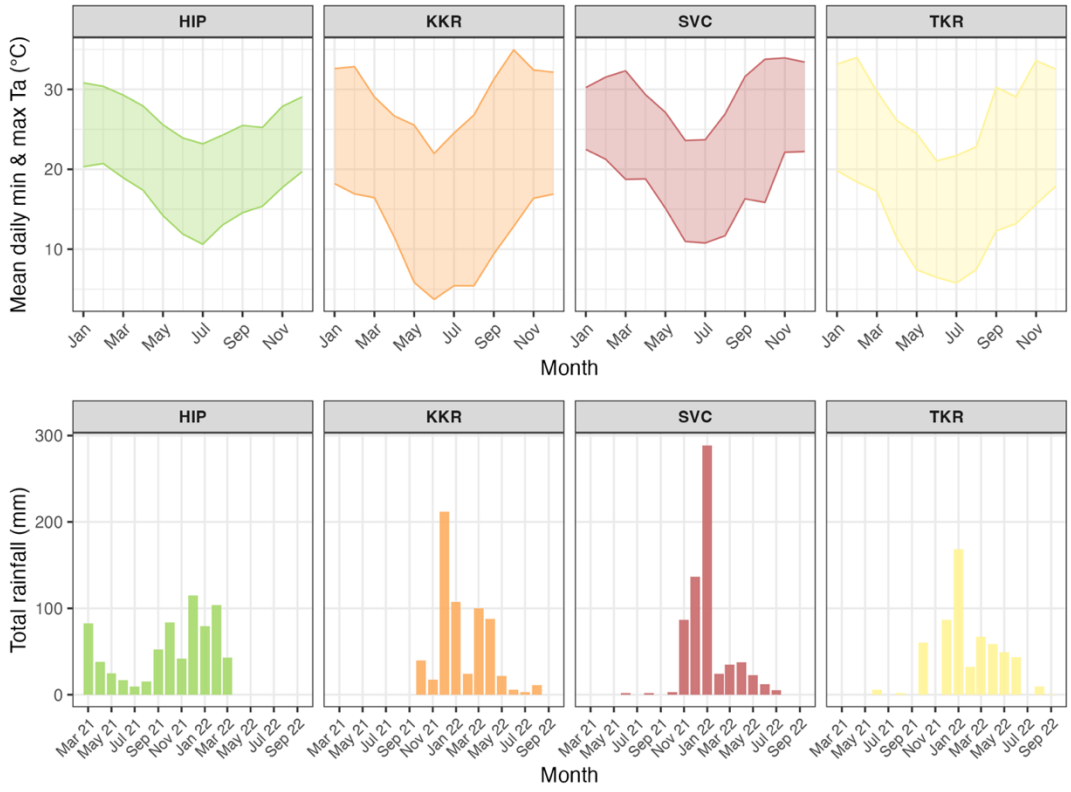


Figure 4.2. Mean daily minimum and maximum air temperature (T_a, °C), and total rainfall (mm) per month recorded at weather stations local to each of the four study sites. Sites correspond with locations in Figure 4.1. See Supplementary Material for weather station details.

4.2.2. Data collection

4.2.2.1. Study animals

Data were collected from 14 wild dogs across the four study sites for a period of up to 15 months, as follows: six animals across three packs at SVC, three animals from a single pack at KKR, two from a single pack at TKR, and three from a single pack at HIP (Table S4.1).

4.2.2.2. Approvals

Approval for this research was granted by the ethics committees of the Zoological Society of London (project BPE/0510), the University of the Witwatersrand (2019/11/65/C), the University of Pretoria (REC048-20), and the Endangered Wildlife Trust (EWTEC2019_008), along with national and regional research authorities (Zimbabwe Parks and Wildlife Management Authority: 153/5/ST/C, Northern Cape Province: OP 1562/2020, North West Province: NW/16145/03/2020, Ezemvelo KZN Wildlife: OP 1562/2020). All procedures involving animal capture, anaesthesia, surgery, recovery, and monitoring followed approved ethical protocols, with full methodological details provided in Woodroffe et al. (2026) (Appendix E, page 160).

4.2.2.3. Wild dog body temperature data

Wild dog body temperature data were collected using miniature temperature-sensitive data loggers, each weighing 3.3g and measuring 25mm x 8mm x 8mm (DST-micro-T with extended memory; Star-Oddi, Gardabaer, Iceland) and coated in inert wax. These loggers record temperature at a five-minute resolution for an estimated 455 days of battery life. Prior to deployment, the loggers were calibrated against a calibration thermometer in an insulated water bath over the range of expected body temperatures (34°C-42°C), with a resulting accuracy of within 0.1°C (Figure S4.1). Study animals were chemically immobilised via darting by experienced wildlife veterinarians, then maintained under anaesthesia at a nearby mobile surgical station. Following aseptic preparation, a small ventral midline incision was made, and a sterilised data logger was implanted retroperitoneally between the abdominal wall and peritoneum. The incision was sutured in layers, and animals received antibiotics, anti-inflammatories, and topical wound treatments. Study animals were recaptured within 19 months of deployment (Table S4.1) to explant loggers for data retrieval, following the same surgical protocol. Where loggers were still recording post-explant (n = 3), they were calibrated a second time to assess for drift; accuracy remained within 0.1°C (Figure S4.1).

4.2.2.4. Wild dog activity data

Wild dog activity data were collected using bespoke accelerometer collars incorporating a “Daily Diary” (DD) sensor unit (Wilson et al., 2008; Wildbyte Technology Ltd, Swansea, UK), a GPS unit (Technosmart, Rome, Italy), and a VHF beacon (Lotek, Wareham, UK). These collars, hereafter called accelerometer collars, were fitted to the implanted individuals, with the exception of one individual (“Limpy”, Table 4.1), which was fitted with a satellite-linked GPS collar (Vectronic Aerospace GmbH, Berlin, Germany). DDs incorporate a triaxial accelerometer and triaxial magnetometer, recording data on changing body posture, rotation, and dynamism (Wilson et al.,

2008). The DDs were programmed to record data at 20Hz for the duration of their battery life (up to an estimated 11 months). GPS units on the accelerometer collars recorded locations every 20 minutes during typical active (crepuscular) periods, and every hour otherwise. Within each pack, at least one non-implanted individual was additionally fitted with a satellite-linked GPS collar (Vectronic Aerospace GmbH, Berlin, Germany).

4.2.3. Weather data

Hourly air temperature data were sourced from the global ERA5 dataset (Hersbach, 2023) using centroid coordinates from each study site. These modelled data were used for consistency due to failures in on-site weather stations, and their accuracy was validated against available on-site measurements, as described in the supplementary material (Appendix C, page 144).

4.2.4. Data processing

The first week of post-capture data were excluded from analyses, to avoid potential alterations in activity or body temperature associated with recovery from immobilisation and implant surgery. Concurrent GPS data from accelerometer and satellite collars were used to identify and exclude periods during which study individuals separated from their packs for at least one day, as such dispersal or excursion events are associated with changes in behavioural state (Woodroffe et al., 2020), which may influence body temperature. Two individuals at the HIP site were housed in enclosures ('bomas', approximately 100m x 80m in size) for species management purposes for several months during the study period (Table S4.1) (Marneweck et al., 2019), which provided an opportunity to assess wild dogs' body temperature when they were not undertaking natural hunting activity. Data collected during these captive periods were hence retained for statistical comparison between body temperature whilst captive versus free-living, but were excluded from other analyses.

Body temperature data were screened for erroneous recordings by searching for instances of abrupt changes (>3°C) that were reversed (within 0.5°C) across the subsequent four data points (20 minutes). No such errors were found. Potential for logger temperature drift over time was also assessed, first visually, followed by breakpoint analysis for one individual ('Johnnie') which displayed possible downward drift, resulting in the exclusion of five months of body temperature data (Figure S4.6).

To measure wild dog activity, we used the metric 'vectorial dynamic body acceleration' (VeDBA), which is a is a reliable proxy for movement-related energy expenditure (Wilson et al., 2020). VeDBA was obtained from the DD accelerometer data via the software DDMT (Daily Diary Multiple Trace;

Wildbyte Technologies Ltd., UK; available from https://github.com/DDMT-Software/DDMT), with a 4 second smoothing window (Shepard et al., 2008).

As light is the primary zeitgeber regulating mammalian circadian rhythms (Golombek and Rosenstein, 2010), and wild dog activity is largely crepuscular (Woodroffe et al., 2017), we transformed clock time to solar time for use in analysis using the package *activity* (Rowcliffe, 2023) in R (R Core Team, 2024), which anchors sunrise and sunset to π/2 and 3π/2 to control for seasonal differences (Vazquez et al., 2019).

4.2.5. Data analysis

Analyses were carried out in R version 4.5.1. (R Core Team, 2024). To bring all predictor variables to the same temporal resolution, we used the R package *zoo* (Zeileis A and G., 2005) to interpolate 5-minute air temperature data from the hourly dataset. VeDBA values (measured in units of gravitational acceleration, g) were summed over the five minutes preceding each body temperature timestamp, to give a cumulative VeDBA measure (VeDBA_sum).

4.2.5.1. Characterising Body temperature profiles

To characterise wild dog body temperature profiles, we calculated individual summary statistics including the diel (24-hour) body temperature mean, maximum, minimum, and range (maximum-minimum). To examine diel patterns, body temperature, air temperature, and VeDBA values were also averaged across days at each solar time (rounded to one decimal place, equivalent to approximately 25 minutes) producing mean diel profiles. The diel period considered throughout was midnight to midnight.

For the two wild dogs taken into temporary captivity during our study, we compared diel body temperature mean, maximum, minimum, and range whilst free-living versus captive, via separate linear models, with individual identity included as a fixed effect.

4.2.5.2. Body temperature modelling

To investigate the relationship between free-living wild dog body temperature, activity, and air temperature, we fitted generalised additive mixed effects models (GAMMs) using the R package *mgcv* (Wood, 2011), with 5-minute Body temperature as the response variable.

For each body temperature observation, we then generated seven lagged VeDBA_sum covariates corresponding to the same time point (lag 0) up to 30 minutes prior (lags 1-6) to incorporate short-term activity history. Air temperature and VeDBA_sum at lags 0-6 were included as thin-plate

spline smoothing terms (Wood, 2011). We specified tensor-product interactions between each VeDBA_sum lag and T_a, a cyclic cubic smooth for solar time, cyclic smooth of day-of-year (DOY) with penalised individual-level deviations (factor-smooth interactions), a random effect for sex, and a random effect for individual. Due to our sample size representing only a single individual at each of three of the four study sites (Table S4.1), we did not include site as a random effect. To avoid overfitting and allow uninformative variables to be effectively removed, we fitted the model with penalisation and term selection (using select = TRUE), which applies an additional penalty that can shrink smoothing terms to zero if they do not contribute to the model (Wood, 2011).

Model fits using Gaussian, inverse Gaussian, and gamma distribution families yielded near-identical results; we therefore retained the Gaussian GAMM for interpretability, and because residual diagnostics indicated no major violations of model assumptions (Figure S4.7). Smoothing parameters were set using the default basis dimensions (*k*) for each smoothing term (Wood, 2011), which provided stable fits and biologically reasonable effect estimates. We evaluated out-of-sample performance using 10-fold h-block cross-validation, assigning non-overlapping 3-h time blocks per individual to folds to avoid temporal leakage. For each fold, we refitted the GAMM on the remaining data and assessed predictions on the held-out block with Root Mean Squared Error (RMSE), Mean Absolute Error (MAE), proportion of variance explained (R^2), and 95% prediction-interval coverage.

We generated partial-dependence predictions for VeDBA_sum at lags 0-6 across a range of observed air temperature values (15, 20, 25, 30, and 35 °C), predicting body temperature across the observed range of each focal VeDBA_sum lag. All non-focal covariates (solar time, day of year, and non-focal VeDBA_sum lags) were held at their median values, and random-effect terms (individual and sex) were excluded from predictions to yield population-level curves.

4.3. RESULTS

Body temperature data were analysed from 13 individuals, comprising a total of 4,865 days whilst free-living, with 1,550 days of concurrent accelerometer collar data available from eight of these individuals (Table S4.1). The larger logger dataset is due to the longer battery life of the temperature-sensitive loggers, along with a number of collar failures. Data for one individual ('Hlokohloko') were excluded due to her free-living sampling period being only five days (after excluding seven days post-implantation and 86 days spent in captivity), compared with 259-448 days of free-living body temperature data and 70-280 days of DD data for each of the remaining animals (Table S4.1).

Table 4.1. Wild dog body temperature (T_b) diel summary statistics for each of 13 individuals monitored in this study as well as global statistics across individuals. Standard deviation (SD) displayed along with means. 'Boma' indicates where two individuals were taken into captivity for reserve management purposes. * = individuals for which concurrent activity data were successfully recorded and were hence included in modelling.

				T_b (°C)						
Site	**Pack**	**Individual ID**	**Status**	**Mean mean ± SD**	**Mean max ± SD**	**Absolute max**	**Mean min ± SD**	**Absolute min**	**Mean range ± SD**	**Max range**
SVC (1)	Chapungu	Beebee*	Free	37.8 ± 0.2	39.3 ± 0.6	41.8	36.2 ± 0.7	33.7	3.2 ± 0.9	5.9
		Canine	Free	37.6± 0.2	39.3 ± 0.6	41.4	35.9 ± 0.7	31.1	3.5 ± 0.9	7.2
		Pug*	Free	38.3 ± 0.2	39.9 ± 0.6	41.9	37.0 ± 0.4	35.6	2.9 ± 0.7	5.1
	Gentleman	Infinity*	Free	38.4 ± 0.3	40.0 ± 0.7	41.7	37.1 ± 0.5	35.8	2.8 ± 0.8	5.7
	Nova	Johnnie*	Free	37.3 ± 0.3	39.0 ± 0.6	41.0	35.4 ± 0.8	33.0	3.6 ± 1.0	7.3
		Zulu*	Free	38.1 ± 0.2	39.7 ± 0.6	42.7	36.6 ± 0.5	33.9	3.1 ± 0.8	6.3
KKR (2)	North	K21	Free	37.9 ± 0.2	39.5 ± 0.8	42.0	36.7 ± 0.5	34.7	2.9 ± 0.9	5.4
		K23	Free	37.9 ± 0.2	39.6 ± 0.8	41.7	36.7 ± 0.5	33.4	2.9 ± 0.9	5.3
		M28*	Free	37.6 ± 0.2	39.6 ± 0.8	42.0	36.1 ± 0.7	32.6	3.5 ± 1.0	7.7
TKR (3)	Korranaberg	BowlingPin*	Free	37.8 ± 0.3	39.4 ± 0.8	41.9	36.4 ± 0.9	32.1	3.0 ± 1.3	8.0
		Limpy	Free	37.8 ± 0.2	39.6 ± 0.9	42.6	36.3 ± 0.8	31.5	3.3 ± 1.3	9.1
HIP (4)	Mbhulunga	Baboonhand*	Free	38.3 ± 0.2	40.0 ± 0.6	42.7	37.2 ± 0.4	35.5	2.8 ± 0.7	4.9
			Boma	38.0 ± 0.2	39.1 ± 0.5	41.3	36.7 ± 0.5	34.4	2.3 ± 0.7	5.8
		TwoTears	Free	38.4 ± 0.2	40.1 ± 0.6	41.6	37.6 ± 0.4	36.6	2.5 ± 0.6	4.1
			Boma	38.3 ± 0.3	39.3 ± 0.5	40.7	37.5 ± 0.3	36.6	1.8 ± 0.5	3.5
		Global	Free	37.9 ± 0.4	39.6 ± 0.8	42.7	36.5 ± 0.8	31.1	3.1 ± 1.0	9.1

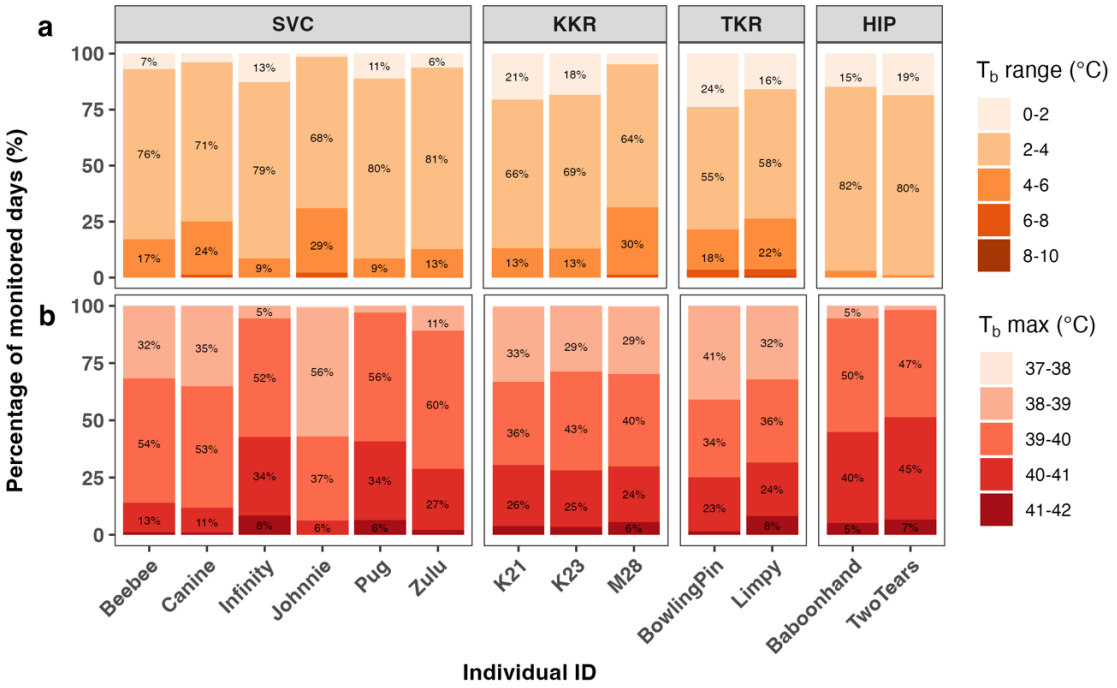


Figure 4.3. Percentage of days within each individual wild dog's monitoring period at which **a** - daily body temperature range (T_b) fell into each of 5 ranges, and **b** - daily maximum body temperature (T_b) fell into each of 5 ranges. Values greater than 5% are displayed. Grouped by site, which correspond with locations in Figure 4.1.

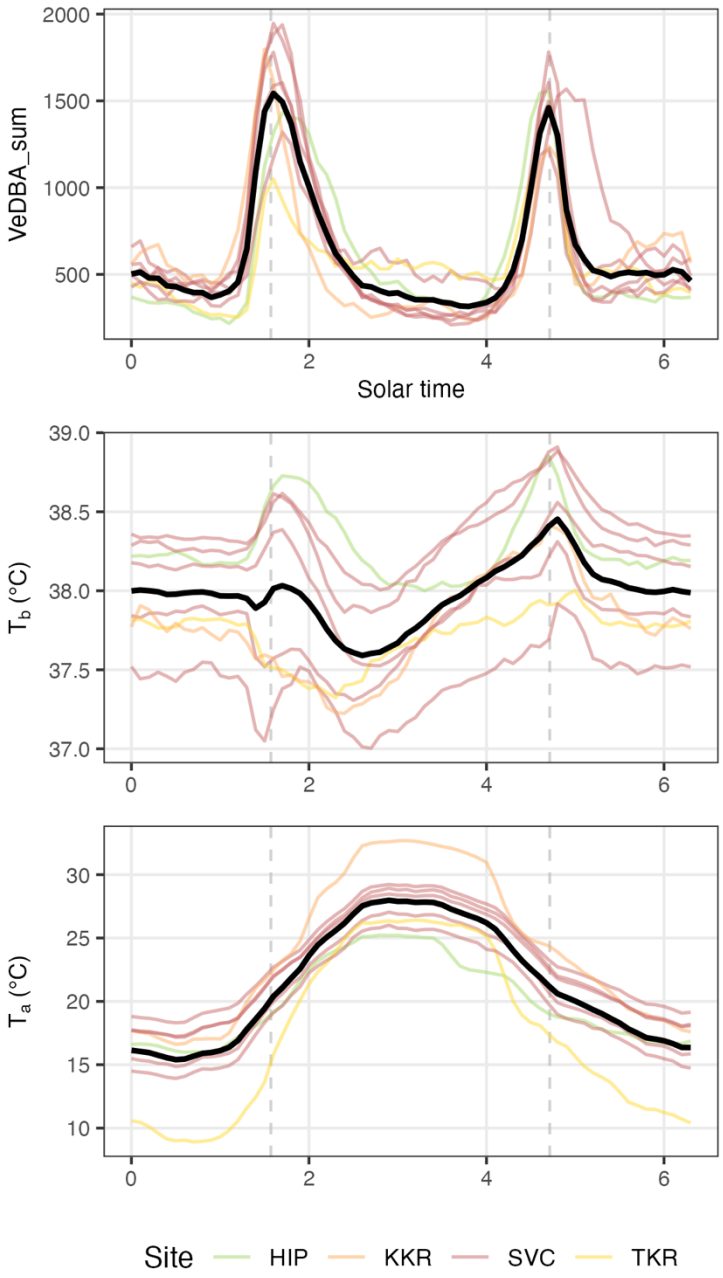


Figure 4.4. Mean diel patterns of VeDBA and body temperature (T_b) across eight African wild dogs, along with air temperature (T_a) during each individual's respective study periods. Data are aligned to solar time (anchoring sunrise and sunset to π/2 and 3π/2, respectively, to control for seasonal differences in light availability (Vazquez et al., 2019). Dashed lines indicate sunrise and sunset. Bold black lines show means across all study animals, while coloured lines represent individual means, coloured by study site. Only periods for which both Tb and VeDBA were collected are displayed (Table S4.1).

4.3.1. Body temperature profiles

Our data revealed marked variation in wild dog body temperature (Table 4.1, Figure 4.3, Figure S4.8). Mean body temperature across free-living individuals was 37.9 (± 0.4°C standard deviation, SD), whilst the highest body temperature recorded was 42.7°C and the lowest was 31.1°C (Table 4.1). Body temperature varied substantially within days, with a maximum observed diel range of 9.1°C (Table 4.1). Across all 13 individuals, body temperature varied by 2-4°C on 55-80% of days and by 4-6°C on 1-30% of days (Figure 4.3a). For 12 of 13 study animals, body temperature

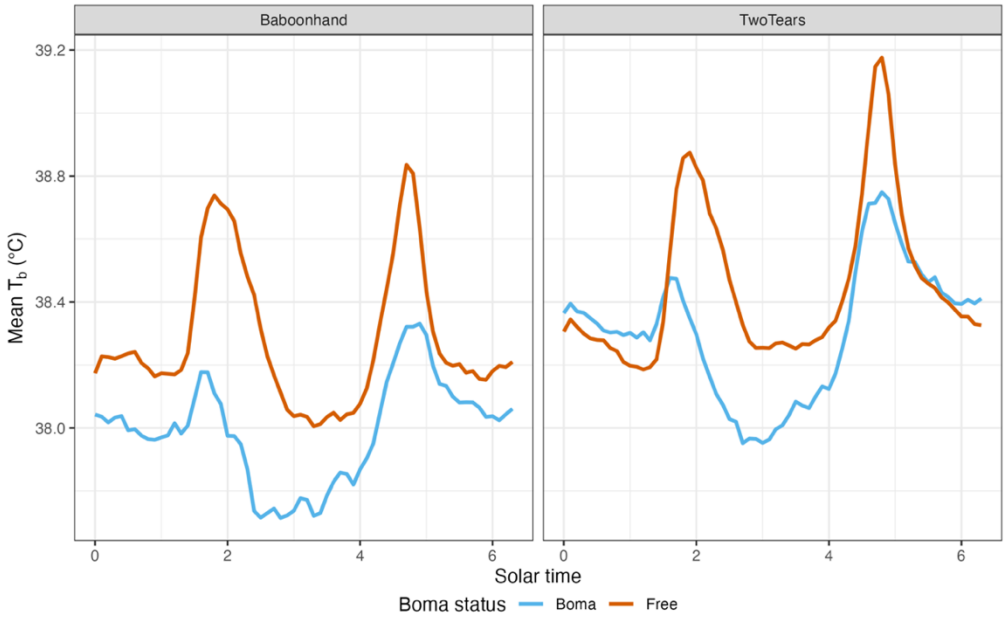


Figure 4.5. Mean diel body temperature (T_b) patterns aligned to solar time (anchoring sunrise and sunset to π/2 and 3π/2 to control for seasonal differences in light availability) for two African wild dogs when free-living ('Free') versus in captivity ('Boma').

exceeded 39°C on the majority of monitored days, reaching between 40 and 41°C on 23-45% of days in 10 individuals (Figure 4.3b).

For the eight individuals with concurrent VeDBA data, mean diel body temperature patterns showed a consistent peak around sunset across all individuals, with an additional peak around sunrise in half of the study individuals (Figure 4.4). Concurrent VeDBA data showed a clear bimodal diel activity pattern across individuals, with peaks occurring around sunrise and sunset, coinciding with the peaks in body temperature (Figure 4.4). Mean diel variation in air temperature experienced by study animals reflected site differences, but showed a universal peak at around mid-day (Figure 4.4).

The two individuals taken into enclosures during the study displayed a bimodal body temperature pattern both when free-living and captive (Figure 4.5). Diel body temperature was, however, lower, and less variable, when captive than when free-living (Figure 4.5, S4.8), with lower diel means (β = -0.23 ± 0.02 SE, $p < 0.001$), maxima (β = -0.83 ± 0.05 SE, $p < 0.001$), minima (β = -0.23 ± 0.03 SE, $p < 0.001$), and ranges (β = -0.60 ± 0.05 SE, $p < 0.001$) when captive, as determined by linear models including individual identity as a fixed effect.

4.3.2. Body temperature modelling

The GAMM explained 42.5% of the variance in body temperature across individuals (adjusted R^2 = 0.425). Significant non-linear relationships were estimated between body temperature and both air temperature and VeDBA_sum (including current, and lagged by up to 30 min; all p<0.001, Table 4.2). Interaction terms indicated that the positive relationship between VeDBA_sum and body temperature varied with air temperature, across lags (Table 4.2). Smooth terms for solar time and day-of-year (DOY) indicated diel and seasonal patterns in body temperature (Figure S4.9). Random intercepts confirmed baseline body temperature differences among individuals but not between sexes (Table 4.2).

Cross-validation indicated that the model predicted body temperature with a mean error of <0.5°C (mean RMSE = 0.49, MAE = 0.37), explaining 42% of the variance, with well-calibrated 95% prediction intervals (coverage ~95%, Table S4.3). These cross-validation performance metrics were consistent across cross-validation folds, indicating stable generalisation (Table S4.3). Predicted

Table 4.2. Generalised Additive Mixed Effects Model (GAMM) output for the association between body temperature (T_b) and activity and environmental variables in eight free-living African wild dogs. T_a = air temperature, VeDBA = Vectorial dynamic body acceleration, DOY = day of year. Thin plate splines are indicated by 's', tensor product interactions are indicated by 'ti'. Lags represent summed VeDBA across 5 minutes from the current time (lag 0), up to 30 minutes prior (lags 1-6).

Variable	edf	F	p-value
s(T_a interpolated)	8.70	763.63	<0.01
s(VeDBA 5-min sum lag 0)	8.51	154.27	<0.01
s(VeDBA 5-min sum lag 1)	8.53	165.65	<0.01
s(VeDBA 5-min sum lag 2)	8.50	98.76	<0.01
s(VeDBA 5-min sum lag 3)	8.41	68.61	<0.01
s(VeDBA 5-min sum lag 4)	8.49	58.36	<0.01
s(VeDBA 5-min sum lag 5)	8.33	50.90	<0.01
s(VeDBA 5-min sum lag 6)	8.40	217.15	<0.01
ti(VeDBA 5-min sum lag 0, T_a interpolated)	11.97	24.44	<0.01
ti(VeDBA 5-min sum lag 1, T_a interpolated)	11.85	25.00	<0.01
ti(VeDBA 5-min sum lag 2, T_a interpolated)	8.63	9.73	<0.01
ti(VeDBA 5-min sum lag 3, T_a interpolated)	8.12	4.89	<0.01
ti(VeDBA 5-min sum lag 4, T_a interpolated)	4.25	1.55	<0.01
ti(VeDBA 5-min sum lag 5, T_a interpolated)	3.59	1.17	<0.01
ti(VeDBA 5-min sum lag 6, T_a interpolated)	8.73	6.94	<0.01
s(Solar time)	7.99	6909.61	<0.01
s(DOY)	7.84	95.15	<0.01
s(DOY, Individual ID)	58.40	66802.42	0.06
s(Sex)	0.00	0.00	<0.01
s(Individual ID)	1.49	0.30	<0.01

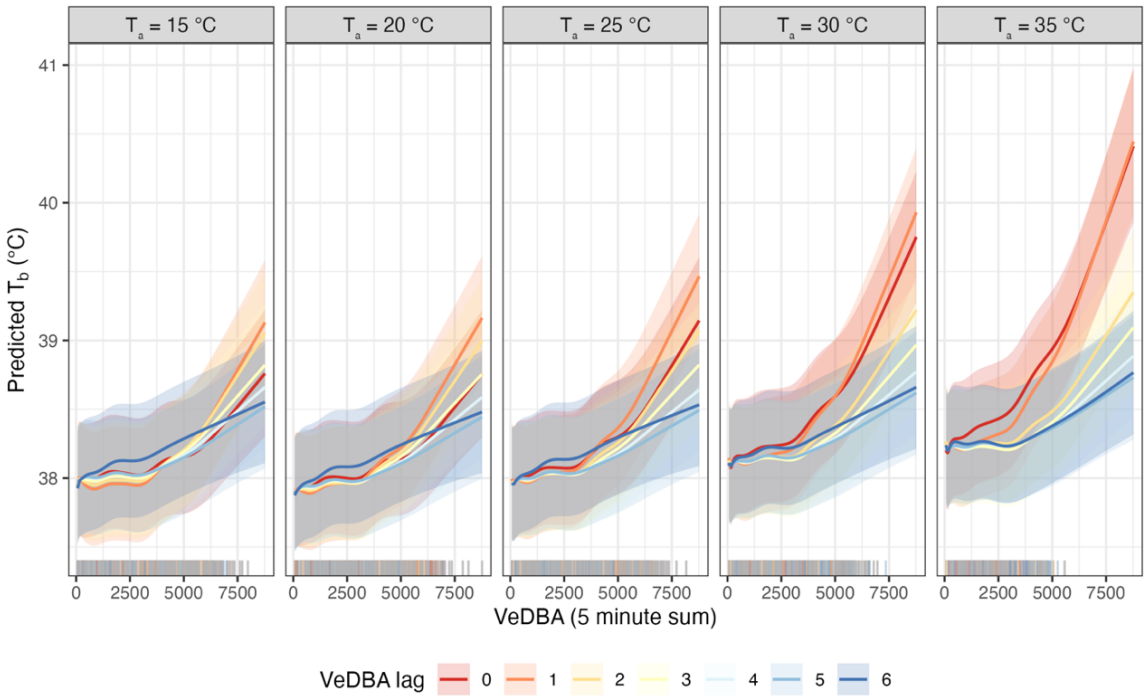


Figure 4.6. Predicted body temperature (T_b) in relation to VeDBA (5-min sums) shown across five observed air temperature values (T_a = 15, 20, 25, 30, 35 °C). Solid lines are GAMM predictions and shaded areas are 95% confidence intervals; rugs show observed VeDBA distributions. Lags represent summed VeDBA across 5 minutes from the current time (lag 0), up to 30 minutes prior (lags 1-6).

body temperature increased non-linearly with activity across all air temperature levels, with a distinct increase in slope at VeDBA_sum values of approximately 3,000 (Figure 4.6), which equates to a mean VeDBA value of 0.5 g over the five-minute interval. The steepest relationships between body temperature and VeDBA_sum, and the highest body temperature values, were predicted at higher air temperature (30-35°C, Figure 4.6). The influence of VeDBA_sum was strongest at short time lags (5-10 minutes), but remained detectable up to lag 6 (30 minutes) (Figure 4.6). Particularly high activity levels (>5,000 VeDBA_sum, corresponding to a mean VeDBA of 0.83 g over a five-minute interval) were rarely observed at the higher air temperature values (Figure 4.6, Figure S4.10).

4.4. DISCUSSION

4.4.1. Wild dog body temperature profiles

Our results revealed both substantial thermal lability and hyperthermia in wild dogs; across 13 individuals at four study sites, mean diel body temperature range was 3.1°C (± 1.0 SD), but reached a maximum range of 9.09°C, whilst mean diel body temperature maximum was 39.6 (± 0.8 SD), with an absolute maximum recorded at 42.71°C (Table 4.1). Body temperature increased with increasing activity, and this increase was steeper at higher air temperatures (Figure 4.6), consistent

with greater heat gain associated with metabolic heat generation and a larger environmental heat load.

Previous research on a range of free-living mammals has shown remarkably consistent diel body temperature rhythms (Fuller et al., 2026), including in elephants (*Loxodonta africana*) (Mole et al., 2018), blue wildebeest (*Connochaetes taurinus*) (Boyers et al., 2019), lions (*Panthera leo*) (Trethowan et al., 2016), cheetah (Hetem et al., 2013), and springbok (*Antidorcas marsupialis*) (Hetem et al., 2009). However, the body temperature rhythms recorded here in wild dogs do not follow this pattern. While an evening peak in body temperature is commonly observed in large mammals, irrespective of activity patterns, and dawn typically represents the diel trough (Fuller et al., 2026), we instead observed pronounced peaks around dawn (Figure 4.4). These morning peaks closely aligned with typical wild dog hunting activity (Figure 4.4), resembling patterns observed in substantially smaller mammals, such as vervet monkeys (*Chlorocebus pygerythrus*) (Lubbe et al., 2014), and meerkats (*Suricata suricatta*) (Fuller et al., 2026). This suggests that wild dog body temperature rhythms may be more strongly driven by activity patterns than other large mammals, including two sympatric large carnivores.

Indeed, we found that wild dog body temperature was strongly and rapidly influenced by activity, with temperatures remaining elevated for up to 30 minutes after intense exercise (Figure 4.6). This relationship is likely linked to the high-intensity cursorial hunting behaviour of wild dogs, reflected in activity peaks around dawn and dusk (Figure 4.4). Gorman et al. (1998) showed that the energetic cost of hunting in wild dogs is approximately 25 times basal metabolic rate, which means that hunting would be associated with substantial heat production. Our comparison of body temperature in the same two individuals under free-living versus temporarily captive conditions (Figure 4.5) further supports the prominent role of hunting behaviour in driving body temperature variation. Although we were unable to directly compare relationships between body temperature, activity, and air temperature between captive and free-living states due to failure of concurrent accelerometer collars (Table S4.1), captivity resulted in lower mean and maximum diel body temperature and reduced variability compared to free-living conditions (Figure 4.5; Figure S4.8), despite the potential stress associated with captivity (Crossey et al., 2020), and known links between stress and body temperature (Tabh et al., 2023). During captivity, hunting was precluded and any movement restricted to an enclosed space (approximately 8,000m^2), while feeding and social behaviours continued. Together, these findings indicate that body temperature in wild dogs is tightly coupled to activity, highlighting the central role of hunting behaviour in shaping their thermal physiology.

Crucially, the degree to which body temperature rose with activity was strongly influenced by air temperature (Figure 4.6). When exercising under high environmental heat loads, wild dog heat dissipation is limited to evaporative cooling, which depends on maintaining adequate water balance. While such exercise-induced hyperthermia in wild dogs under high air temperatures in a treadmill study was initially proposed as an adaptive heat storage strategy to save water that would otherwise be required to dissipate heat through evaporative cooling (Taylor et al., 1971), hyperthermia increases the risk of heat illness and death. We recorded wild dogs reaching body temperatures in excess of 39°C on the majority of days studied (Figure 4.3), and all free-living individuals reached body temperatures ≥ 41°C during the study (Table 4.1). Domestic dogs (*Canis lupus familiaris*) have been shown to experience similarly elevated body temperatures (measured rectally) following exercise, with increases likewise exacerbated by air temperature, reaching body temperatures of up to 41.4°C in sled dogs (Phillips et al., 1981) and 42.1°C in racing greyhounds (McNicholl et al., 2016). Whilst we do not know what body temperature constitutes lethal risk to wild dogs, 50% of domestic dogs in a laboratory experiment died following rectal temperatures of 41.7°C (Adolph, 1947), and 41-41.5°C has been suggested as a critical body temperature threshold for heat illness in domestic dogs (Carter and Hall, 2018, McNicholl et al., 2016). Our findings hence raise concern regarding potential fitness consequences of exercise-induced hyperthermia under high air temperatures in wild dogs.

4.4.2. Implications for the impacts of climate change on wild dogs

In light of these results, the reduction in wild dog activity at higher air temperature previously observed (Pomilia et al., 2015, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017, Rafiq et al., 2023) likely reflects a form of behavioural thermoregulation which avoids potentially dangerous exercise-induced hyperthermia. A comparable decline in activity with increasing air temperature has been attributed as such in another large canid, the dingo (*Canis dingo*) (Tatler et al., 2021). Fitness consequences resulting from behavioural thermoregulation have been documented across taxa, including reduced body mass (van de Ven et al., 2019, Vane et al., 2025), poorer body condition (Gardner et al., 2016), fewer mating opportunities (Campagna and Le Boeuf, 1988), reduced parental care (Sharpe et al., 2019), lower offspring provisioning (Wiley and Ridley, 2016), and decreased survival (van de Ven et al., 2020). Therefore, whilst this behavioural response in wild dogs may represent an adaptive short-term response to avoid hyperthermia, any resulting reduction in prey capture and food intake could impose longer-term fitness costs, unless hunting effort can be compensated during cooler conditions.

However, wild dogs already concentrate hunting during the coolest periods of the day (Woodroffe, 2011) and show only limited increases in nocturnal activity in response to high temperatures (Rafiq et al., 2023, Rabaiotti and Woodroffe, 2019). This likely reflects constraints on nocturnal activity, as wild dogs rely on sufficient light for hunting and are largely restricted to moonlit nights (Cozzi et al., 2012, Rabaiotti and Woodroffe, 2019, Ngatia et al., *in review-b,* Rasmussen et al., 2012). Increased nocturnality may also elevate overlap with dominant nocturnal competitors such as lions and hyaena (*Crocuta crocuta*) (Rasmussen et al., 2012). Hotter conditions may therefore instead effectively narrow the available hunting window for wild dogs, potentially reducing food intake, and therefore limiting pup provisioning and provisioning of babysitters during the denning period. Such constraints may contribute to the reduced reproductive success observed when wild dogs raise pups in hotter weather (Woodroffe et al., 2017, Abrahms et al., 2022). Reduced provisioning could disproportionately impact breeding females – and consequently pups – given that they spend more time babysitting than other pack members (Malcolm and Marten, 1982) and may incur additional thermophysiological costs associated with lactation (Speakman, 2008). The species' seasonal breeding aligning with the coolest time of the year (McNutt et al., 2019) may hence represent an adaptive response to limit the physiological impact of high air temperatures on both breeding females and young.

4.4.3. Future directions

Investigation of hunting success, food intake, and den provisioning across contrasting climatic conditions will be necessary to further disentangle the mechanisms through which air temperatures influence wild dog demography. A reduction in hunting activity does not necessarily equate to reduced food intake, and it has been suggested that wild dog prey species are similarly thermally constrained and therefore easier to capture under hot conditions (Creel et al., 2016). Our findings, however, suggest that the high-intensity cursorial hunting behaviour of wild dogs imposes disproportionate thermophysiological strain, with wild dog body temperature influenced by activity in a manner not observed in prey species such as springbok (Hetem et al., 2009), blue wildebeest (*Connochaetes taurinus*) (Fick et al., 2006), and gemsbok (*Oryx gazella gazella*) (Boyers et al., 2019). As this relationship is exacerbated under elevated environmental heat loads, rising air temperatures may constrain wild dog hunting performance, potentially altering predator-prey dynamics and exacerbating climate-related risks for this endangered carnivore.

We used a relatively simple proxy for energy expenditure in this study, interpreting high VeDBA_sum values as indicative of hunting behaviour (Redcliffe et al., 2024). However, this activity metric also inherently encompasses other behaviours, including feeding and social rallying (Estes

and Goddard, 1967). Behavioural classification of comparable wild dog accelerometer data identified thresholds for trotting at 0.4 g, running at 0.9 g, and sprinting at 1.4 g (Redcliffe et al., 2024). We observed a marked increase in the steepness of predicted body temperature responses at VeDBA_sum values above approximately 3,000 over five minutes (Figure 4.6), which corresponds to a mean VeDBA of 0.5 g over the sampling interval. While direct application of the behavioural classification rules from Redcliffe *et al.* (2024) to our dataset would require validation, this threshold indicates a level of sustained or cumulatively intense activity over the sampling interval (e.g., sustained fast trotting, or a combination of trotting and running) that is associated with steep increases in body temperature. However, a VeDBA_sum of 3,000 could reflect a combination of behaviours rather than a single locomotor mode. We also recorded few instances of very high activity (VeDBA_sum > 5,000; mean VeDBA ≈ 0.83 g) at high air temperatures (≥35°C; Figure 4.6). Behavioural classification would therefore be valuable to disentangle the contributions of specific behaviours to body temperature variation.

Although our models explained 42% of observed variation in wild dog body temperature, we were unable to account for all potential contributors to wild dog body temperature. Given the possibility of kleptoparasitism by lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) (Carbone et al., 2006, van der Meer et al., 2011, Creel and Creel, 1996), stress-induced hyperthermia during prey handling may occur in wild dogs, as proposed in cheetahs (Hetem et al., 2013), explaining some of the additional body temperature variation. Identifying hunt and kill behaviours from accelerometery data, as performed by Redcliffe *et al.* (2024), would be key to investigate this possibility. In domestic dogs, body temperature responses during exercise vary among individuals, with darker greyhounds exhibiting greater exercise-induced increases in body temperature, likely due to differences in solar radiation absorption associated with coat colour (McNicholl et al., 2016). Likewise, springbok with dark coats have higher diel body temperature maxima and ranges than those with lighter coats (Hetem et al., 2009). Comparable mechanisms may contribute to the individual variation in body temperature observed among wild dogs in this study (Table 4.2), given the substantial variation in coat colour and pattern within the species (Daniels et al., *in review*), although radiative heat gain by coats is not only a function of colour (Mitchell et al., 2018, Walsberg, 1983). Individual variation may also be partly driven by inter-site differences, given that our full dataset included only a single individual at three of the four study sites (Table 4.1, Table S4.1). Such differences could reflect local adaptation to respective climates (Meek et al., 2022), although we note that the morning peaks in body temperature recorded in our study were not unique to a single site, nor were they universal within the site at which multiple individuals were monitored (SVC, Figure 4.4).

It has been suggested that the physiological challenge for large mammals under climate change will arise from a combination of increasing environmental heat and reduced water availability (Fuller et al., 2026). Water availability is therefore likely to be particularly important for wild dog population persistence, as body water lost through evaporative cooling during exercise must be replenished (Fuller et al., 2021). Notably, the lowest mean diel body temperatures recorded across individuals in our study occurred following morning peaks in activity (Figure 4.4), which may indicate subsequent visits to water. Heterothermy in Arabian oryx (*Oryx leucoryx*) and aardvark (*Orycteropus afer*) has been attributed to low water availability, resulting in diel body temperature ranges of up to 7.7°C and 11.7°C, respectively, driven by both lower minima and higher maxima (Weyer et al., 2020, Hetem et al., 2010). In comparison, we recorded an absolute maximum body temperature of 42.71°C, an absolute minimum of 31.06°C, and a maximum diel range of 9.09°C in wild dogs (Table 4.1). Reconstruction of wild dog movement paths using accelerometer data and GPS locations via dead reckoning (Bidder et al., 2015) would allow visits to water to be examined directly, improving understanding of these patterns and their implications for water availability and management under climate change.

4.4.4. Conclusion

Our findings demonstrate that free-living wild dogs have body temperature rhythms atypical of large mammals, experiencing substantial exercise-induced hyperthermia, with environmental heat load amplifying this response. The combination of high air temperature and intense locomotor effort appears to impose a thermophysiological constraint that likely limits hunting activity during the heat of the day, through behavioural thermoregulation. As climate change intensifies thermal extremes across Africa, understanding how these physiological limits shape behaviour and demographic outcomes will be critical for predicting the species' resilience and informing conservation management. Similar thermophysiological constraints may also operate in other cursorial predators that rely on sustained locomotion during hunting, suggesting that rising temperatures could have broader implications for coursing predators.



CHAPTER 5 | Mapping risk and resilience: a multi-method modelling approach to forecasting the persistence of an endangered carnivore

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AUTHOR CONTRIBUTIONS

JFL, DR, and RW conceived the study and developed the methodology. JFL curated the data, performed the analyses, and wrote the manuscript. DR contributed to analyses. AD and RW provided supervision, and critically reviewed and edited the manuscript. This author list is currently unconfirmed and will be finalised for publication.

Mapping risk and resilience: a multi-method modelling approach to forecasting the persistence of an endangered carnivore

ABSTRACT

Climate change and land-use change threaten biodiversity through both direct effects on population dynamics and indirect effects on habitat suitability, yet these processes are rarely integrated in large-scale forecasts. We assessed the vulnerability of the endangered African wild dog (*Lycaon pictus*) across continental Africa by combining mechanistic demographic projections with correlative habitat suitability modelling. We adapted a published individual-based model (IBM), parameterised using long-term data from two contrasting populations, to simulate population trajectories under three climate scenarios (SSP1-2.6, SSP3-7.0, SSP5-8.5). We compared these projections with habitat suitability model (HSM) outputs incorporating climate, land cover, and human population change, and developed a composite metric to identify areas of concordant risk and resilience. Population declines were predicted across all scenarios, with the magnitude of decline strongly dependent on demographic context. More severe declines were consistently predicted under the scenario derived from a human-impacted system, suggesting reduced resilience where anthropogenic pressures are high. Spatially, the greatest declines were projected in key strongholds, including the Kavango Zambezi Transfrontier Conservation Area and Niokolo-Koba National Park, while parts of East Africa, particularly central Kenya and Ethiopia, were predicted to experience comparatively smaller declines. Comparison with habitat suitability projections revealed regions where multiple pressures are likely to converge, as well as areas of divergence between modelling approaches. In many regions, demographic models projected greater declines than habitat models, indicating that correlative approaches alone may underestimate climate-driven risk. These findings highlight the importance of combining mechanistic and correlative frameworks to capture complementary pathways of environmental change, and provide a more robust basis for identifying conservation priorities and potential climate refugia for wide-ranging species.

5.1. INTRODUCTION

Climate change has long been highlighted as a prominent driver of ongoing and forecast biodiversity loss (Roman-Palacios and Wiens, 2020, Beever et al., 2011, Bellard et al., 2012). Direct impacts of climate change on individual organisms – such as altered survival, reproduction, or phenology – combine with indirect effects arising from changes in habitat quality, species interactions, and human disturbance, to shape species' responses to shifting climatic conditions (Walther et al., 2002, Ockendon et al., 2014). The combination of these effects make understanding and predicting species' responses to climate change a complex but pressing challenge in biodiversity conservation, with different modelling frameworks capturing different elements of these processes.

Perhaps the most dominant of these frameworks is correlative Habitat Suitability Modelling (HSM), also called Species Distribution Modelling (SDM), for which a substantial body of literature exists predicting range shifts under future climate change scenarios (Jones and Harris, 2025, Mitchell et al., 2024, Zamora-Gutierrez et al., 2018, Lawson et al., 2023, Zhang et al., 2025). These models statistically link species occurrence to environmental variables (Pearson and Dawson, 2003), allowing spatially-explicit predictions across a range of extents, and the incorporation of other forecast threats, such as a land-use change. HSMs can be constructed relatively easily, even with limited occurrence data, making them widely accessible. They do not, however, explicitly model the mechanism(s) by which species are impacted by climate (Schurr et al., 2012), and as such suitability above a subjective threshold is often interpreted as predicted persistence of a species (Hellegers et al., 2025), without capturing the population dynamics driving extinction risk.

Demographic, or mechanistic, models instead explicitly simulate population dynamics such as survival, reproduction, and dispersal, and as such, present a promising avenue for predicting impacts of environmental change (Urban et al., 2016, Stillman et al., 2015). One such modelling framework, individual-based modelling (IBM), has seen increased uptake in simulating the impacts of habitat change (Crispim-Mendes et al., 2025, Glass et al., 2024, Bond et al., 2023), social dynamics (Bauduin et al., 2020), and reintroduction feasibility (Andersen et al., 2021, Lovell et al., 2025, Ovenden et al., 2019, Atzeni et al., 2026, Premier et al., 2025). Crucially, IBMs can incorporate empirically derived climate-demography relationships, allowing temperature or precipitation to directly influence vital rates within simulated populations (Rabaiotti et al., 2023, Correa et al., 2024, Conquet et al., 2025, Bond et al., 2023). However, such models typically require detailed longitudinal data on known individuals collected over multiple years (Stillman et al., 2015).

We therefore conceptualise HSMs as primarily capturing indirect climate impacts mediated through changes in environmental suitability, while IBMs capture direct impacts of climate on demographic rates and population persistence (Pearson and Dawson, 2003, Schurr et al., 2012, Stillman et al., 2015). Many assessments of climate change vulnerability rely on a single modelling framework, often used to inform spatial prioritisation of conservation efforts (Urban et al., 2016, Araujo and Peterson, 2012), despite calls for integration of methods in forecasting (Zurell et al., 2016, Fordham et al., 2012). Where such models already exist, integrating and comparing demographic and correlative projections across broad spatial extents would aid in determining whether different approaches identify the same high-risk regions, or whether particular modelling frameworks systematically under- or overestimate extinction risk. Such integration of habitat suitability and population dynamics is recommended for formal conservation assessments, including under the IUCN red listing guidelines for assessing the threat of climate change (IUCN Standards and Petitions Committee, 2024)

The African wild dog (*Lycaon pictus*, hereafter "wild dog") is a wide-ranging and highly social endangered carnivore (Woodroffe et al., 2025), that has been identified as sensitive to both climatic variation (Chapter 4, Woodroffe et al., 2017, Rabaiotti et al., 2021) and human disturbance (O'Neill et al., 2020, Pretorius et al., 2019, Jackson et al., 2016). A climate-sensitive IBM has been developed for the species, incorporating empirically derived temperature effects on fecundity, juvenile survival, and adult survival (Rabaiotti et al., 2023). However, this model was parameterised for a single region and did not generate spatially explicit predictions of climate risk beyond that extent, nor did it incorporate additional environmental pressures, such as land-use change, that may indirectly affect demography. By contrast, correlative HSMs incorporating both climate and land-use change forecast substantial reductions in wild dog habitat suitability across key regions of the continent (Chapter 3). Determining whether these indirect, suitability-based projections align with direct demographic responses to climate change is critical for ongoing continental conservation planning (IUCN/SSC, 2015, IUCN/SSC, *in prep-a,* IUCN/SSC, 2024). Moreover, given the relative ease with which HSMs can be developed, evaluating whether they represent an adequate surrogate for more data-intensive demographic models will help to expedite forecasts of climate change impacts on other species.

Here, we adapt the published IBM (Rabaiotti et al., 2023) to simulate relative differences in wild dog population responses to projected climate change across continental Africa. We parameterise the model using long-term demographic data from two contrasting sites and initialise all simulated populations at the same standardised carrying capacity, allowing the effects of projected climate

change on population dynamics to be compared independently of current abundance and distribution. We then compare these mechanistic projections with correlative estimates of habitat-suitability change derived in Chapter 3, generating both a composite metric of climate risk and an assessment of spatial concordance and divergence between modelling frameworks. In doing so, we evaluate the implications of these complementary modelling approaches for climate-risk assessment and conservation prioritisation, both for wild dogs and more broadly.

5.2. METHODS

All data manipulation and analyses were carried out in R version 4.4.0 (R Core Team, 2024), using the package *Terra* (Hijmans, 2024) for spatial processing. Visualisation took place in QGIS version 3.4.05 (QGIS.org, 2024).

5.2.1. Population modelling

5.2.1.1. Model structure

The population model was adapted from a published single sex, individual based model (IBM) for wild dogs (Rabaiotti et al., 2023). Within the model, the population is composed of multiple territories and a number of packs – each territory can contain one wild dog pack, comprising a single dominant female (>12 months of age); subdominant adult females (>12 months of age), and juvenile females (3-12 months of age) (Rabaiotti et al., 2023). Individuals were included only from 3 months of age due to the difficult in reliably counting pups prior to this stage (Woodroffe, 2011).

The model runs using a monthly timestep – within each timestep the following six phases take place: mortality, dispersal, ageing, births (where applicable), pack fate (consisting of three levels: inheritance of dominance status, pack break up, or pack continuity), re-colonisation of vacant territories (Rabaiotti et al., 2023). We adjusted the published model to treat breeding as a seasonal event, with attempts scheduled at fixed 12-month intervals, consistent with wild dog breeding taking place during the coolest period of the year throughout most of their geographic range (McNutt et al., 2019). We therefore did not include an inter-birth interval parameter, in contrast with Rabaiotti et al. (2023). Full details of model structure and processes are provided in Rabaiotti et al. (2023).

5.2.1.2. Model parameterisation

In order to capture documented variation in wild dog demography and responses to air temperature, we parameterised the IBM using two demographic scenarios, based on published long-term life-history data from wild dog populations in central Kenya (37°2′ E, 0°6′ N) and

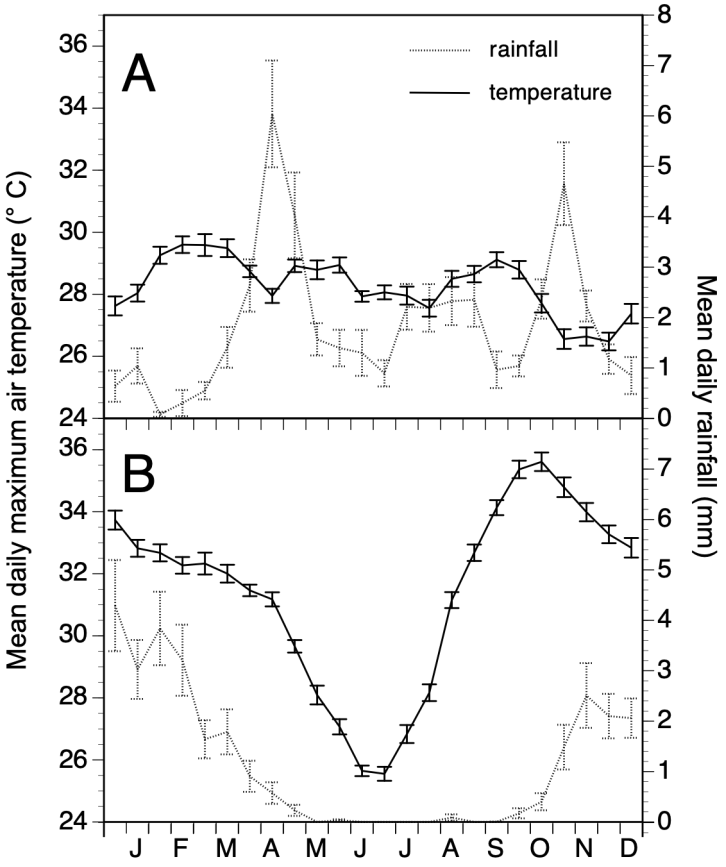


Figure 5.1. Figure adapted from Woodroffe et al. (2017)*:* Within-year variation in weather conditions at study sites in (A) Kenya and (B) Botswana. Data are averaged across half-month periods for the years 2001-8. Error bars indicate standard errors. Data for the Kenya site were collected at Mpala Research Centre, in the middle of the study area, data for the Botswana site were collected at a weather station at Maun airport, roughly 30km from the study area boundary and within the same ecosystem.

northern Botswana (19°52’ S, 23°63’ E). The Kenya site experiences relatively high human impact, covering a mix of privately owned ranches and community land, while the Botswana site mostly comprises a national protected area, and hence experiences relatively little human pressure. The Botswana site has distinct seasons, and higher maximum air temperatures than the Kenya site, which is relatively aseasonal (Figure 5.1).

Data on litter size and juvenile survival at were taken from Woodroffe et al. (2017) for Kenya and from Abrahms et al. (2022) for Botswana, while adult mortality and pack size data for both sites were sourced from Rabaiotti et al. (2021). Dispersal (Woodroffe et al., 2020) and age (Rabaiotti et al., 2021) data were available only for the Kenyan population and were therefore applied to both demographic scenarios. Parameters for model inputs were calculated through re-analysis of these data using a monthly timestep, using Generalized Linear Models for pup survival and litter size, and Cox Proportional Hazards Models for adult survival and dispersal, as detailed in Appendix S1 of Rabaiotti *et al*., (2023).

Accordingly, and in line with published literature, the IBM incorporated the following relationships under both demographic scenarios: juvenile survival declined with increasing denning season temperature (defined as the mean temperature during the first three months of life) and increased

Table 5.1. Mean values and standard error (SE) of the normal distributions from which the input parameters in the IBM were drawn, for each of two demographic scenarios (Kenya and Botswana). Calculated using Generalized Linear Models for pup survival and litter size, and Cox Proportional Hazards Models for adult survival and dispersal, as detailed in Rabaiotti et al., (2023). Litter size and juvenile survival data were sourced from Woodroffe et al. (2017) for Kenya and from Abrahms et al. (2022) for Botswana, adult mortality and pack size data for both sites were sourced from Rabaiotti et al. (2021). Dispersal (Woodroffe et al., 2020) and age (Rabaiotti et al., 2021) data were available only for the Kenyan population and were therefore applied to both demographic scenarios.

		Value ± SE	
Variable	**Coefficient**	**Kenya**	**Botswana**
Adult mortality	Intercept	0.0155 ± 0.0040	0.0211 ± 0.0060
	Impact of temperature	0.1689 ± 0.0827	-
	Impact of pack size	-0.1680 ± 0.0578	-0.2967 ± 0.1226
	Impact of dominance	-0.6145 ± 0.3076	-
	Impact of age	0.0162 ± 0.0011	
Juvenile survival	Intercept	-1.4240 ± 0.6465	-0.8889 ± 0.2954
	Impact of temperature	-0.7057 ± 0.2937	-0.1666 ± 0.0396
	Impact of litter size	0.5482 ± 0.1565	0.1318 ± 0.0555
Litter size	Intercept	0.8776 ± 0.0684	1.0121 ± 0.0379
	Impact of temperature	-	-0.0438 ± 0.0208
	Impact of pack size	0.04553 ± 0.0233	0.0476 ± 0.0121
Dispersal	Intercept	0.0064 ± <0.0001	
	Impact of pack size	0.1059 ± 0.0240	

with litter size; adult survival increased with pack size; litter size increased with pack size (Woodroffe et al., 2017, Rabaiotti et al., 2023). In the Botswana demographic scenario, litter size additionally decreased with increasing denning season temperature (Abrahms et al., 2022). Finally, in the Kenya demographic scenario, adult survival decreased with mean temperature over the preceding three timesteps (Rabaiotti et al., 2021). The parameter values and effect sizes reflected the site-specific datasets (Table 5.1).

5.2.1.3. Climate projections

As in Chapter 3 of this thesis, CHELSA CMIP6 ISIMIP3 climatologies were used for both current and future climate projections (Karger, 2021).

Raster layers of projected current (year 1981-2010) mean daily maximum temperature for each of the 12 months of the year were downloaded, along with equivalent future projections for the time period 2071-2100 for all available global circulation models (GCMs) (GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, MRI-ESM2-0) at each of the three available Shared Socioeconomic Pathways (SSPs): SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5, hereafter referred to as SSPs 1-2.6, 3-7.0, and 5-8.5, respectively. SSP 1-2.6 is a sustainability-focused, low-emissions scenario, with global cooperation and land conservation, and increase in global mean temperature limited to

approximately 2°C by 2100 (IPCC, 2021). SSP 3.7-0 is a high-emissions, high-population scenario, with regional conflict and extensive land-use change, leading to warming above 3°C by 2100 (IPCC, 2021). SSP 5-8.5 is a fossil-fuel driven, high-emissions scenario with more limited population growth, characterised by technological development and extreme warming of over 4°C by 2100 (IPCC, 2021). For each SSP, consensus mean daily maximum temperature layers for each month were created by taking the mean per-pixel of the five GCM projections.

Three temperature layers for each SSP were created from these CHELSA data for use in the IBM: change in mean maximum annual temperature (T_c), annual maximum temperature range (T_r), and change in daily maximum temperature during the denning season (T_d). To create the T_c layers, a mean of the 12 monthly mean daily maximum temperature layers was created for current and future projections, and the resulting current layer subtracted from each of the future equivalents. The T_r layers were created by subtracting the coolest future month from the hottest future month. For the T_d layers, a layer representing mean of the coolest three months (McNutt et al., 2019) was created for current and future projections, and the resulting current layer subtracted from each of the future equivalents.

The nine resulting layers (T_c, T_r, and T_d for each of the three SSPs) were then resampled to a pixel size of 9,000km^2, with each pixel hereafter representing a site where a single wild dog population might reside. This pixel size was selected as a conservative, intermediate estimate of population area, reflecting the wide variation in observed pack densities across current populations (c. 350-3,000+ km² per pack), and is consistent with reported ranges in population area sizes (Woodroffe et al., 2025). The T_c and T_d layers were rounded to the nearest 0.1°C, whereas the T_r layers were rounded to the nearest 0.5°C due to their broader range (T_c: 1.17-6.70°C; T_d: 0.33-6.39°C; T_r: 1.20-29.15°C). Rounded values of T_c, T_r, and T_d were then extracted from all nine layers across pixels covering continental Africa, and unique combinations of the three variables identified across scenarios for inclusion in the IBM.

5.2.1.4. Model implementation

For each unique combination of temperature variables (T_c, T_r, and T_d), and each demographic scenario (Kenya and Botswana), the model was run with 100 iterations. Nine territories were used for each model run, in reflection of the median number of wild dog packs found in populations across the species' current range (Woodroffe et al., 2025), and consistent with Rabaiotti et al. (2023). Following Rabaiotti et al. (2023), wild dogs could disperse between the nine territories

within the population, but, as each population was treated as a separate model run (representing separate 9,000km^2 pixels), they were assumed not to disperse between populations.

As in the published model, we adopted a burn-in period of 100 timesteps, wherein T_c and T_d were held at an average of 0°C, denoting no change in temperature from current conditions (Rabaiotti et al., 2023). The model was thereafter run for 1080 timesteps, i.e. 90 years (from the current climate projections for the period 1981-2010, to the future climate projections for the period 2071-2100). Across these 1080 timesteps, T_c and T_d were implemented to increase linearly from a mean of 0 to a mean of the final respective projected values, representing steady warming over time (with stochastic variation). T_r was implemented to scale monthly temperature variation according to seasonality. The mean temperature in each time step (month) of the model was hence determined by the month, T_c, and T_r.

5.2.1.5. Model outputs

For each model run, population size was extracted at the end of burn-in, and every subsequent five years until the final timestep. For each combination of input temperature variables (T_c, T_r, and T_d) mean population size across the 100 iterations was calculated at each five-year interval. Mean starting (post burn-in) and final population size were converted to a percentage change across the 90 years.

These outputs were then used to produce maps of predicted population size change under each demographic scenario by matching the input temperature variables (T_c, T_r and T_d) to the corresponding raster pixel values across continental Africa under each SSP. To facilitate combination with the HSM outputs, IBM outputs were then averaged across the two demographic scenarios to derive mean predictions of population size change under each SSP within each pixel. Finally, a composite SSP layer was generated by averaging across the three SSPs from the demographic scenario average.

5.2.2. Habitat suitability modelling

The habitat suitability model (HSM) was sourced from Chapter 3 of this thesis. The HSM is a multi-scale Boosted Regression Tree model, built using points sampled from an expert-designated wild dog range map (Figure S5.2) along with predictor variables comprising climate, land cover, protected area status, and human density (Chapter 3). The HSM was constructed using spatially blocked 5-fold cross validation and was evaluated by Area Under the Curve (mean 0.984, standard deviation [SD] 0.007), True Skills Statistic (mean 0.763, SD 0.072), and Kappa Statistic (mean 0.762, SD 0.060).

Habitat suitability prediction layers across continental Africa were generated for the current time period (1981-2010), along with each of the three SSPs for the future (2071-2100) time period, accounting for forecast climate, land cover, and human population density change. These layers represented mean habitat suitability (across cross-validation folds) on a scale of 0 to 1 within each 100km^2 pixel. The current prediction was then subtracted from each of the future predictions, resulting in layers representing predicted habitat suitability change on a scale of -1 to 1, where 0 represents no change in suitability. To ensure comparability with the IBM outputs – where populations were initialised at carrying capacity and therefore could not increase – pixels with predicted increases in suitability (>0) were reclassified to 0, restricting interpretation to projected declines in suitability.

5.2.3. Wild dog geographical range

Wild dog geographical range has been extensively mapped by local experts participating in IUCN/SSC regional and national workshops across Africa, classifying the species' historical range into a number of current range categories (Figure S5.1) (IUCN/SSC, 2024, IUCN/SSC, 2015, IUCN/SSC, *in prep-a*). Of these, we predominantly focused on predictions within expert-designated current *resident* and *recoverable* range (Figure S5.1), with the following definitions:

- *Resident* range: where wild dogs are known to be resident, with regular detection over several years of complete packs and/or evidence of breeding.
- *Recoverable* range: known to be absent, but where habitat and prey remain over sufficiently large areas, meaning either natural or assisted recovery of wild dogs might be possible within the next ten years with reasonable conservation action.

5.2.4. Combining and comparing IBM and HSM predictions

Within each polygon comprising the *resident* and *recoverable* range categories, the mean values of predicted population change (from each demographic scenario, and the scenario average) and habitat suitability change were extracted for each SSP prediction layer. The resulting values were then rounded (0 decimal places for population change [values of 0 to -100%]; 2 decimal places for habitat suitability change [values of 0 to -1]) and ranked from least (1) to most (28 [maximum assuming no ties]) predicted loss according to each metric, with equal (rounded) values assigned the same rank. The predicted population change ranks (demographic scenario average only) and habitat suitability change ranks were then: 1. Summed to produce a 'combined change' metric to determine loss as predicted by both the IBM and HSM methods, and 2. Subtracted from one another (population change minus habitat suitability change), producing a measure of 'change discrepancy' to compare spatial differences in the IBM and HSM predictions.

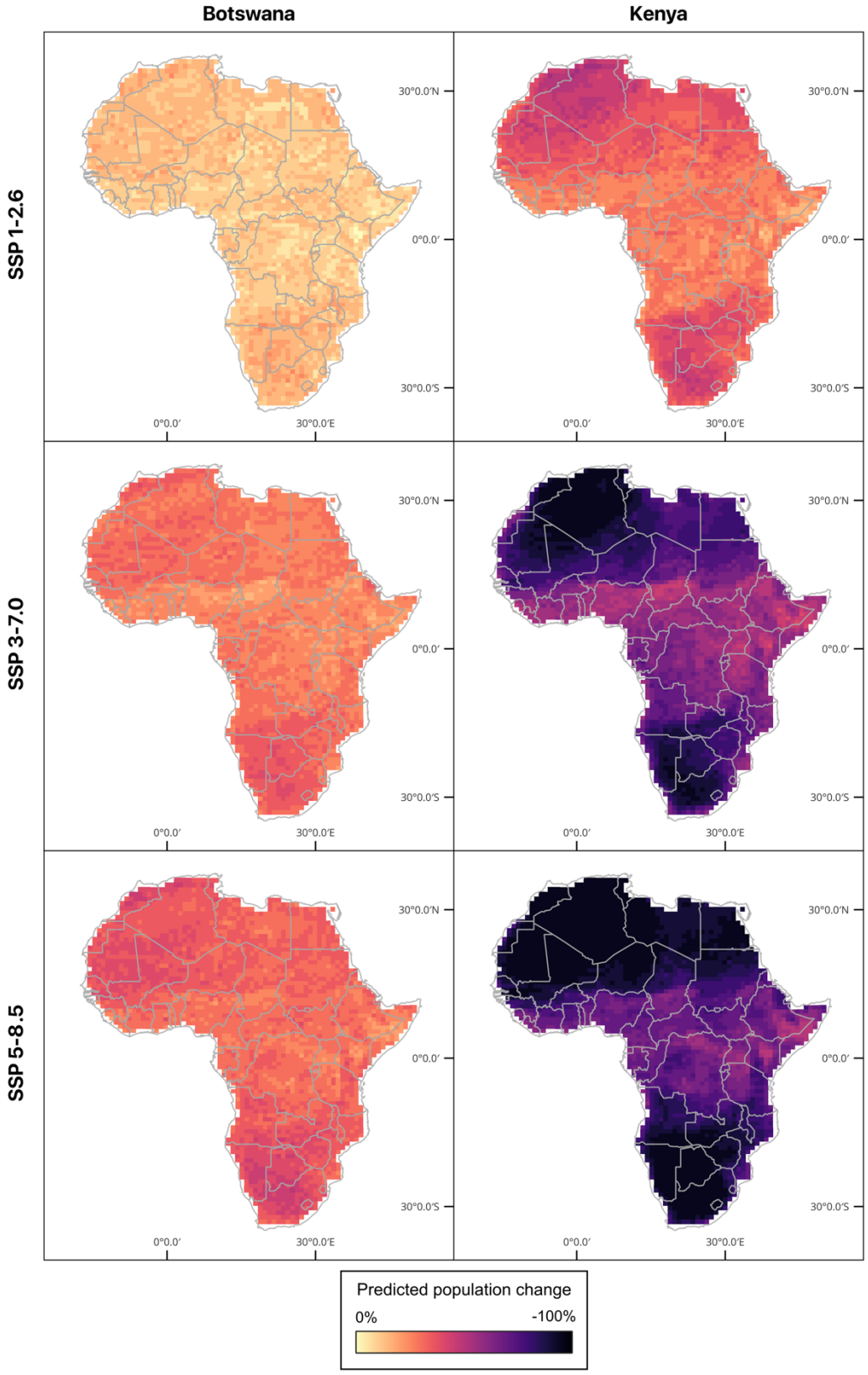


Figure 5.2. Mean predicted African wild dog population change over 90 years under each of three SSPs and two demographic scenarios (Botswana and Kenya) for simulated populations within each 9,000km^2 pixel. Simulations were based on climate data alone and do not consider habitat suitability or current wild dog distribution. Each pixel represents an independent site; to facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site.

5.3. RESULTS

5.3.1. IBM continental predictions

The IBM predicted that African wild dog population sizes would decline across continental Africa under all three SSPs and both demographic scenarios (Figure 5.2). Predicted declines were smallest under the low-emissions scenario, SSP 1-2.6 (Botswana scenario range: -0% to -26%; Kenya scenario range: -14% to -59%), and largest under the fossil-fuel driven high-emissions scenario, SSP 5-8.5 (Botswana scenario range: -18% to -50%; Kenya scenario range: -50% to -100%) (Figure 5.2). Declines were mostly steady across the simulated 90-year period, with higher final mean maximum daily temperatures associated with steeper declines (Figure 5.3). Population decline was consistently steeper across timesteps under the Kenya demographic scenario, resulting in lower final population sizes at all final temperature changes (Figure 5.3). Spatial patterns of decline across the continent were largely consistent across SSPs and demographic scenarios, indicating more severe declines in Northern, West, and Southern Africa than in East Africa, and the least severe declines at higher altitudes and close to the equator (Figure 5.2). More extreme declines were, however, consistently forecast under the Kenya demographic scenario than the Botswana demographic scenario (Figure 5.2).

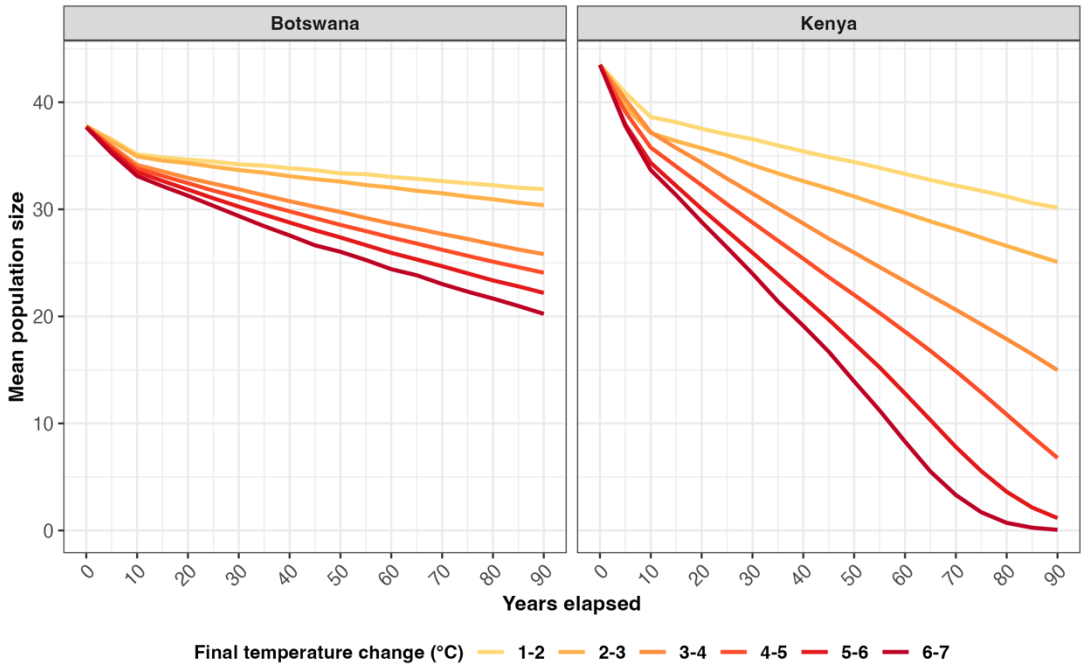


Figure 5.3. Mean predicted African wild dog population size over the 90-year (post burn-in) modelled timespan for simulated populations starting at a consistent carrying capacity of nine packs. Lines are coloured by the final increase in mean maximum daily temperature (°C) reached in year 90, relative to year zero.

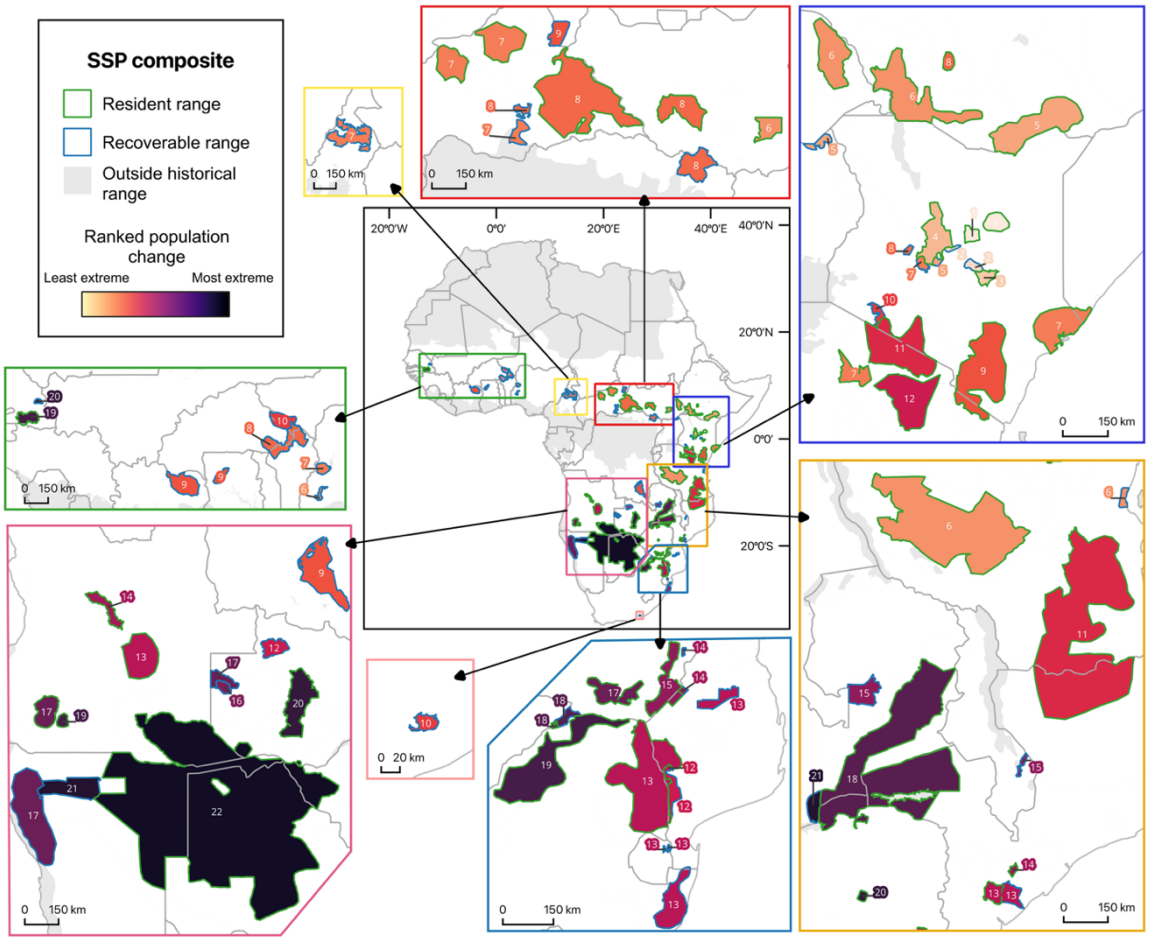


Figure 5.4. Ranked mean African wild dog population change across SSPs and demographic scenarios over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Ranks range from 1 (least extreme decline) to 26 (most extreme decline), with equal ranks assigned to polygons of the same mean value.

5.3.1.1. IBM predictions within *resident* and *recoverable* range

Predictions across SSPs and demographic scenarios broadly followed the same spatial patterns (Figure 5.2). When considering the IBM outputs, we therefore focus on predictions under the SSP composite, and compared outcomes using rankings of predicted decline within *resident* and *recoverable* range polygons (Figure 5.4). This approach allows comparison among polygons while avoiding reliance on absolute population decline values, which differ across SSPs and demographic scenarios. However, figures S5.4-S5.9 in the supplementary material present population change predictions separately for each range polygon under each SSP and demographic scenario.

The most extreme percentage population decline in *resident* range was predicted within the Kavango Zambezi Transfrontier Conservation Area and adjoining land (hereafter referred to as the KAZA landscape) at the nexus of Angola, Zambia, Zimbabwe, Botswana, and Namibia (Figure 5.4, rank 22). This was followed by Kafue National Park in Zambia (Figure 5.4, rank 20), Niokolo Koba

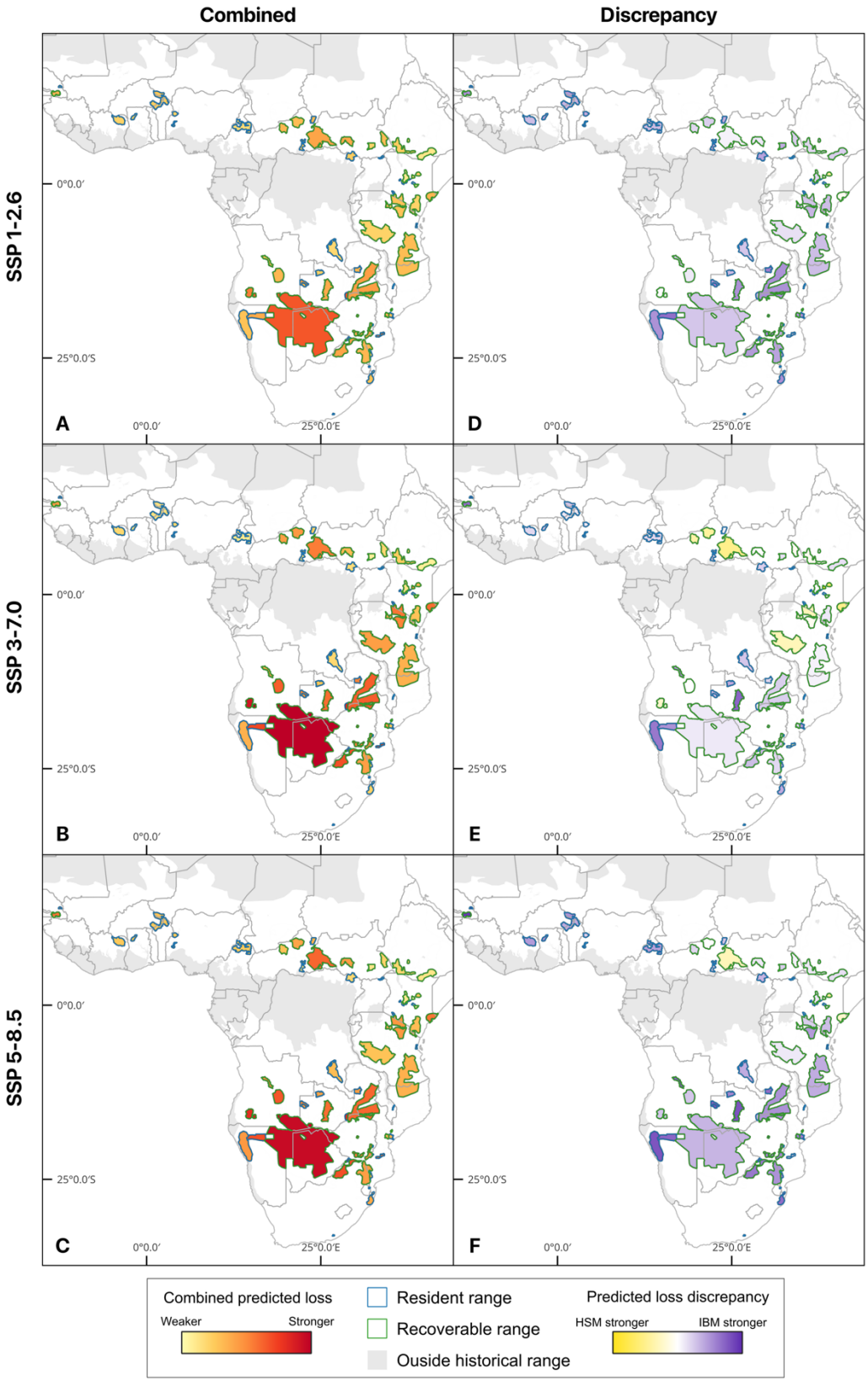


Figure 5.5. A-C: predicted African wild dog loss within resident and recoverable range according to combined population change and habitat suitability change under each of three SSPs. D-F: discrepancy between population change and habitat suitability change predictions within resident and recoverable range under each of three SSPs.

National Park in Senegal, the Waterberg region of South Africa, Mupa National Park in Angola (all jointly ranked 19; Figure 5.4), and the Luangwa Valley in Zambia (Figure 5.4, rank 18). Within *recoverable* range, the most extreme losses were predicted within Boundou Reserve in Senegal (Figure 5.4, rank 20) and Siavonga Open Area in Zambia (Figure 5.4, rank 21). The least extreme predicted declines, across both *resident* and *recoverable* range, were found in the highlands of central Kenya (Figure 5.4, ranks 1-4).

5.3.2. Combining IBM and HSM predictions

The combined IBM and HSM predictions are shown in Figure 5.5. They followed broadly the same spatial patterns across SSPs, with the strongest loss predicted within the KAZA landscape and the weakest loss predicted in central Kenya and southern Ethiopia across SSPs (Figure 5.5 A-C).

5.3.3. Comparing IBM and HSM predictions

Across regions, the IBM tended to indicate relatively greater declines than the HSM when comparing ranked changes in population size and habitat suitability. This pattern was particularly evident in Namibia, Zambia, and Senegal across SSPs (Figure 5.5 D-F). In contrast, central and coastal Kenya were consistently ranked as areas of greater relative decline in habitat suitability (Figure 5.5D-F), as were the Central African Republic under SSP 3-7.0 and SSP 5-8.5 (Figure 5.5 E-F), and the Rungwa-Ruaha landscape of Tanzania and Angola's Bicuar National Park under SSP 3-7.0 (Figure 5.5E).

5.4. DISCUSSION

Our results indicate that climate change poses an increasing threat to the persistence of African wild dogs, but that the nature and severity of this risk vary across their remaining range. While some regions are projected to be subject to substantial risk, others may retain relatively suitable conditions and function as future strongholds. By incorporating demographic and habitat-based projections, this study provides a more nuanced basis for identifying conservation priorities under future climate and land-use change, while demonstrating the strengths and limitations of each approach when used in isolation.

5.4.1. IBM predictions

Under both demographic scenarios, the IBM projected declines in population size across SSPs across much of the continent (Figure 5.2). As some level of climate warming is predicted across Africa under all SSPs (Figure S5.2), this result is consistent with the established mechanistic links between elevated air temperatures and reduced vital rates in wild dogs (Woodroffe et al., 2017,

Rabaiotti et al., 2021, Abrahms et al., 2022). The severity of predicted decline scaled with emissions scenario (least extreme under SSP 1-2.6; most extreme under SSP 5-8.5), indicating that future climate trajectory could determine wild dog persistence in parts of their geographical range (Figure 5.2).

Simulations under the Botswana demographic scenario indicated greater resilience to warming, with smaller projected declines across all three emission pathways (Figure 5.2) and consistently larger final population sizes (Figure 5.3). This difference reflects the implemented variation in demographic parameters: although temperature has been empirically observed to negatively affect juvenile survival in both Botswana and Kenya, its effects were less severe in Botswana (Woodroffe et al., 2017), despite an additional temperature effect on litter size not observed in Kenya (Abrahms et al., 2022) (Table 5.1). Temperature has also been documented to negatively impact adult survival in Kenya, whereas this relationship was not detected in Botswana (Rabaiotti et al., 2021) and so was not included in the Botswana demographic scenario (Table 5.1). Comparing these contrasting demographic scenarios highlights how differences in climate-demography relationships can scale up to influence projections of population persistence, and provides a basis for exploring the ecological drivers of this variation.

The Botswana site lies mainly within a formally protected landscape characterised by low human pressure and high connectivity (Cozzi et al., 2020), whereas the Kenya site occurs within a mixed-use, human-dominated landscape (Woodroffe, 2011), where most wild dog deaths are caused by domestic dog diseases and human-wildlife conflict (Rabaiotti et al., 2021, Ngatia et al., *in review-a*). The comparatively lower declines predicted under the Botswana scenario therefore suggest that lower anthropogenic pressure and stronger connectivity may buffer wild dogs against climate-driven demographic impacts, highlighting the potential role of protected areas in enhancing resilience. Prior studies have also highlighted the role of protected areas in sustaining biodiversity under climate change (Johnston et al., 2013, Thomas and Gillingham, 2015).

It is also possible that the wild dog population inhabiting the more seasonal Botswana site, and thus exposed to greater temperature extremes (Figure 5.1), is better adapted to this regime than the population in Kenya, and therefore more resilient to further increases in temperature and seasonality. Such population-level differences in thermal sensitivity would be consistent with evidence that local adaptation to climatic conditions is widespread and can shape responses to warming (Meek et al., 2022). Investigating populations in more extreme environments, such as Senegal and the Central African Republic (CAR) (Figure S5.1), would help to disentangle the extent to which local adaptation may buffer populations against climate change.

5.4.1.1. IBM predictions within *resident* and *recoverable* range

Southern Africa is projected to experience more substantial warming than other parts of the wild dog's range, including during the critical denning season (Figure S5.2). Consistent with this pattern, the largest projected population declines within *resident* range were concentrated in this region (Figure 5.4), with the most extreme losses consistently forecast in the KAZA landscape across SSPs and demographic scenarios (Figures S5.4-S5.9). The KAZA landscape currently supports the largest remaining wild dog population, holding nearly one third of the global total (Woodroffe et al., 2025). Substantial climate-driven reductions in this region could therefore have disproportionate consequences for the species' global abundance and conservation status.

However, the magnitude of decline projected here should not be interpreted as equivalent to the probability of actual population extinction. Although KAZA is projected to experience the greatest proportional losses from the standardised carrying capacity, its large actual population size provides an important demographic buffer against extinction. In the original IBM, larger populations withstood higher temperature thresholds before collapsing (Rabaiotti et al., 2023), suggesting that the KAZA population may retain greater resilience to climate-driven demographic deterioration than smaller populations. Even following a substantial decline, the KAZA population may remain considerably larger than many other resident populations and may therefore be less immediately vulnerable to demographic and environmental stochasticity, and local extinction. Nevertheless, this buffer should not be interpreted as protection from long-term risk, as sustained declines in a population that represents such a large proportion of the global total would still have major consequences for the species' range-wide status.

Substantial declines were also predicted in Niokolo Koba National Park in Senegal (Figure 5.4), which represents the last remaining population of wild dogs in West Africa and is currently estimated to comprise only 30 adults across four packs (Woodroffe et al., 2025). Given its small population size and geographic isolation, this population is likely to be particularly vulnerable to climate-driven demographic change (Woodroffe et al., *in review*). Its risk profile therefore differs fundamentally from that of KAZA. Whereas KAZA's large existing population may provide a substantial extinction buffer despite severe projected proportional declines, Niokolo Koba has little demographic margin for further loss. Even moderate reductions in adult survival or recruitment could leave the population vulnerable to demographic stochasticity and rapid extinction. Thus, although the projected proportional decline in Senegal may be less extreme than that in KAZA, absolute extinction risk is likely greater due to its much smaller present population.

These projections underscore the urgency of targeted monitoring and conservation action in West Africa, where the loss of the Niokolo Koba population would constitute a regional extinction. Reintroductions within the current recoverable range in Senegal would likely be exposed to similar climate-driven declines (Figure 5.4). However, other areas of recoverable range in West Africa are projected to experience less extreme warming (Figure S5.2) and were correspondingly predicted to be substantially less vulnerable to climate impacts (Figure 5.4). These regions may therefore represent more favourable candidates for future reintroduction efforts to strengthen West Africa's wild dog population.

Across scenarios, the smallest projected population declines occurred in central Kenya (Figure 5.4; Figures S5.4-S5.9), an aseasonal region expected to experience comparatively modest temperature increases (Figure S5.2; Figure S5.3). This relative resilience likely reflects both lower projected warming, linked to the region's high altitude, and reduced seasonal temperature extremes characteristic of equatorial systems. However, our implementation of the IBM did not incorporate the documented effect of temperature on inter-birth interval in this population (Woodroffe et al., 2017), which would likely amplify climate-driven impacts on reproduction and population growth. As a result, the apparent resilience projected in central Kenya may be somewhat overstated. Notably, the original IBM formulation – which incorporated temperature effects on inter-birth interval – projected more severe declines under warming, although differences in model implementation limit direct comparability (Rabaiotti et al., 2023).

While this study aimed to map relative climate vulnerability across space, future work incorporating empirically derived population sizes for each resident range area, along with site-specific demographic responses where documented, would enable projections of absolute population losses and more realistic estimates of extinction risk.

5.4.1.2. IBM caveats

We parameterised the IBM using two demographic scenarios derived from long-term empirical studies in contrasting regions of the current wild dog range. In extrapolating these temperature-demography relationships to areas where such relationships have not been quantified, we assumed that broadly comparable responses would apply across the species' range. Demographic sensitivity to temperature may, however, vary across ecological contexts as a result of local adaptation, differences in prey availability and competitor density, or interactions with anthropogenic pressures. Consequently, projected outcomes for individual populations should not be interpreted as definitive predictions of realised population size or persistence.

Nevertheless, comparable demographic sensitivity to temperature has been documented at an additional site in Zimbabwe (Woodroffe et al., 2017), and behavioural responses to temperature have been recorded across several sites in Kenya, Zimbabwe, and South Africa (Ngatia et al., *in review-b*), indicating that thermal sensitivity is geographically widespread. These observations support the use of the model for identifying broad-scale patterns of relative climate vulnerability, while not excluding the possibility that the magnitude of response will differ among populations.

The two demographic scenarios implemented here produced broadly similar spatial patterns of risk despite differing in the underlying demographic mechanisms relating to adult and juvenile survival, although the magnitude of projected responses varied between scenarios (Figure 5.2). Focusing on mean ranked predictions across the two scenarios provided an intermediate representation of relative risk and reduced reliance on either individual demographic relationship. However, assessing the generality and local accuracy of these relationships would require comparable long-term demographic data from additional regions. Such data are currently lacking, and monitoring efforts in other parts of Africa remain in their early stages (Aebischer et al., 2020, Horion et al., 2024).

Our implementation of the IBM, consistent with the published iteration, incorporates temperature-driven demographic relationships only. These projections therefore likely represent a conservative estimate of climate-related risk, as changing precipitation regimes and increasing extreme events are also known to influence survival and recruitment in other species (Ockendon et al., 2014). Expansions in wild dog home range have already been linked to droughts within the vulnerable KAZA landscape (West et al., 2024), potentially increasing energetic costs, exposure to dominant competitors, and the risk of human-wildlife conflict. Equally, reduced dispersal success and redirected movements into human-dominated areas have been observed alongside flooding within the Okavango delta of KAZA (Hofmann et al., 2024), highlighting how both climatic extremes may exacerbate anthropogenic pressures on populations.

In addition, our implementation of the IBM assumed linear warming, which does not reflect the non-linear temperature trajectories and potential acceleration of regional warming projected under different emissions pathways (IPCC, 2021). Moreover, the IBM does not include concurrent changes in land use, human population density, and other anthropogenic pressures. In many regions, habitat loss, fragmentation, and conflict are likely to compound the demographic impacts of warming (Abrahms et al., 2023; Williams et al., 2019), meaning that realised declines could exceed those projected here. Conversely, populations were treated as closed within pixels, with dispersal limited to territories inside each pixel. In reality, connectivity among neighbouring

landscapes may facilitate rescue effects and reduce local extinction risk (Van Schmidt and Beissinger, 2020), particularly in well-connected regions. Thus, while the IBM provides a mechanistic estimate of temperature-driven vulnerability, realised outcomes will depend on the interaction between climate change, other anthropogenic pressures, starting population size, and landscape connectivity.

The IBM outputs should therefore be viewed primarily as decision-support tools rather than precise forecasts of future population trajectories. Their principal value lies in identifying areas in which temperature-related demographic pressures may be comparatively high, supporting the prioritisation of monitoring, validation, and conservation intervention. Conservation decisions should combine these projections with local knowledge, contemporary population data, and site-specific assessments rather than treating projected declines or persistence as certain outcomes.

5.4.2. Combined IBM & HSM predictions

By combining predictions from two distinct modelling approaches, we capture both direct and indirect pathways of climate change impact, synthesizing projected changes in population size and shifts in habitat suitability. Our composite metric therefore provides a more comprehensive assessment of vulnerability, linking species-specific mechanistic responses to temperature with concurrent projections of land-use change and human population growth. The influence of these distinct methodologies is evident in the combined outputs. For instance, although Southern Africa emerges as the region facing the greatest overall projected loss, combined impacts are strongest under SSP 3-7.0 – the pathway characterised by the most extensive land conversion and human population growth – rather than SSP5-8.5, which represents the highest level of warming (Figure 5.5A-C; Figure S5.2), underscoring the importance of incorporating land-use change into climate risk assessments.

We suggest that the resulting predictions of combined predicted loss within wild dog *resident* and *recoverable* range are hence the most robust available option for considering spatial prioritisation of wild dog conservation efforts under climate change. In particular, areas of concordant high loss predicted across both methods represent robust priorities for conservation investment because the independent models converged on elevated risk. The KAZA landscape, is projected to experience the greatest combined loss across SSPs (Figure 5.5 A-C), reflecting both substantial temperature-driven population declines (Figure 5.4) and concurrent reductions in habitat suitability (Chapter 3). As the largest remaining stronghold for wild dogs globally (Woodroffe et al., 2025), this landscape represents a critical conservation priority. KAZA is the world's largest

transboundary conservation area, comprising a mosaic of national parks, other protected areas, and unprotected lands with varying degrees of human influence (Hofmann et al., 2021). Landscape permeability for dispersing wild dogs is correspondingly heterogeneous, with human presence substantially constraining wild dog movement in parts of the region (Hofmann et al., 2023, Hofmann et al., 2021). Accordingly human-caused mortality accounted for the vast majority of disperser deaths in one study within the landscape (Cozzi et al., 2020). We suggest that buffering wild dog populations in this region against the effects of climate change may therefore depend on reducing anthropogenic mortality, particularly through conflict mitigation strategies to increase tolerance and support coexistence between people and wild dogs.

From a global conservation perspective, it is equally important to safeguard areas projected to be least impacted by climate change, as these regions may become critical refugia if other populations decline or are lost. Under this framework, populations in Kenya and Ethiopia emerge as priorities irrespective of emissions scenario (Figure 5.5 A-C). Wild dog populations in southern Ethiopia remain comparatively understudied relative to those in Southern Africa (Asfaw et al., 2025, Tsegaye and Mengesha, 2023), and increased monitoring will be essential to assess their long-term viability. In central Kenya, wild dogs persist largely outside formally protected areas within human-dominated landscapes. Although levels of human-wild dog conflict have historically been low (Woodroffe et al., 2005), populations have previously experienced local extinction due to infectious disease (Ngatia et al., *in review-a*). Continued investment in disease management, including vaccination of domestic dogs (Woodroffe et al., 2012), will therefore be critical to maintaining this potential stronghold under climate change.

5.4.3. Contrasting IBM & HSM predictions

The discrepancies in the magnitude of predicted loss between the two modelling approaches highlight the intrinsic differences between the two approaches, and underscore the importance of combining multiple frameworks for large-scale projections, ideally in complement to one another, as each may capture processes overlooked by the other.

Across the majority of wild dogs' geographical range, projected population declines from the IBM were more severe than the corresponding losses in habitat suitability predicted by the HSM (Figure 5.5 D-F). This contrast was particularly pronounced in regions forecast to experience substantial warming, including Namibia, Senegal, and Zambia (Figure 5.5 D-F; Figure S5.2), emphasising the value of incorporating species-specific mechanistic relationships with climate (Stillman et al., 2015, Urban et al., 2016). Reliance on HSM outputs alone to forecast wild dog

persistence under climate change could therefore underestimate climate-driven demographic risk, with important consequences for conservation planning. This divergence is especially striking in critically endangered populations such as Niokolo Koba National Park in Senegal (Figure 5.5 D-F), which may appear climatically suitable under HSM projections (Chapter 3) yet are predicted to experience substantial population declines across SSPs under the IBM (Figures S5.4-S5.9). Similarly, reintroduction strategies informed solely by habitat suitability may overestimate long-term viability under more extreme warming in sites such as Etosha National Park in Namibia and Bangweulu National Park in Zambia (Figure 5.5F).

Conversely, in some regions the magnitude of predicted habitat suitability loss exceeded projected population declines from the IBM. This pattern was particularly pronounced in the CAR under SSP3-7.0 and SSP5-8.5 (Figure 5.5 E–F). The CAR supports the last wild dog populations in the Central African region (Aebischer et al., 2020), and its further decline would represent not only a regional biodiversity loss but also the erosion of an irreplaceable genetic resource (Ramage, *in review*). Similarly, although populations in central Kenya are projected to experience relatively limited demographic decline, they are not immune to environmental change; the HSM predicts reductions in habitat suitability in parts of this landscape (Figure 5.5E-F), and this population has already experienced two severe outbreaks of domestic dog diseases (Ngatia et al., *in review-a*). In these areas, stronger signals from the HSM than the IBM emphasise the importance of incorporating projected land-use change and human population growth alongside climatic drivers (Williams et al., 2019).

5.4.4. Conclusions

Our findings indicate that climate change is likely to reshape spatial patterns of vulnerability across the African wild dog's range, threatening current strongholds while highlighting understudied regions that may offer comparatively favourable conditions for long-term persistence. For wild dogs, effective conservation action to facilitate climate adaptation will depend not only on reducing direct anthropogenic pressures in landscapes at highest risk of climate related impacts, such as the KAZA landscape, but also on monitoring and safeguarding potentially comparatively resilient populations in East Africa. More broadly, by combining mechanistic demographic projections with spatially explicit habitat suitability predictions, we identify regions where climate-driven declines may be compounded by land-use change. More broadly, this multi-method approach demonstrates how incorporating direct and indirect pathways of climate risk can provide a stronger foundation for spatial prioritisation and conservation planning for wide-ranging species under accelerating global change.



CHAPTER 6 | DISCUSSION



6.1.THESIS AIMS

Human-driven environmental change is reshaping biodiversity through the combined effects of climate change and land-use change, with consequences that operate across spatial scales from individuals to populations and landscapes (Foden et al., 2018). In Africa, these pressures are expected to intensify as temperatures rise, land conversion continues, and human populations expand (Archer et al., 2018), placing especially strong pressure on large carnivores with extensive space requirements and low population densities (Ripple et al., 2014, Wolf and Ripple, 2017). African wild dogs provide a valuable case study for understanding these dynamics, because their persistence is likely to be shaped by both landscape-level habitat availability and apparent sensitivity to environmental heat (Woodroffe et al., 2017). This thesis therefore set out to examine how heat and habitat together influence wild dog population persistence, from current habitat suitability to future demographic vulnerability. The ultimate aim of this work is to provide insights to inform conservation strategies for this, and other, species under environmental change, both at local and range-wide scales.

To meet these aims, I addressed the following knowledge gaps:

1. Uncertainty in the current distribution of suitable habitat across wild dogs' historical range, as identified by expert-designated mapping processes (Chapter 2)
2. Limited understanding of how projected climate and land-use change will jointly influence future habitat suitability for wild dogs across the African continent (Chapter 3)
3. A lack of mechanistic understanding of the physiological vulnerability of wild dogs to environmental heat, particularly the factors influencing thermoregulation (Chapter 4)
4. Limited understanding of how differing observed relationships between environmental heat and demography translate into population-level impacts across space (Chapter 5)
5. A lack of combined forecasts of combined effects of environmental change across the species' vast historical range (Chapter 5)

6.2. KEY FINDINGS

In **Chapter 2**, I used habitat suitability modelling to assess whether suitable wild dog habitat may exist beyond the species' known distribution. The results suggested that substantial areas of suitable habitat remain, representing up to 24.6% of the historical range, including large portions of expert-designated possible, unknown, and recoverable areas. Notably, suitable conditions were identified within poorly surveyed regions, including parts of Angola, Ethiopia, Mozambique, and

Somalia. Habitat suitability was most strongly associated with protected area coverage, intermediate rainfall, and low human density, highlighting the combined importance of ecological conditions and anthropogenic pressures. By translating expert-derived range maps into a quantitative, spatially explicit framework, this chapter identified priority areas for targeted surveys and potential reintroduction; however, any such actions require careful local assessment prior to implementation. Although these predictions do not represent realised occupancy, they highlight regions where populations may persist undetected, or where recovery efforts may be most effective.

In **Chapter 3**, I extended the habitat suitability framework developed in Chapter 2 to assess how projected climate and land-use change may alter suitable habitat for wild dogs across the continent. The results indicated that suitability is likely to decline across much of the species' current resident range under future scenarios, particularly under higher-emissions and land-use pathways, although some localised increases were identified at the margins of the range. These changes were driven by both climatic and land-cover shifts, with rising temperatures and expansion of cropland associated with reduced suitability. Importantly, projected changes were spatially heterogeneous, with key strongholds such as the Kavango-Zambezi (KAZA) landscape and Chinko Conservation Area identified as particularly vulnerable. These findings suggest that environmental change will reshape the spatial distribution of suitable habitat, rather than simply reduce its overall extent. As in Chapter 2, these projections represent potential rather than realised distributions, and should be interpreted as a tool to guide conservation planning rather than direct forecasts of population persistence.

In **Chapter 4**, I investigated the physiological basis of potential thermal constraints on wild dogs by examining body temperature in relation to activity and environmental heat. The results showed that body temperature is highly labile and strongly influenced by both activity and air temperature, with rapid increases occurring during periods of high activity, particularly under warmer conditions. These findings support the hypothesis that high environmental temperatures constrain wild dog behaviour through thermoregulatory limits, with reduced activity at high air temperatures likely reflecting behavioural responses to avoid overheating. Such constraints may reduce hunting opportunities and, in turn, limit energy intake and reproductive investment, providing a plausible mechanism linking air temperature to observed demographic patterns. Although some uncertainty remains regarding the extent to which these effects can be offset by behavioural flexibility, the results suggest that rising temperatures will impose increasing

physiological constraints on wild dogs. This highlights the importance of considering direct thermal effects, alongside habitat change, when assessing climate change impacts on mammals.

In **Chapter 5**, I assessed the vulnerability of wild dogs to projected changes in both climate and land-use across the African continent, by combining demographic projections with habitat suitability modelling. Population declines were predicted under all climate scenarios, but the magnitude of these declines was strongly influenced by the demographic scenario, highlighting the importance of local ecological and anthropogenic context in shaping climate sensitivity. More severe declines were consistently predicted under the demographic scenario derived from a more human-impacted system, suggesting that populations in such contexts may be less resilient to warming. Spatially, the most pronounced declines were predicted in key strongholds such as the KAZA landscape and Niokolo-Koba National Park, while populations in parts of East Africa, particularly central Kenya and Ethiopia, appeared relatively less impacted. When combined with habitat projections, these results identified regions where multiple pressures are predicted to converge and increase risk, as well as areas that may act as refugia, emphasising the need for context-specific conservation planning under future environmental change.

Taken together, these chapters show that African wild dog population persistence under environmental change is shaped by interacting constraints of environmental heat and habitat availability. Habitat suitability models identify which areas are likely to be habitable now, and how they may shift under environmental change, while physiological results provide a mechanistic basis for thermal sensitivity that likely constrains hunting behaviour and energy balance, leading to population-level impacts. In combination, these results indicate that, in the absence of effective conservation action, environmental change is likely to drive widespread but spatially variable declines across the species' range. This highlights that conservation responses must operate across scales, requiring both range-wide prioritisation of vulnerable and resilient populations, and targeted local interventions to mitigate site-specific threats.

6.3. WILD DOG CONSERVATION AT A CONTINENTAL SCALE

The projections of wild dog habitat suitability and population viability generated in Chapters 3 and 5 paint a concerning picture for the species' future across the continent. Nevertheless, these outcomes could be mitigated by effective conservation action. Forecasting the combined impacts of environmental change provides an opportunity to plan ahead and incorporate these predictions into conservation strategies.

6.3.1. Accelerating understanding

Wild dog conservation planning would first benefit from an improved understanding of the species' current distribution, which can be guided by the outputs of Chapter 2. Following appropriate local validation of these maps, and consideration of additional factors such as prey distribution, targeted surveys in promising areas of uncertain range could substantially improve knowledge of wild dog status. Populations have already been confirmed in previously uncertain areas within the last decade (Kosmas et al., 2023, Monterroso et al., 2020), suggesting further undiscovered populations may persist. Identifying such populations could significantly alter the species' current status and highlight areas requiring conservation attention. Conversely, confirming absence in these regions would allow for refinement of range maps and highlight potential areas for future recovery. Importantly, the projections developed in Chapters 3 and 5 span all range categories, providing a basis for forecasting the persistence of any newly identified populations.

Alongside potentially undiscovered populations, several known wild dog populations remain significantly understudied. In particular, there is a paucity of data from populations in West, Central, and the Horn of Africa regarding space use, population size, trends, and threats (Woodroffe et al., *in review,* Aebischer et al., 2020, Asfaw et al., 2025, Tsegaye and Mengesha, 2023). The absence of occurrence data from these regions necessitated the use of pseudo-presence points in the habitat suitability models developed in Chapters 2 and 3. Collection of empirical occurrence data would allow these models to be refined using observed data, improving the accuracy of fine-scale predictions by reducing uncertainty associated with false presences. Similarly, long-term demographic data from these regions would enable the individual-based modelling framework (Chapter 5) to be parameterised locally, providing more representative predictions of climate-related risk, and improving evaluation of generalisability of the existing predictions.

Notably, parts of these understudied regions, including Senegal, the Central African Republic, and South Sudan, represent the very hottest areas of the species' current range (Figure 6.1). Targeted research in these locations would therefore not only improve conservation assessment and forecasting, but also provide critical insight into how wild dogs persist under extreme thermal conditions, complementing the mechanistic findings presented in Chapter 4. The comparatively greater resilience of populations under the Botswana demographic scenario in Chapter 5, relative to those under the Kenya scenario, may reflect local adaptation to a hotter and more seasonal environment (Atkins and Travis, 2010). Further research in these, even more extreme environments could therefore help to test for evidence of local adaptation or, conversely, identify

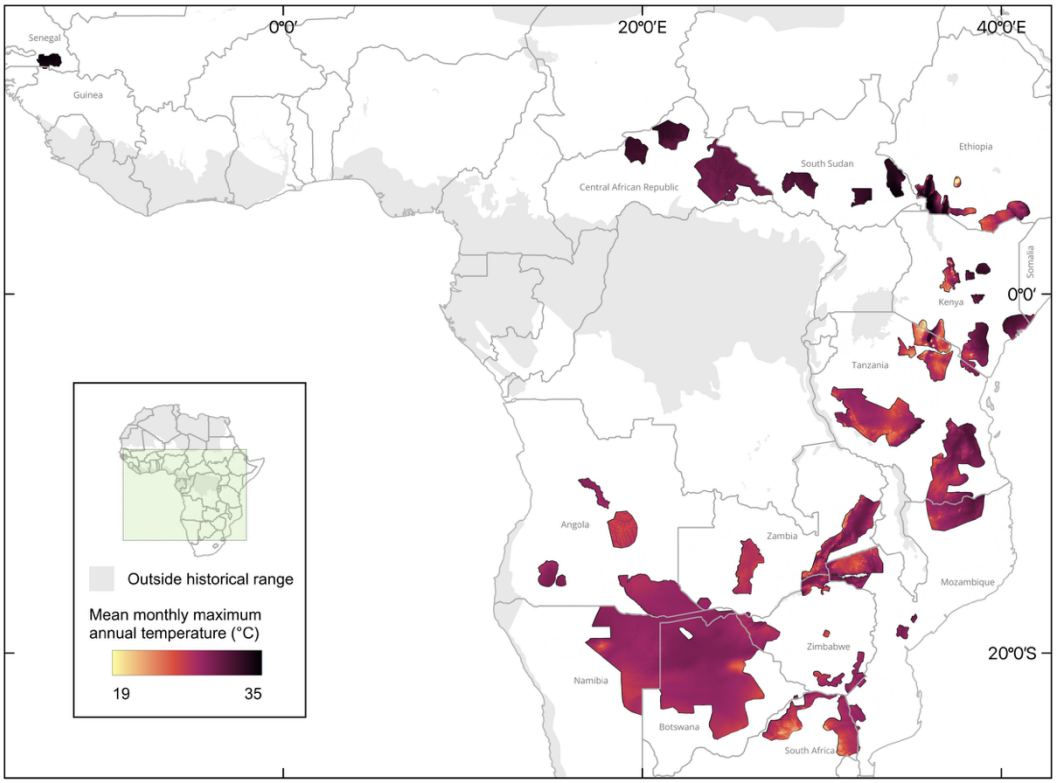


Figure 6.1. Mean of the monthly maximum annual temperature (°C) within wild dog resident range according to current CHELSA climatology (Karger et al., 2017). Country names are displayed for wild dog range states.

populations that are particularly vulnerable to further warming. West Africa's last known wild dog population, found in Senegal's Niokolo-Koba National Park (Figure 6.1), is in most urgent need of conservation attention. With an estimated population of just four packs, this remnant population is at risk of extinction before these dynamics have even begun to be understood (Woodroffe et al., *in review*).

6.3.2. Spatial planning

The results of this thesis highlight that the conservation of African wild dogs under environmental change will require difficult trade-offs across the species' range. Climate-driven risk is not confined to populations that are already small and isolated, but also extends to some of the species' largest and best-protected strongholds. Conservation decisions may therefore need to balance efforts to limit substantial losses from large populations against interventions intended to prevent the extinction of smaller, more immediately vulnerable populations.

Both habitat suitability and population viability analyses identified the KAZA landscape as an area of particularly high relative vulnerability to environmental change (Chapter 5). KAZA is a largely protected landscape and currently supports almost one third of the global wild dog population. Its large population size and extensive protected area network provide important safeguards against

many threats, including habitat loss and demographic stochasticity. However, the substantial declines projected for this landscape demonstrate that even large, well-protected populations cannot be assumed to be secure under climate change. Protection of habitat and maintenance of a large population may increase resilience and delay population collapse, but they do not prevent climate-driven changes in survival and recruitment. KAZA therefore illustrates how climate change may erode the security of populations currently regarded as strongholds, including in landscapes where opportunities to address the underlying threat through conventional site-based protection may be limited.

However, the large projected proportional declines in KAZA should not be interpreted as implying that it faces the greatest immediate probability of climate-driven extinction. Its large current population provides a substantial demographic buffer, meaning that is likely to withstand greater absolute and proportional losses before reaching critically low abundance than smaller populations. Nonetheless, sustained declines could progressively diminish the resilience that the KAZA population currently derives from its size, and in supporting such a large precentage of the global population, substantial losses there could have disproportionate consequences for the species' global abundance and conservation status, even if the population itself remains extant.

In contrast, the wild dog population in Niokolo-Koba National Park is already small, isolated, and depleted. Even comparatively modest reductions in survival, recruitment, or habitat suitability may therefore substantially increase its extinction risk. The contrast between KAZA and Niokolo-Koba illustrates that the magnitude of projected decline and the probability of extinction are not equivalent. A large population may experience a severe proportional decline while retaining some demographic resilience, whereas a much smaller population may be pushed towards extinction by a less pronounced environmental response. Meanwhile, regions such as central Kenya and southern Ethiopia were projected to be comparatively least vulnerable and may therefore function as important areas of future persistence or climate refugia. These spatial patterns, revealed through the combination of demographic and habitat projections, can help identify where climate-related pressures may be greatest and where conservation investment may offer the greatest potential for long-term persistence.

Reintroductions of wild dogs could play an important role in restoring former range and bolstering population size, and may be guided by the results from Chapters 2 and 5. Crucially, reintroductions into areas projected to undergo substantial declines in habitat suitability or population viability under climate change would be inadvisable (Chapters 3 & 5). If guided by the results presented in Chapters 3 and 5, reintroductions would require additional, thorough local assessment, including

evaluation of threats, prey availability, and the genetic suitability of source populations (Ramage, *in review*). Recent reintroductions to Mozambique and Zambia, using individuals from the South African metapopulation, have shown encouraging success (Bouley et al., 2021; Zambian Carnivore Program, 2022), whereas a reintroduction in Malawi resulted in the loss of an entire pack due to poisoning (African Parks, 2023). These contrasting outcomes reflect the inherent challenges of reintroduction efforts and highlight the importance of site-specific considerations. Nevertheless, given the widespread vulnerability of the species, there is a strong argument for prioritising the protection and persistence of existing populations before expanding into new areas.

Maintaining and improving connectivity both within and between wild dog populations will become increasingly important under environmental change, both in enabling potential shifts in geographic range and in facilitating dispersal and genetic flow as population sizes decline. Although connectivity was not explicitly modelled in this thesis, suitable habitat is projected to become increasingly fragmented (Chapter 3), and human-caused mortality during dispersal is already high (Cozzi et al., 2020, Woodroffe et al., 2020). In addition, improved population viability was predicted under the more connected demographic scenario (Chapter 5), potentially indicating the importance of landscape permeability. Modelling connectivity across the species' range would therefore provide a valuable tool for identifying key movement pathways and critical gaps in the landscape. Protecting and restoring movement corridors, reducing barriers to dispersal, and mitigating anthropogenic mortality in matrix habitats will be essential for sustaining connectivity under future environmental change.

6.4. WILD DOG CONSERVATION AT A LOCAL SCALE

6.4.1. Mitigating change

Addressing the threat of climate change to a given species, or to biodiversity more broadly, presents a significant challenge. Climate change is a global process, largely driven by emissions from regions often distant from those most affected by its impacts (IPCC, 2022). Direct mitigation therefore requires coordinated international action to reduce greenhouse gas emissions, which is unlikely to be achieved in response to the conservation needs of any single species. Conservation efforts can nonetheless contribute to this goal through advocacy, policy engagement, and the protection of carbon-rich ecosystems (Griscom et al., 2017).

In contrast, land-use change may represent a more tractable threat, as it is more directly and more rapidly shaped by national and sub-national governance and policy. There is growing evidence that conservation initiatives can influence land-use trajectories, for example through spatial planning

tools which guide land-use decisions and balance conservation and development (Jantz et al., 2025). Outputs from Chapter 3 could therefore aid in informing conservation-based advocacy and spatial planning to guide future land-use decisions. However, land use across much of the wild dog's historical range remains highly dynamic and contested. Rapid human population growth and increasing demand for land and resources present significant challenges for balancing human livelihoods with wildlife conservation (United Nations, 2024, Holechek et al., 2017). In addition, conservation land management can be complex and politically contingent. For example, the public-private partnership model in protected area management in Chad has recently been rescinded and reinstated, illustrating the potential fragility of such governance structures (African Parks, 2025).

6.4.2. Mitigating the impacts of climate change

The results from Chapter 5 indicate that wild dogs inhabiting areas with higher levels of anthropogenic pressure are likely to be more vulnerable to the effects of climate change. This aligns with findings from Rabaiotti *et al*. (2021), which show that increased mortality on hotter days at a site in Kenya was associated with infectious disease and human-wildlife conflict, rather than being directly caused by heat itself. Further evidence from Ngatia *et al*. (*in review*) suggests that wild dog and domestic dog ranges overlap more extensively on hotter days, increasing the risk of disease spillover. Together, these findings indicate that the effects of climate change on wild dog mortality may be lessened by addressing these direct anthropogenic threats, providing a tangible means of mitigating an otherwise diffuse and large-scale driver of population decline. Local conservation action will therefore be essential across the species' range, with interventions such as vaccination of wild and domestic dogs (Prager et al., 2011, Fitzpatrick et al., 2012), conflict mitigation (Mkonyi, 2022), and snare removal (Becker et al., 2024) playing key roles in supporting long-term persistence.

In Chapter 4, I describe a physiological basis for the impact of environmental heat load on wild dog hunting behaviour, whereby high activity levels in warm conditions elevate body temperature toward potentially dangerous levels. This suggests that wild dog thermophysiology may constrain hunting activity in hot weather, contributing to the species' characteristic crepuscular patterns alongside limitations imposed by moonlight availability (Cozzi et al., 2012, Ngatia et al., *in review-b*), and to reduced activity at higher air temperatures (Pomilia et al., 2015, Rabaiotti and Woodroffe, 2019, Woodroffe et al., 2017). As environmental temperatures rise, this crepuscular window of thermally suitable hunting time is therefore likely to contract. This highlights an important interaction between climate change and prey depletion, whereby wild dogs may face

both reduced time available for hunting, and diminished prey availability, both of which reduce the probability of a successful hunt (Creel et al., 2025). Addressing the drivers of prey depletion, and restoring depleted herbivore populations, will therefore be critical to ensuring a sufficient prey base to support wild dog persistence under future environmental change.

6.5. REMAINING KNOWLEDGE GAPS

Several important avenues of research remain to fully understand how wild dogs will be affected by, and persist under, climate change. While Chapter 4 began to disentangle the mechanism by which environmental heat influences behaviour through its effects on body temperature, it did not directly quantify hunting behaviour or determine the extent to which physiological constraints limit performance or food intake. Evidence from Ngatia *et al*. (*in review-b*), building on Rabaiotti *et al*. (2019), suggests that wild dogs exhibit limited behavioural plasticity, with incomplete compensation for reduced daytime hunting through increased nocturnal activity across multiple sites. Further research is therefore needed to determine how these behavioural responses translate into energetic outcomes, and whether reduced hunting time under high temperatures ultimately constrains food intake. Addressing this gap will be critical for understanding the extent to which environmental heat limits wild dog fitness and population persistence.

The mechanism by which environmental heat influences wild dog reproductive success similarly remains unclear (Woodroffe et al., 2017, Abrahms et al., 2022). One possible pathway is through the observed reduction in hunting activity, which may limit cooperative care of young in hot conditions, as observed in other cooperative breeders (Wiley and Ridley, 2016, Bourne et al., 2023), or result in reduced body mass gain in pups, as seen in other taxa (Cunningham et al., 2013, van de Ven et al., 2020). The physiological costs of lactation may additionally increase under high environmental temperatures (Speakman, 2008), further constraining reproductive investment. As hunting becomes more energetically costly at high air temperatures, packs may also face a trade-off between time spent hunting and pup guarding (Courchamp et al., 2002), potentially reducing pup attendance and increasing vulnerability to predation (Malcolm and Marten, 1982). Disentangling the potential roles of such mechanisms will be key to understand how climate change may influence reproductive success and population persistence.

Wild dogs commonly visit water sources during and after hunting, both drinking and entering the water. Recent research shows that wild dogs range closer to water under hotter conditions (Ngatia, *in review*), highlighting the potential importance of water availability. Such behaviour suggests a role for water in facilitating evaporative cooling, potentially alleviating the high body temperatures

reached during energetically demanding hunting activity (Chapter 4). Further investigation into water use, particularly its influence on body temperature, will be essential to determine its importance for thermoregulation, and can be achieved through the recreation of fine-scale movement paths from accelerometer data (Bidder et al., 2015). If access to water proves critical for persistence under climate change, this would have important implications for the artificial water provisioning currently implemented in parts of the species' range (Sandoval Serés, 2024).

Although rainfall covariates were included in the habitat suitability models developed in Chapters 2 and 3, this thesis primarily focuses on the relationship between wild dog physiology and demography and environmental temperature. Previous research suggests that rainfall is less consistently linked to reproductive behaviour and success in this species (Woodroffe et al., 2017, McNutt et al., 2019), however, projected changes in rainfall patterns, including increased frequency of droughts and flooding, are likely to influence wild dog persistence under climate change (West et al., 2024, Hofmann et al., 2024) and should be incorporated into future modelling frameworks.

6.6. WIDER IMPLICATIONS

Other wide-ranging large mammals are likely to face similar constraints on habitat availability under environmental change, as demonstrated here for wild dogs. Across Africa, projected climate and land-use change are expected to alter land cover in ways that will also affect sympatric species, such as leopards (*Panthera pardus*) (Mitchell et al., 2024). This work therefore has broader implications for African megafauna, as well as for species occupying similar ecological niches in other regions. Beyond habitat-mediated effects, the direct impacts of environmental heat identified here highlight additional taxa at risk. As wild dog hunting behaviour appears constrained by thermal and energetic limits, other cursorial predators with similarly high energetic demands, such as the dhole (*Cuon alpinus*) and grey wolf (*Canis lupus*), may face comparable constraints, although such effects have not been observed in the cheetah (*Acinonyx jubatus*) (Hetem et al., 2013). Importantly, declines in predator populations under environmental change may also drive trophic cascades, with wider consequences for ecosystem structure and function (Ripple et al., 2024).

Cooperative breeders may represent a further group of concern. Numerous studies have documented negative effects of high temperatures on behaviour and reproduction in such species, including meerkats (*Suricata suricatta*) (van de Ven et al., 2020), dwarf mongooses (*Helogale parvula*) (Vane et al., 2025), banded mongooses (*Mungos mungo*) (Khera et al., 2025), alpine

marmots (*Marmota marmota*) (Tafani et al., 2013), southern pied babblers (*Turdoides bicolor*) (Bourne et al., 2023), and sociable weavers (*Philetairus socius*) (Mares et al., 2017). Together, this suggests that cooperative breeders may be particularly vulnerable to climate change, and that further investigation across taxa is warranted, particularly concerning endangered cooperative breeders.

In this thesis, I show that environmental change threatens wild dogs through both indirect and direct pathways, operating via habitat change (Chapter 3) and the influence of environmental heat on physiology (Chapter 4) and demography. Chapter 5 demonstrates that these pathways can either reinforce one another or diverge spatially, highlighting the importance of considering processes across scales, from individuals to populations and landscapes (Schurr et al., 2012, Urban et al., 2016). Crucially, reliance on habitat suitability models alone may underestimate climate-driven risk where mechanistic effects are not accounted for (Stillman et al., 2015). Incorporating both correlative and mechanistic approaches therefore provides a more robust framework for assessing species vulnerability under environmental change, and could benefit risk assessments across a wide range of taxa (Fordham et al., 2012). Such an approach supports more holistic conservation planning, linking local-scale interventions (e.g. reducing anthropogenic mortality) with landscape-scale strategies to protect and restore habitat.

6.7. CONCLUSION

This thesis predicts that African wild dog population persistence under environmental change is likely to be shaped by the interaction of environmental heat and habitat availability, operating across scales from individual physiology to population dynamics and spatial distribution. By integrating habitat suitability modelling, physiological data, and demographic projections, this work provides a mechanistic and spatially explicit understanding of how climate and land-use change jointly influence species vulnerability. These findings highlight that the impacts of environmental change are spatially heterogeneous, placing both key strongholds and already vulnerable populations at risk, and providing a basis for targeted conservation action. More broadly, this work demonstrates how interacting environmental constraints may shape species persistence, with relevance to other species facing similar climatic and habitat constraints. Ensuring the persistence of the endangered African wild dog under ongoing environmental change will require conservation strategies that are spatially informed, proactive, and responsive to both local drivers and landscape-level change.



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APPENDICES



APPENDIX A – CHAPTER 2 SUPPLEMENTARY MATERIAL

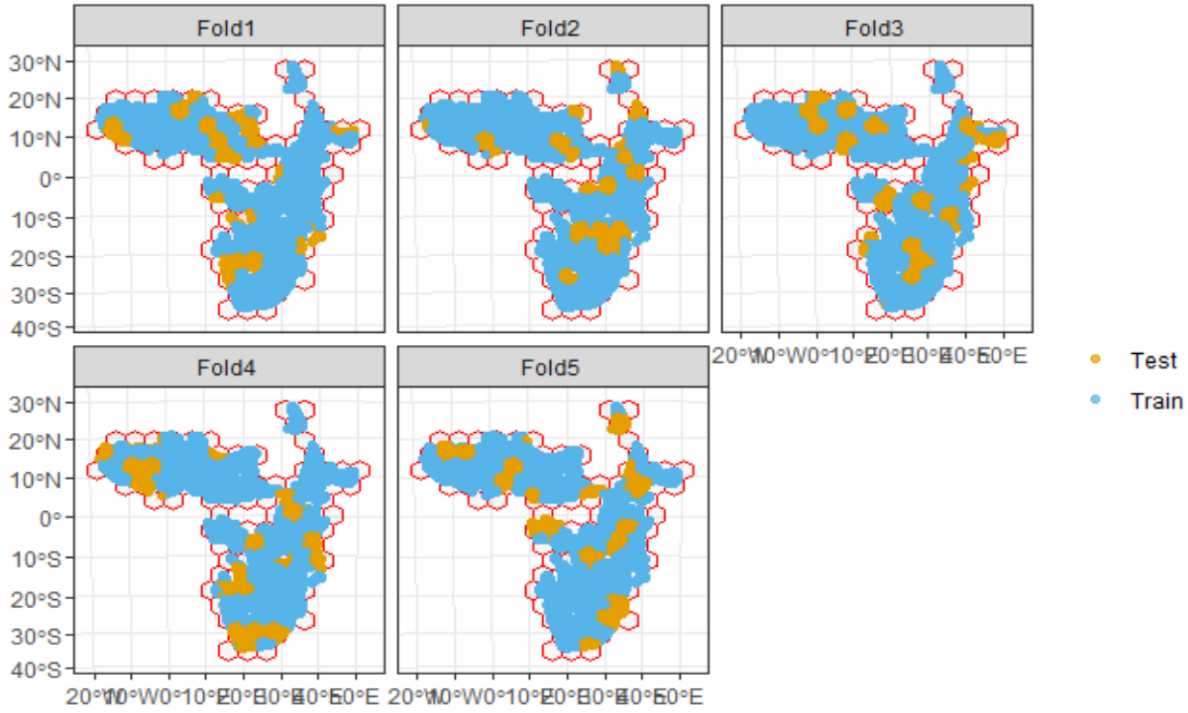


Figure S2.1. Spatially-blocked cross-validation folds used in Boosted Regression Tree models. Generated using the R package *blockCV* (Valavi et al., 2019)

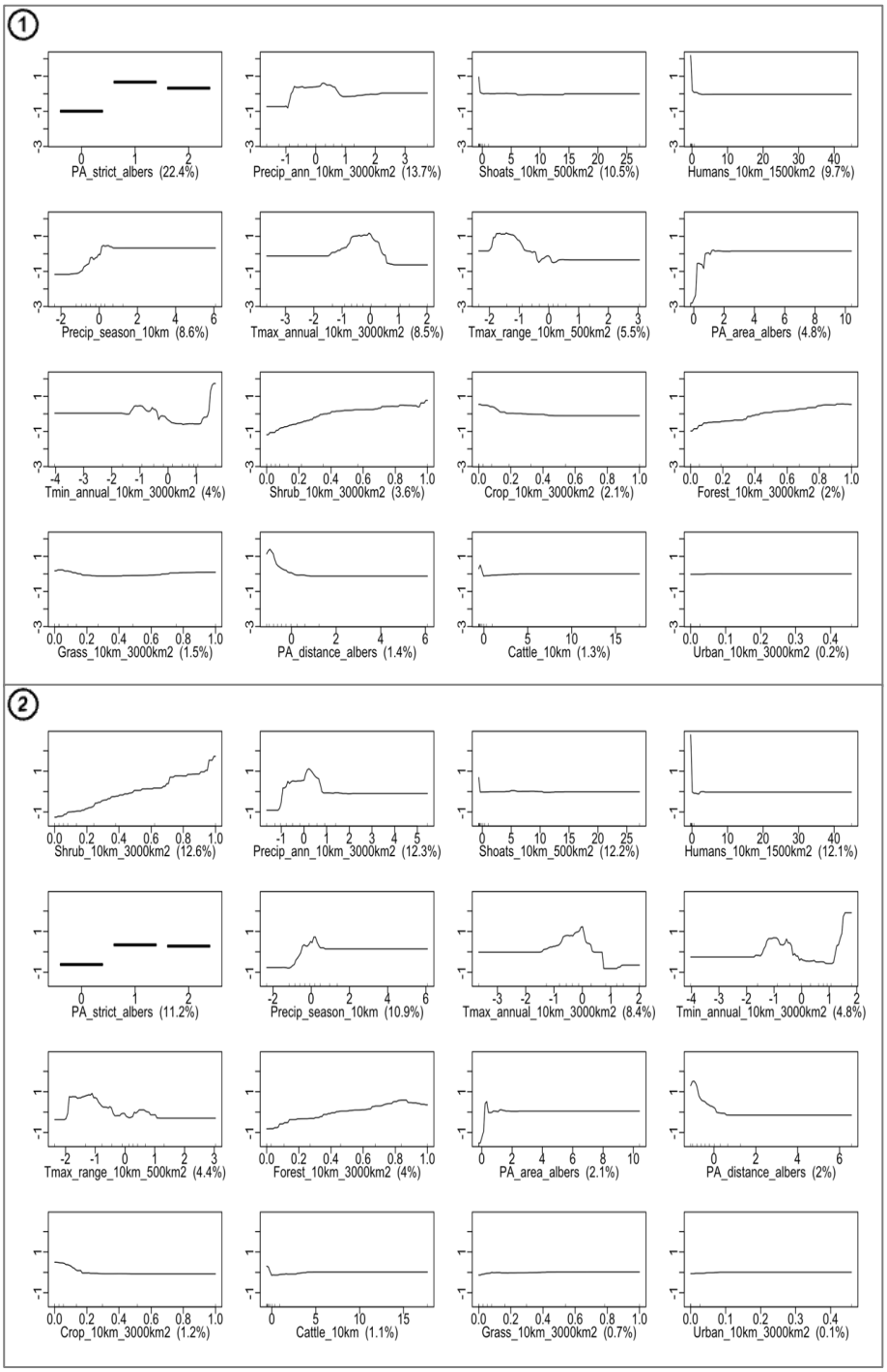


Figure S2.2 (1). Response curves for all predictors used in folds one and two of five cross-validated Boosted Regression Tree model folds. Percentages in brackets are relative importance of each variable in that fold. Generated using the R package *dismo* (Hijmans et al., 2023).

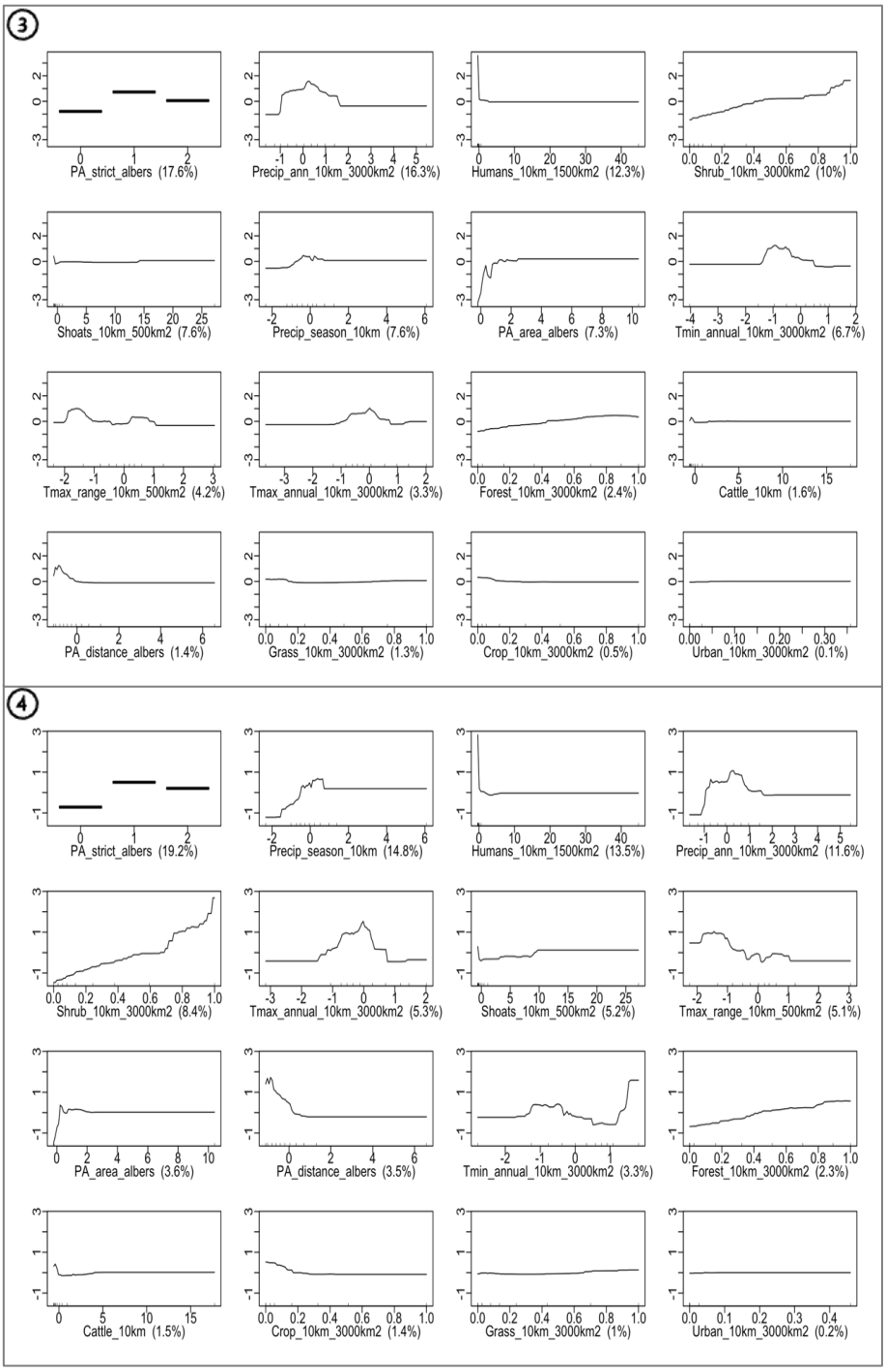


Figure S2.2 (cont). Response curves for all predictors used in folds three and four of five cross-validated Boosted Regression Tree model folds. Percentages in brackets are relative importance of each variable in that fold. Generated using the R package *dismo* (Hijmans et al., 2023).

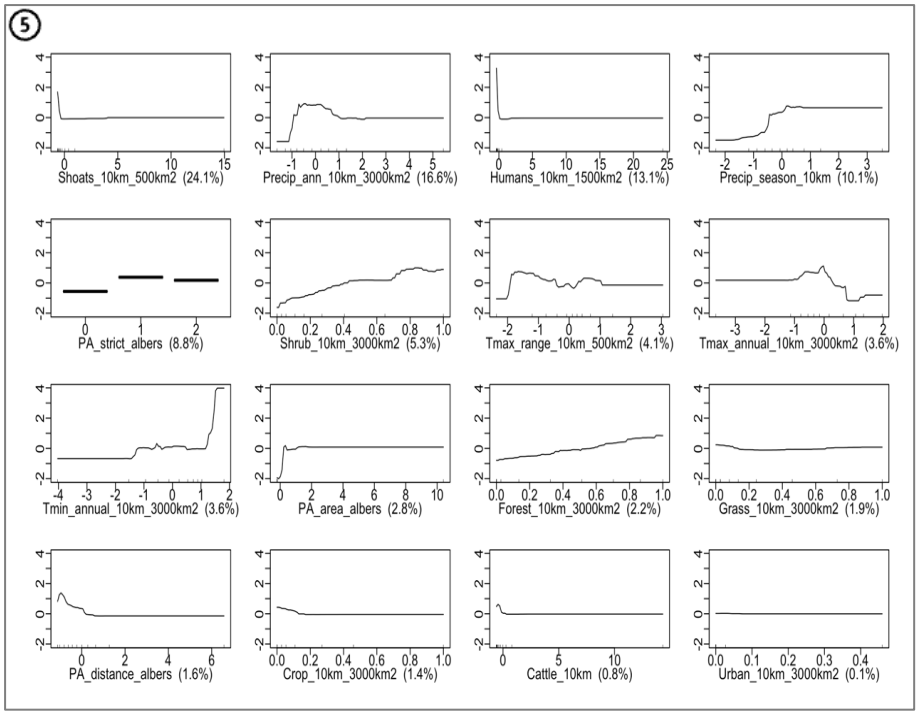


Figure S2.2 (cont). Response curves for all predictors used in fold five of five cross-validated Boosted Regression Tree model folds. Percentages in brackets are relative importance of each variable in that fold. Generated using the R package *dismo* (Hijmans et al., 2023).

Tables S2.1-S2.5 can be found in an associated excel spreadsheet, along with corresponding shapefiles; each table contains predicted habitat suitability and mean predictor variable values within each polygon of the following expert-designated range categories (Table 2.1):

Table S2.1 – possible range

Table S2.2 – recoverable range

Table S2.3 – unknown range

Table S2.4 – resident range

Table S2.5 – extirpated range

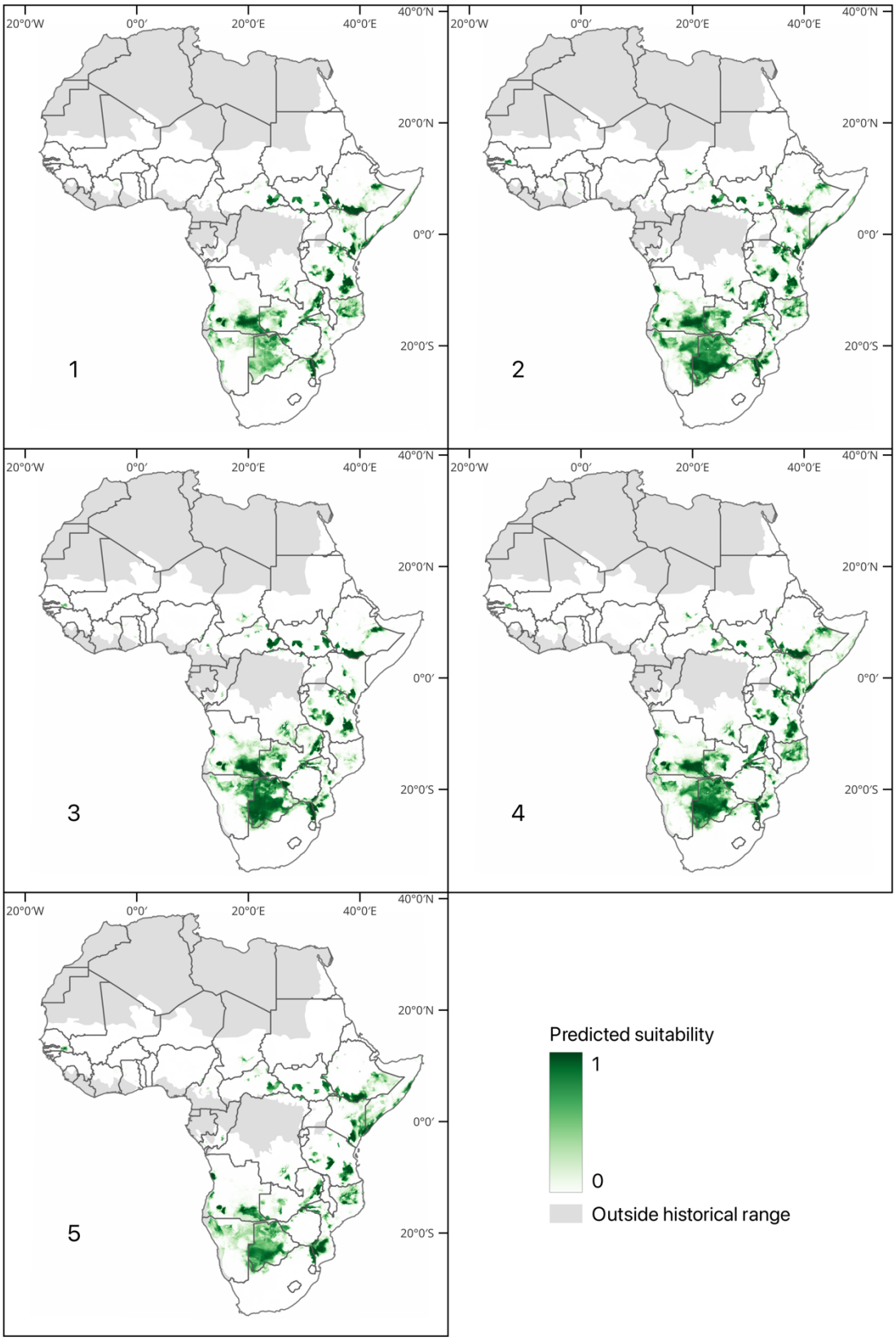


Figure S2.3. Modelled African wild dog habitat suitability across the species' historical range, as predicted by five-fold cross-validated multi-scale Boosted Regression Tree models. Each map represents projected suitability for each of the five folds.

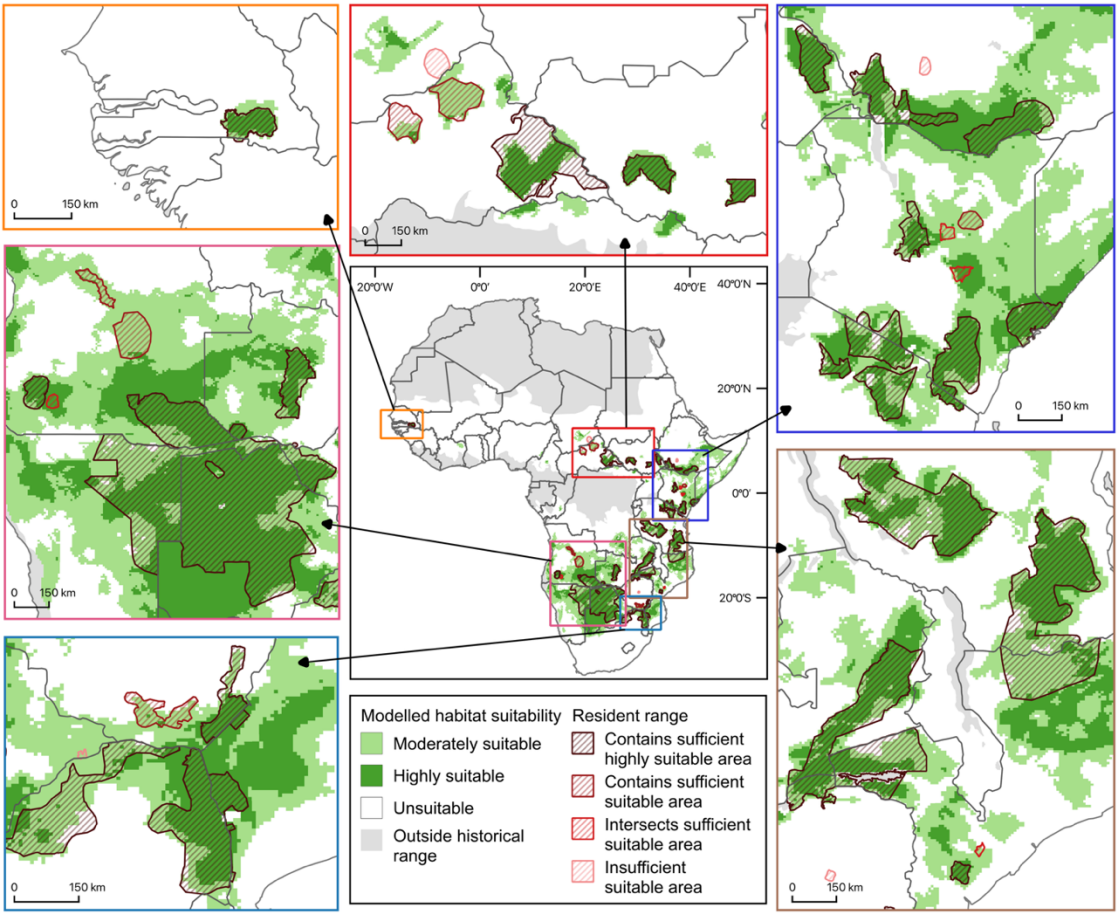


Figure S2.4. Modelled wild dog habitat suitability within expert-defined *resident* range polygons (Woodroffe et al., 2025) as predicted by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable. Sufficient suitable area defined as at least 3,000 km^2 of moderate or high suitability.

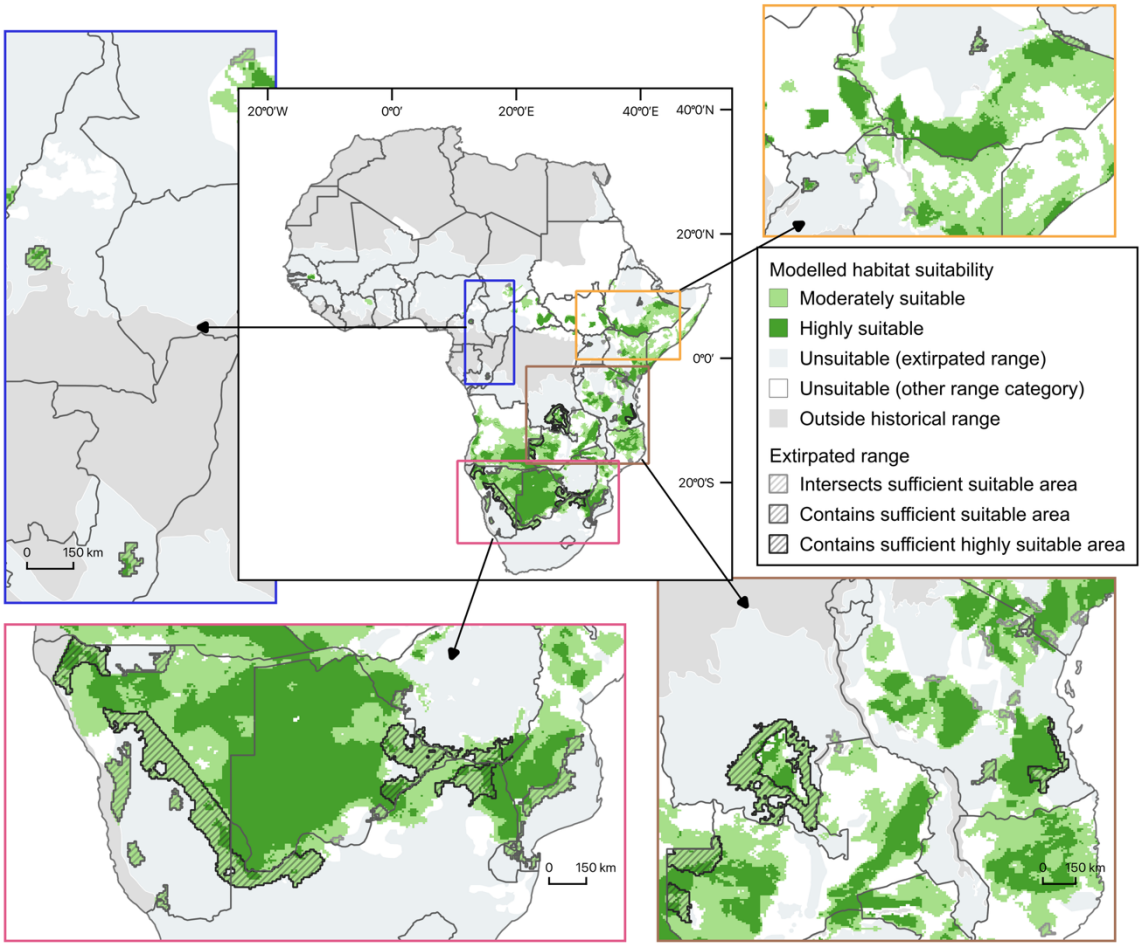


Figure S2.5. Modelled wild dog habitat suitability within expert-defined *extirpated* range polygons (Woodroffe et al., 2025) as predicted by multi-scale Boosted Regression Tree models. Moderately suitable areas represent pixels in the 75th–90th percentile of suitability values; pixels above the 90th percentile were considered highly suitable. Sufficient suitable area defined as at least 3,000 km^2 of moderate or high suitability.

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APPENDIX B – CHAPTER 3 SUPPLEMENTARY MATERIAL

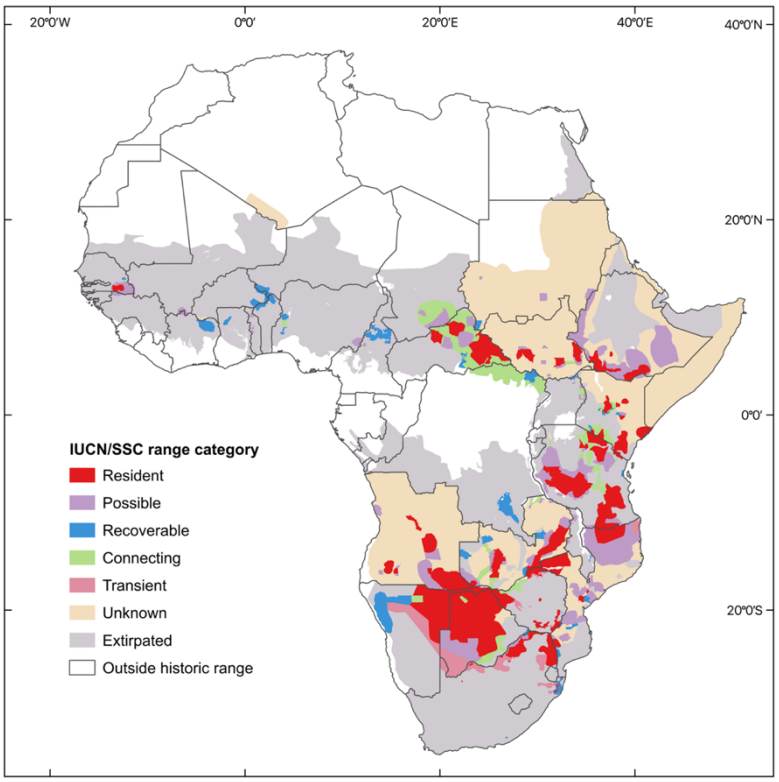


Figure S3.1. *Lycaon pictus* historical range and current range categories, as defined and mapped by species experts participating in regional workshops (IUCN/SSC, *in prep-a,* IUCN/SSC, 2024, IUCN/SSC, 2015).

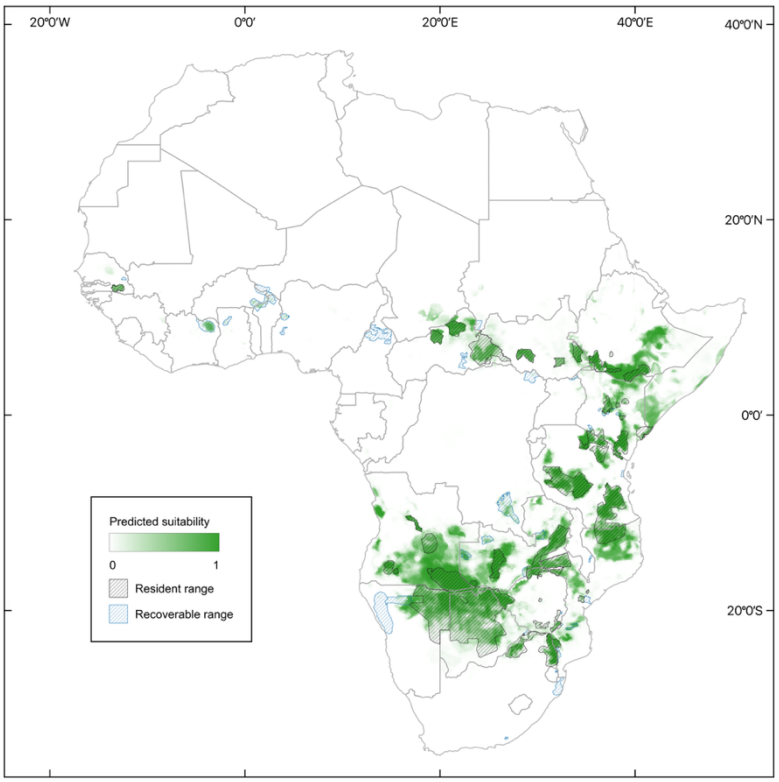


Figure S3.2. Predicted current habitat suitability for wild dogs, as averaged from by five cross-validated multi-scale Boosted Regression Tree models. Expert-defined resident and recoverable range polygons (IUCN/SSC, *in prep-a,* IUCN/SSC, 2015, IUCN/SSC, 2024) are displayed.



Figure S3.3. Changes in predictor layers relative to current, within pixels for which there is a predicted increase or decrease in suitability of wild dog habitat of at least 0.25. Shown for six future scenarios based on multi-scale Boosted Regression Tree models projected across continental Africa.

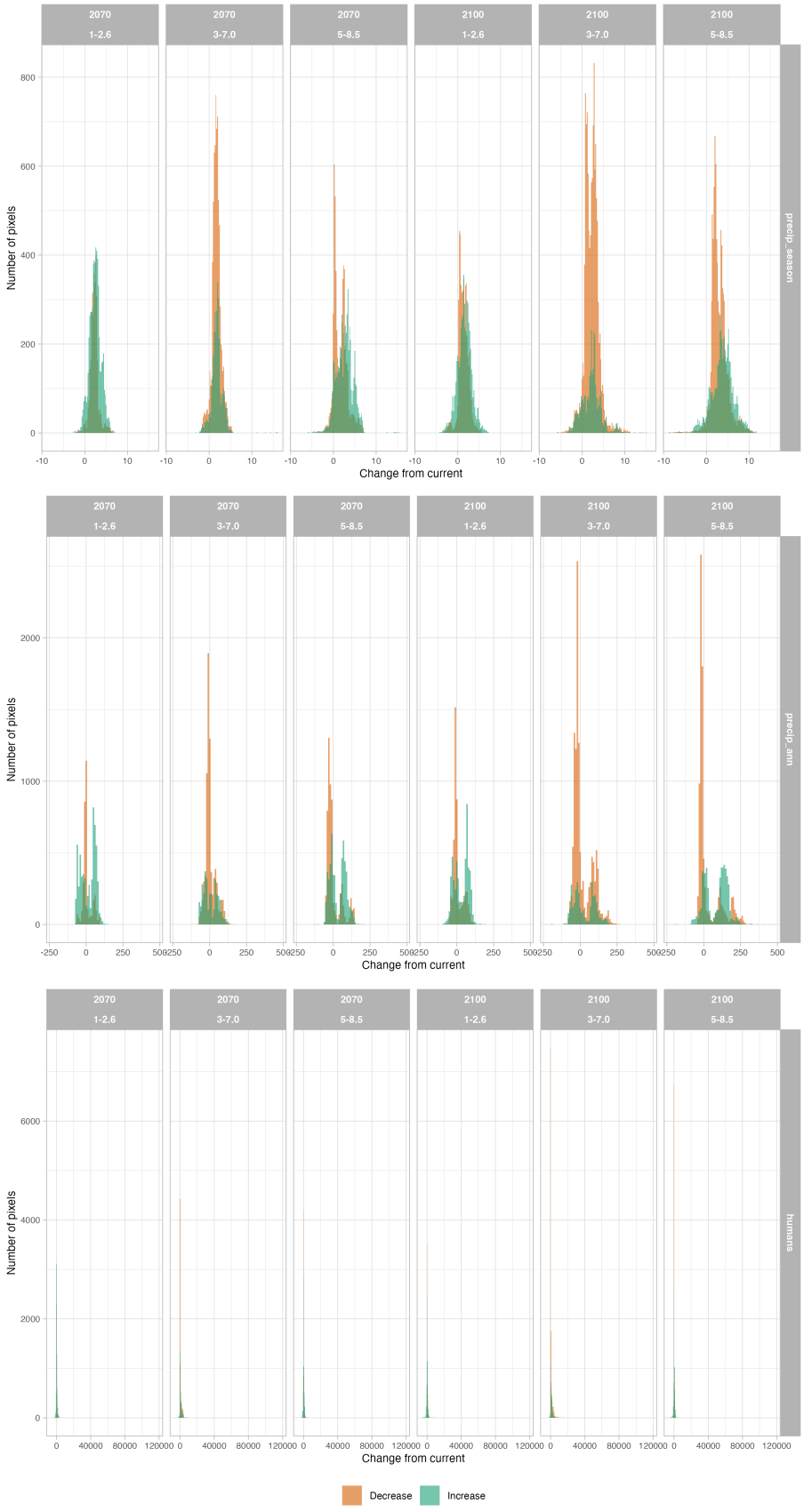


Figure S3.3 (cont). Changes in predictor layers relative to current, within pixels for which there is a predicted increase or decrease in suitability of wild dog habitat of at least 0.25. Shown for six future scenarios based on multi-scale Boosted Regression Tree models projected across continental Africa.

Tables S3.1-S3.6 can be found in an associated excel spreadsheet, along with corresponding shapefiles; each table contains predicted change in habitat suitability with coinciding mean changes in predictor variable values within each polygon expert-designated resident and recoverable range under each of the following future scenarios:

Table S3.1 – 2041-2070 SSP 1-2.6

Table S3.2 – 2041-2070 SSP 3-7.0

Table S3.3 – 2041-2070 SSP 5-8.5

Table S3.4 – 2071-2100 SSP 1-2.6

Table S3.5 – 2071-2100 SSP 3-7.0

Table S3.6 – 2071-2100 SSP 5-8.5

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APPENDIX C – CHAPTER 4 SUPPLEMENTARY MATERIAL

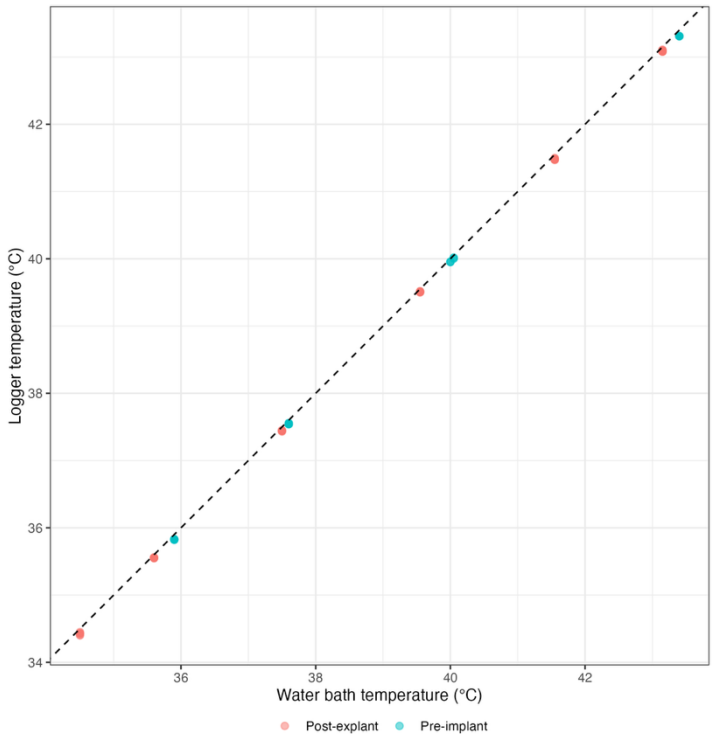


Figure S4.1. Calibration data for temperature-sensitive data loggers against water bath recordings. Displayed for loggers for which calibration took place both pre-implant (red) and post-explant (blue) to assess for potential drift in temperature values over time. All values are within 0.1°C.

Table S4.1. Summary of wild dog body temperature (T_b) and concurrent accelerometer collar (DD) data collected across four sites. Site numbers in brackets correspond with locations in Figure 4.1; SVC = Savé Valley Conservancy (Zimbabwe), KKR = !Khamab Kalahari Reserve (South Africa), TKR = Tswalu Kalahari Reserve (South Africa), HIP = Hluhluwe-iMfolozi Park (South Africa). Numbers in brackets refer to periods when animals were in captivity for reserve management purposes. Retrieval indicates when individuals were recaptured and loggers retrieved. The first week of data was excluded for all individuals, along with all data for individual 'Hlokohloko' due to short resulting free-living sampling period, a large proportion of data for individual 'Johnnie' due to apparent logger drift (Figure S5), and short periods for individuals 'Beebee' and 'Canine' due to separations from respective packs.

								T_b days		DD days	
Site	Pack	Individual ID	Sex	Deployment	Captivity	Death	Retrieval	Included	Excluded	Included	Excluded
SVC (1)	Chapungu	Beebee	M	17/05/2021	NA	NA	30/11/2022	431	13	169	13
		Canine	M	15/05/2021	NA	NA	30/11/2022	439	8	NA	NA
		Pug	F	17/06/2021	NA	NA	20/11/2022	406	7	191	7
	Gentleman	Infinity	M	16/06/2021	NA	19/12/2022	19/12/2022	407	7	280	7
	Nova	Johnnie	F	14/05/2021	NA	NA	26/11/2022	275	172	139	7
		Zulu	M	14/05/2021	NA	NA	26/11/2022	440	7	277	7
KKR (2)	North	K21	M	29/09/2021	NA	NA	26/09/2022	355	7	NA	NA
		K23	M	29/09/2021	NA	NA	13/09/2022	342	7	NA	NA
		M28	M	29/09/2021	NA	NA	28/09/2022	357	7	70	7
TKR (3)	Korranaberg	Bowling pin	M	22/06/2021	NA	NA	15/12/2022	447	7	165	7
		Limpy	F	14/06/2021	NA	NA	15/12/2022	448	7	NA	NA
HIP (4)	Mbhulungu	Baboonhand	M	23/03/2021	14/12/2021	NA	23/03/2022	259 (+99)	7	259	7 (+32)
		Hlokohloko	F	23/03/2021	04/04/2021	29/06/2021	29/06/2021	0	12 (+86)	0	12 (+86)
		Two Tears	M	23/03/2021	14/12/2021	NA	23/03/2022	259 (+99)	7	NA	NA
								4,865 (+198)	268 (+86)	1,550	74 (+118)

Weather data

Portable weather stations (HOBO Weather Station, Onset Computer Corporation, Pocasset, USA) were installed at each site to record dry-bulb temperature, relative humidity, wind speed, solar radiation, and black globe temperature at 1 m height and 1-hour intervals. However, technical failures resulted in substantial data gaps and unreliable records. Alternative weather data were therefore collated from local sources. At KKR and TKR, hourly air temperature T_a and rainfall data were obtained from onsite weather stations managed by the reserves (Figure 4.1). At HIP, monthly total rainfall was available from reserve management, while daily minimum and maximum T_a were obtained from the Riverview weather station, 21 km from the park boundary, via the South African Weather Service. At SVC, daily minimum and maximum T_a and daily rainfall totals were sourced from the Middle Sabi Research Station, 12 km away (Figure 4.1).

Because this combination of hourly, daily, and monthly records provided inconsistent temporal resolution across sites, we instead obtained hourly modelled T_a and rainfall data from the global ERA5 reanalysis dataset (Hersbach, 2023), extracted using the centroid coordinates of each site. ERA5 T_a correlated strongly with local measurements at both hourly (KKR and TKR; Table S4.2, Figure S4.2) and daily (all sites; Table S4.2, Figure S4.3) resolutions. Monthly rainfall totals also correlated reasonably well (Table S4.2, Figure S4.4), although daily rainfall correlations were weak, particularly at SVC (Table S4.2, Figure S4.5). Consequently, rainfall data were excluded from subsequent models.

Table S4.2. Pearson's correlation coefficients between ERA5 modelled weather data and onsite or local instrument-derived weather data for each of four sites (Fig 1). Dashes indicate a lack of available onsite or local data for comparison. SVC = Savé Valley Conservancy (Zimbabwe), KKR = !Khamab Kalahari Reserve (South Africa), TKR = Tswalu Kalahari Reserve (South Africa), HIP = Hluhluwe-iMfolozi Park (South Africa).

Site	Monthly rain	Daily rain	Daily Max T_a	Daily Min T_a	Hourly T_a
KKR	0.97	0.51	0.81	0.91	0.84
TKR	0.85	0.56	0.95	0.93	0.91
SVC	0.70	0.07	0.82	0.84	-
HIP	0.65	-	0.96	0.96	-

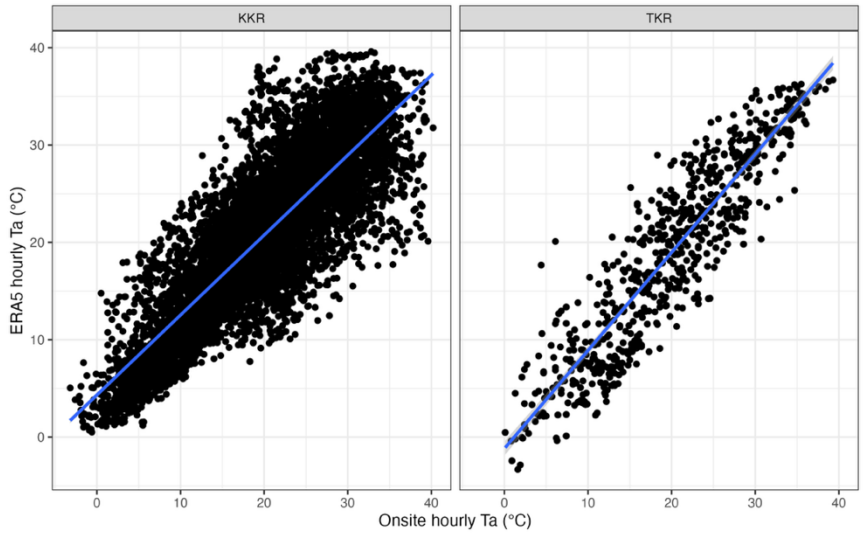


Figure S4.2. Relationship between ERA5 modelled hourly air temperature and onsite hourly air temperature records from !Khamab Kalahari Reserve (KKR) and Tswalu Kalahari Reserve (TKR) across respective study periods. Blue lines represent fitted linear models.

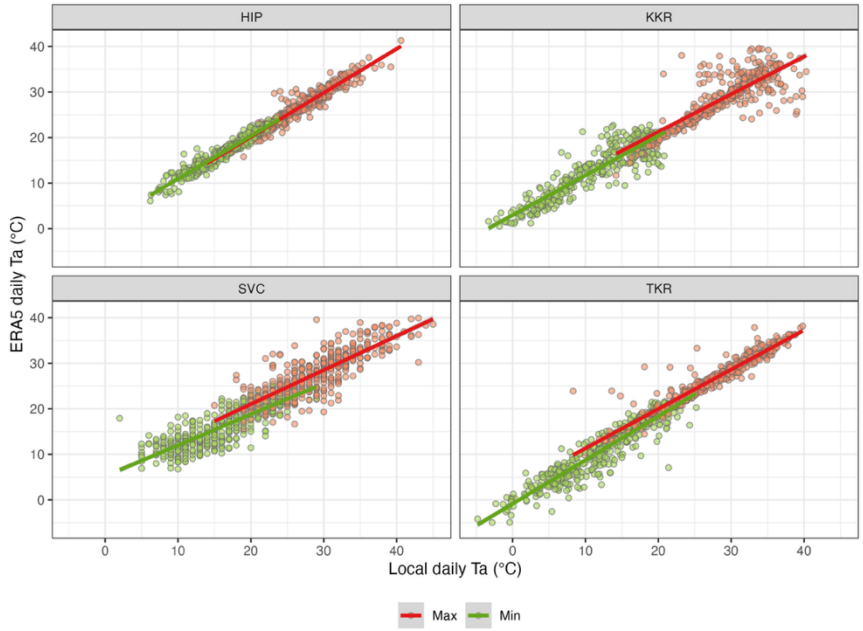


Figure S4.3. Relationship between ERA5 modelled daily minimum and maximum air temperature and onsite temperature records from each of four study sites across respective study periods. Lines represent fitted linear models.

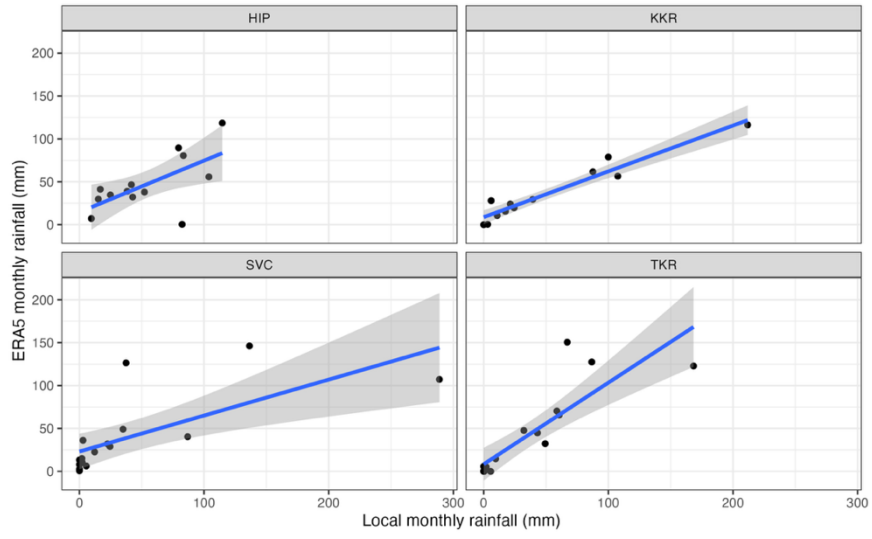


Figure S4.4. Relationship between ERA5 modelled monthly rainfall and onsite rainfall records from each of four study sites across respective study periods. Lines represent fitted linear models with associated standard error shading.

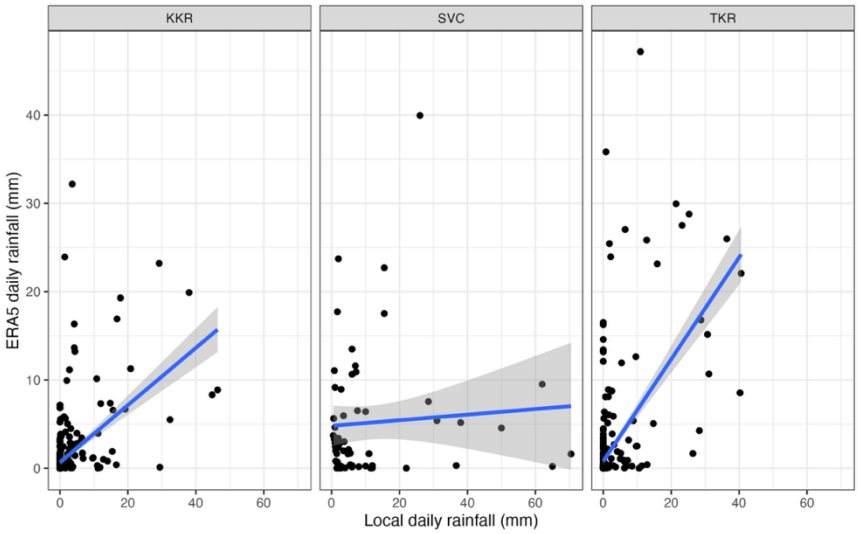


Figure S4.5. Relationship between ERA5 modelled daily rainfall and onsite rainfall records from each of three study sites across respective study periods. Lines represent fitted linear models with associated standard error shading. Daily rainfall data were unavailable for the fourth site (HIP).

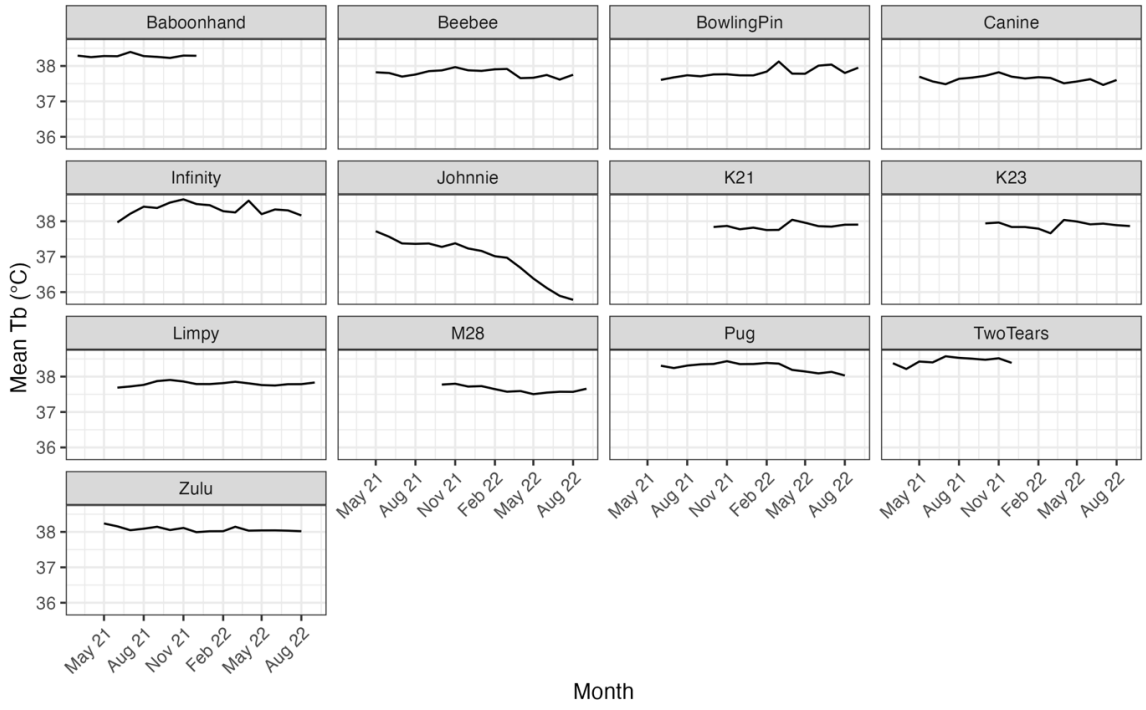


Figure S4.6. Mean monthly body temperature (T_b) for each study individual. Data from 20/02/2022 onwards for individual "Johnnie" was excluded, as determined by breakpoint analysis.

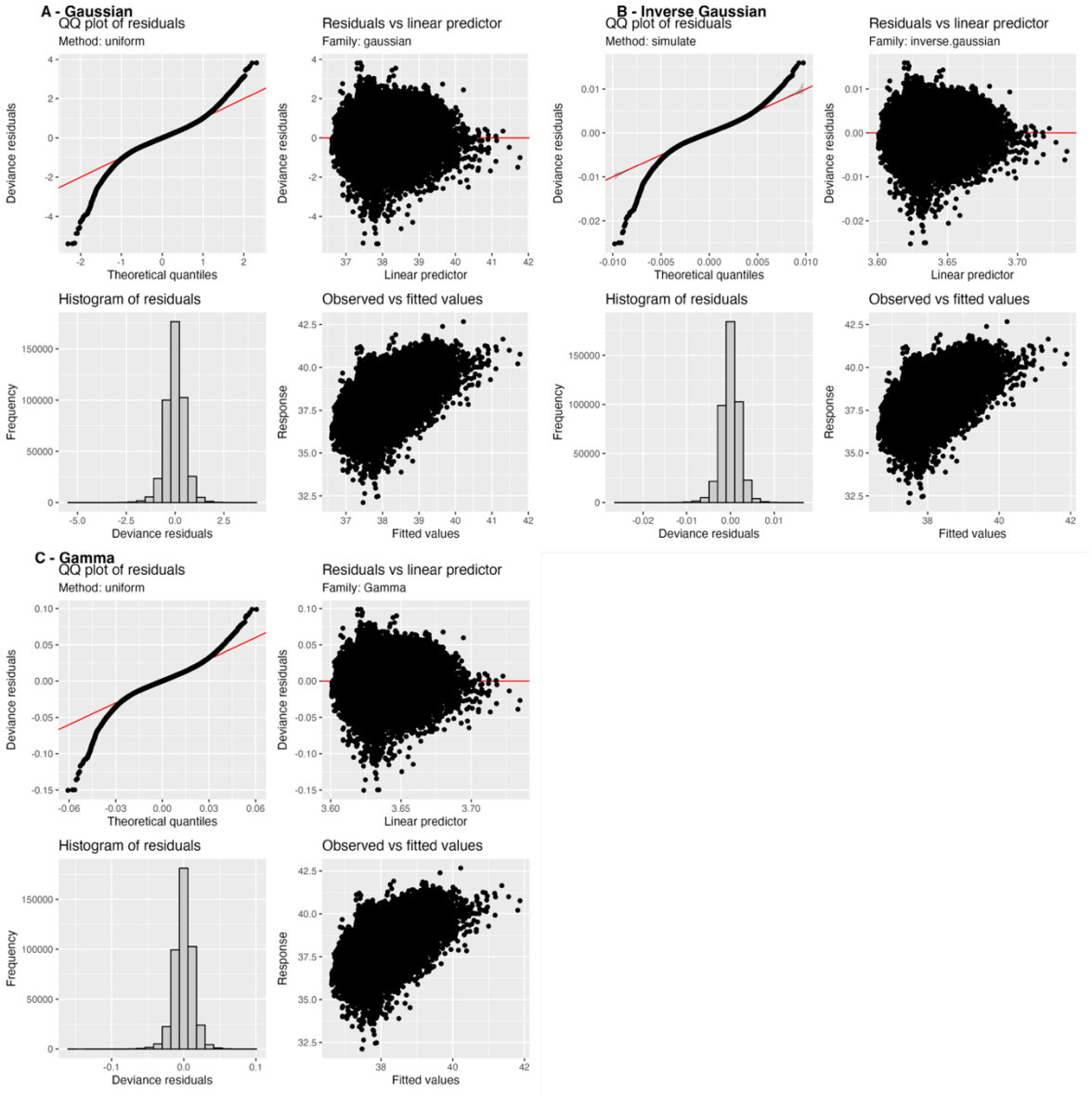


Figure S4.7. GAMM diagnostics generated using the *appraisal* function in the *gratia* package (Simpson, 2024) for each of three families: Gaussian (A), Inverse Gaussian (B), and Gamma (C).



Figure S4.8. Daily body temperature (T_b) for each of 13 wild dogs at four sites. Thick lines represent daily means; shading represents daily minima and maxima. Facet titles indicate site and individual ID. "Boma" indicates where two individuals were taken into captivity for reserve management purposes.

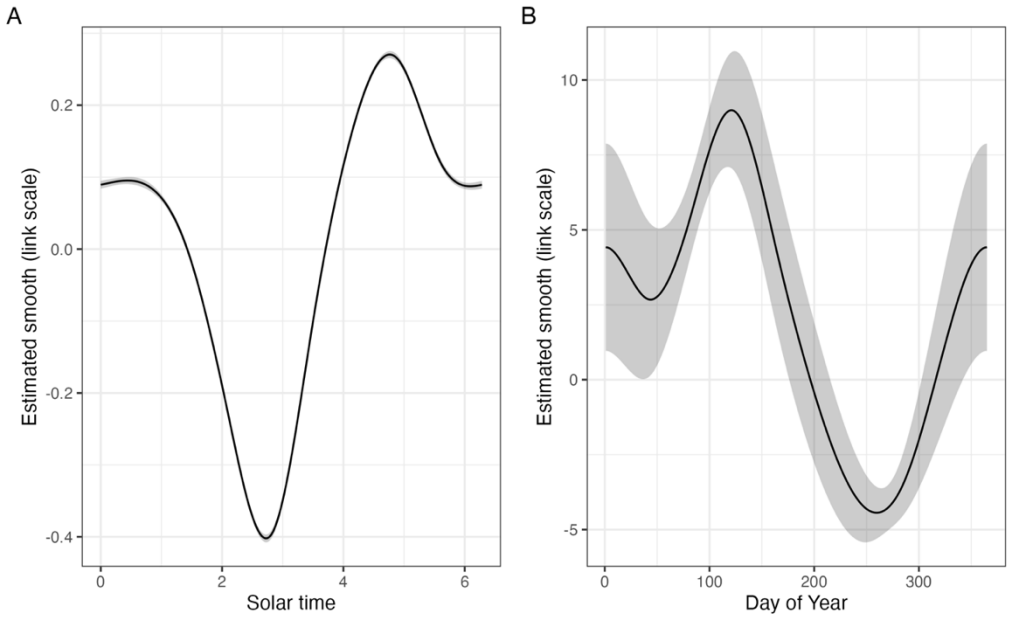


Figure S4.9. Estimated smooth effects of (A) solar time and (B) day-of-year (DOY) on wild dog body temperature (T_b) from the generalised additive model. Solid lines represent model estimates on the link (identity) scale; shaded areas indicate approximate 95% confidence intervals.

Table S4.3. Results from Generalised Additive Mixed Effects Model (GAMM) 10-fold h-block cross-validation modelling the relationship between body temperature (T_b) and activity and environmental variables in eight free-living African wild dogs.

Fold	n	RMSE	MAE	R^2	Coverage
1	44,318	0.49	0.36	0.41	0.95
2	44,346	0.50	0.37	0.42	0.94
3	44,317	0.48	0.36	0.42	0.95
4	44,352	0.51	0.38	0.40	0.94
5	44,352	0.48	0.36	0.43	0.95
6	44,340	0.48	0.37	0.41	0.95
7	44,352	0.50	0.37	0.41	0.95
8	44,323	0.49	0.37	0.41	0.95
9	44,305	0.47	0.35	0.45	0.95
10	44,265	0.50	0.38	0.40	0.94
Overall	**443,270**	**0.49**	**0.37**	**0.42**	**0.95**

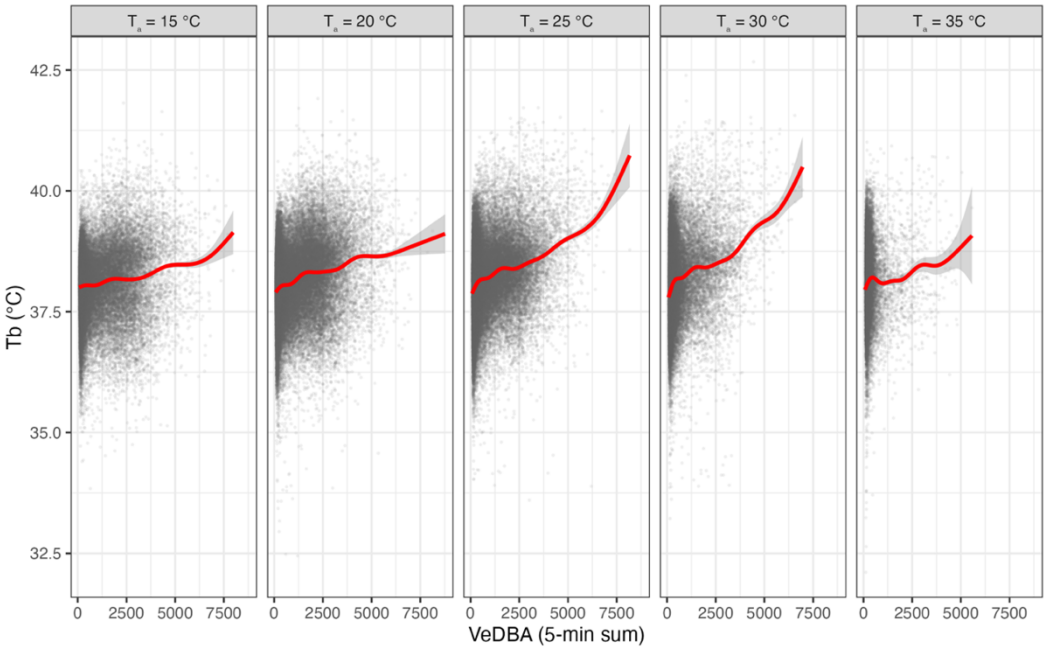


Figure S4.10. Raw body temperature (T_b) data plotted against activity (VeDBA) at each of five given air temperatures (T_a, within 2°C). Lines indicate fitted generalised additive models (GAMs). Shading represents 95% confidence intervals.

References

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SIMPSON, G. 2024. gratia: Graceful ggplot-Based Graphics and Other Functions for GAMs Fitted using mgcv. R package version 0.10.0, <https://gavinsimpson.github.io/gratia/>.

APPENDIX D – CHAPTER 5 SUPPLEMENTARY MATERIAL

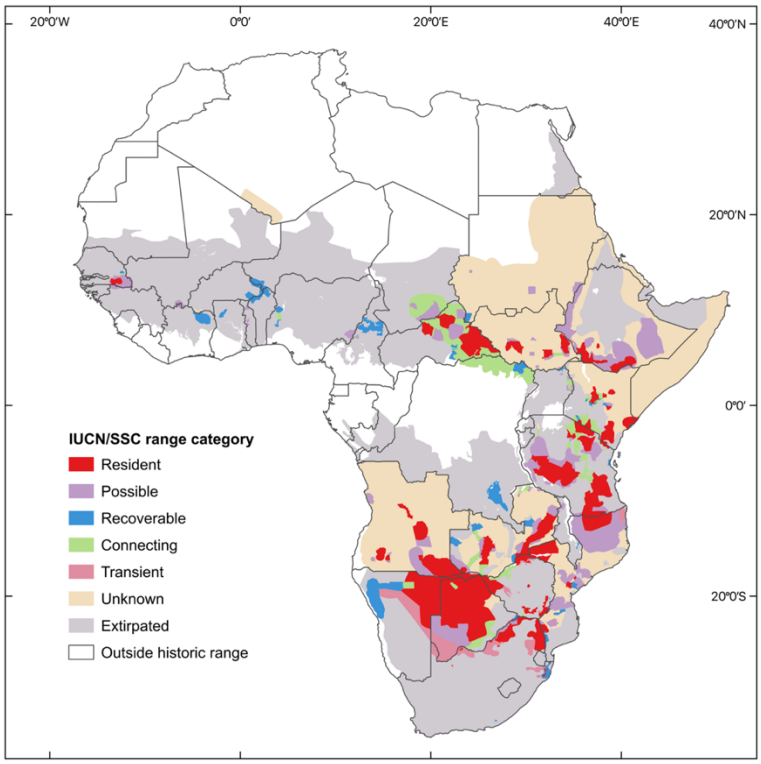


Figure S5.1. African wild dog historical range and current range categories, as published alongside the species IUCN Red List assessment (Woodroffe et al., 2025), defined and mapped by species experts participating in regional workshops (IUCN/SSC, 2015, IUCN/SSC, *in prep-a,* IUCN/SSC, 2024).

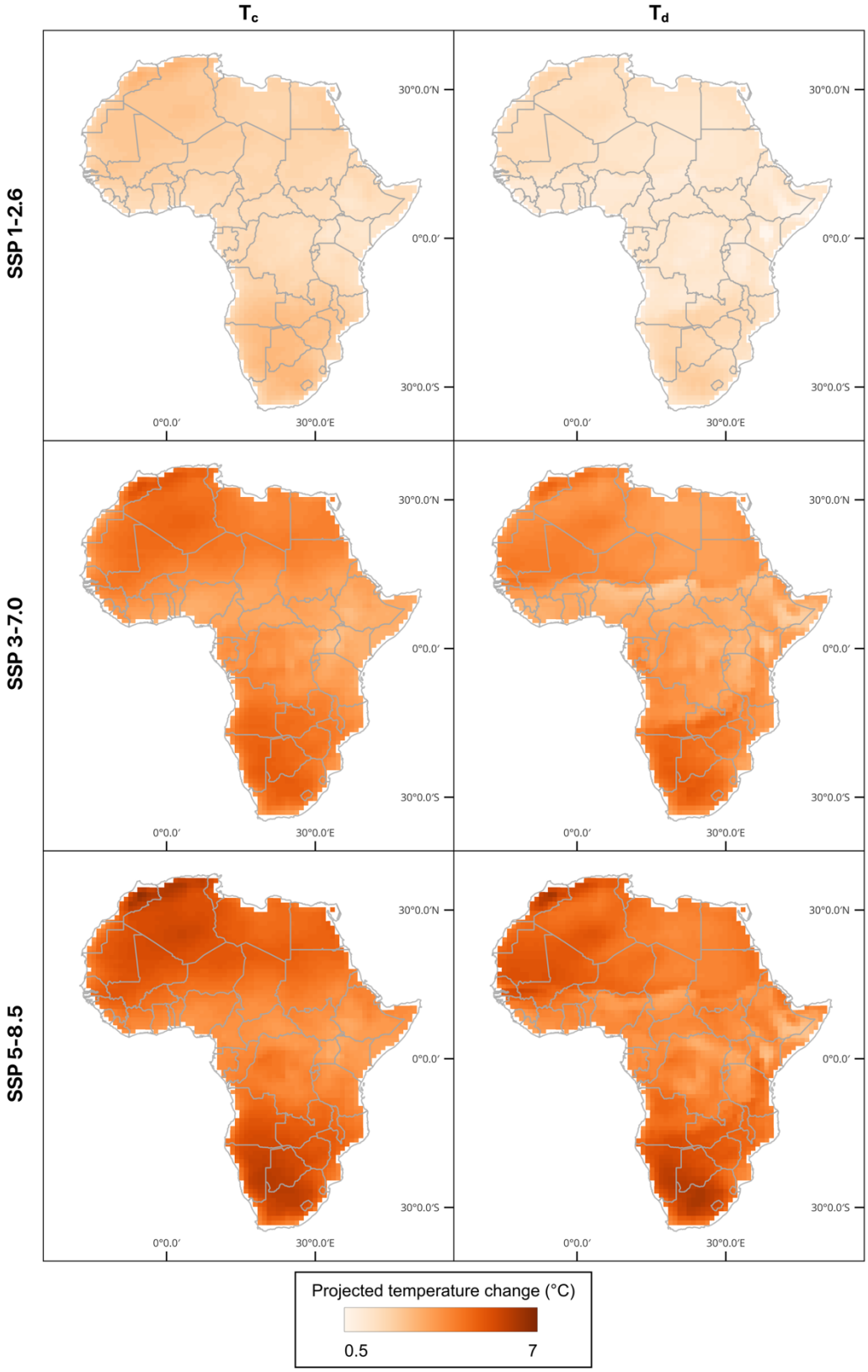


Figure S5.2. Mean change in daily maximum temperature across continental Africa under three SSP scenarios, as projected by five global circulation models (GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0) for the period 2071–2100 relative to 1981–2010 (Karger, 2021). T_c represents change in annual mean daily maximum ambient temperature; T_d represents change in mean daily maximum ambient temperature during the coolest three consecutive months (the African wild dog denning season).

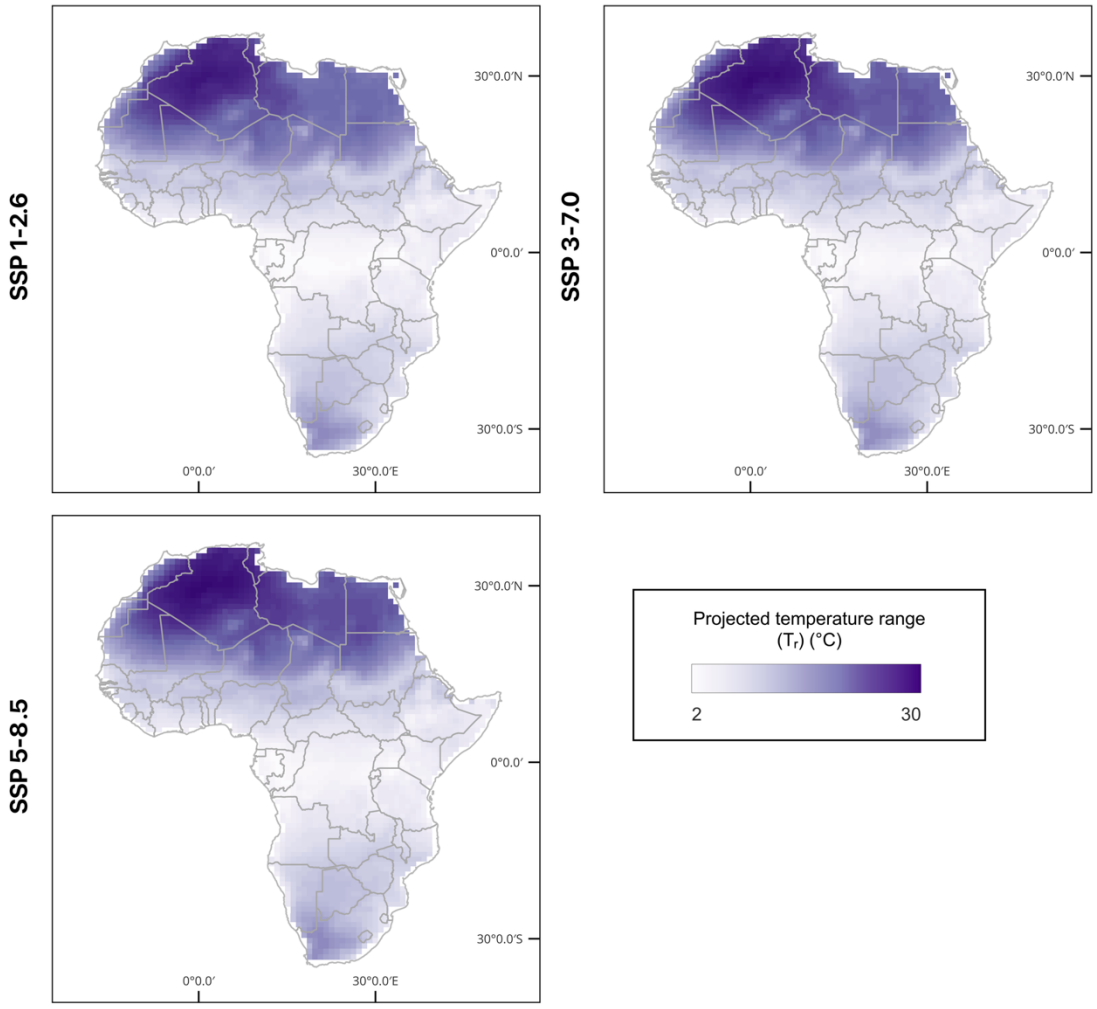


Figure S5.3. Projected mean temperature range across continental Africa under three SSP scenarios, as projected by five global circulation models (GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0) for the period 2071–2100 **(Karger, 2021).** Temperature range (T_r) represents the difference in mean daily maximum temperature between the coolest and hottest month.

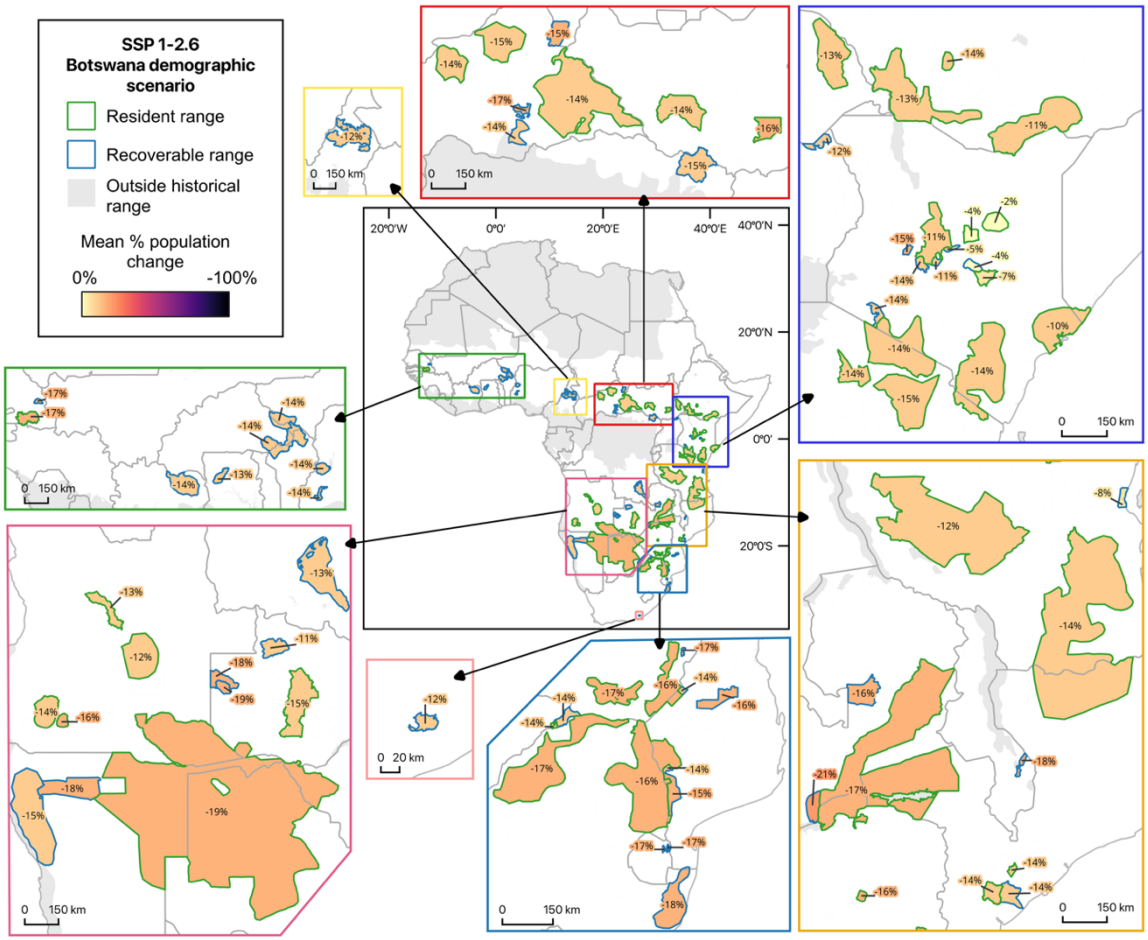


Figure S5.4. Mean predicted African wild dog population change under SSP 1-2.6 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Botswana site.

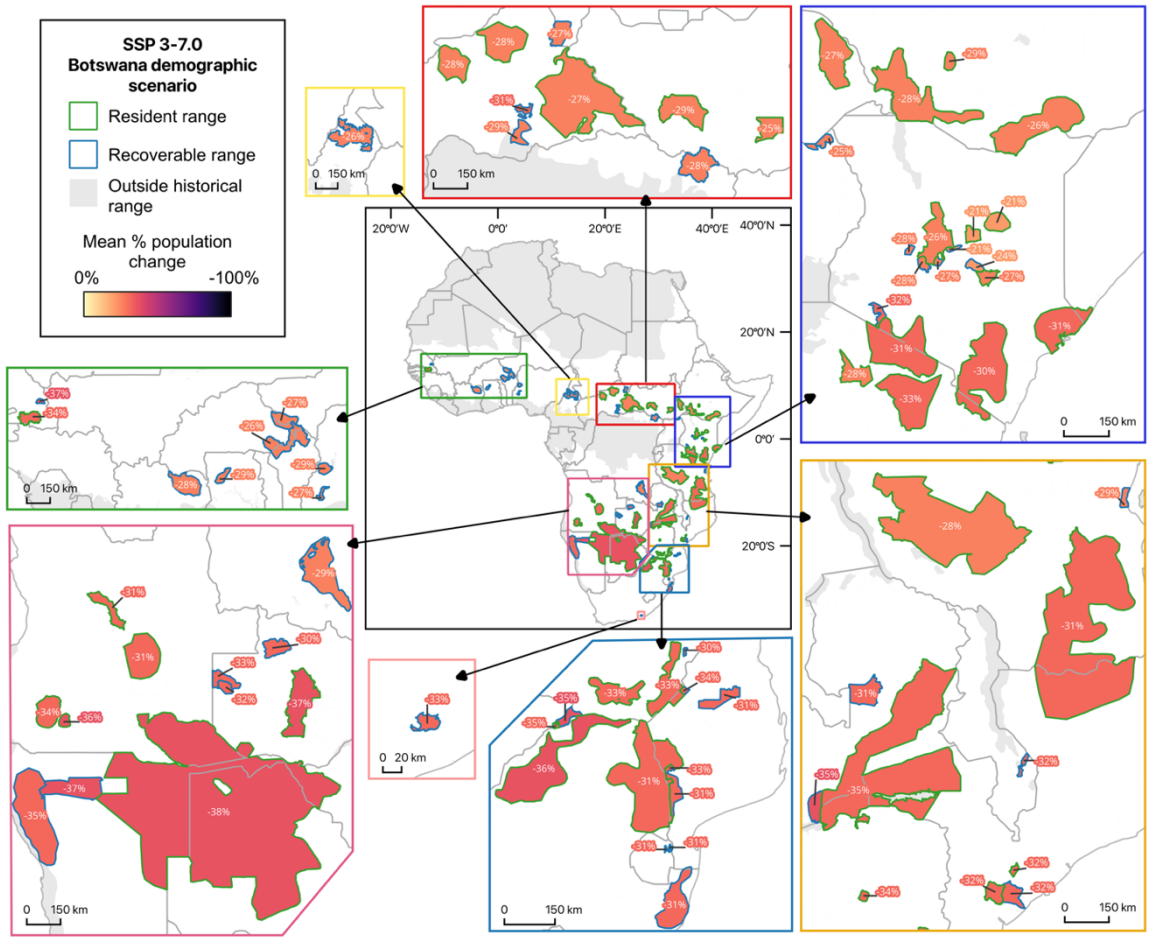


Figure S5.5. Mean predicted African wild dog population change under SSP 3-7.0 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Botswana site.

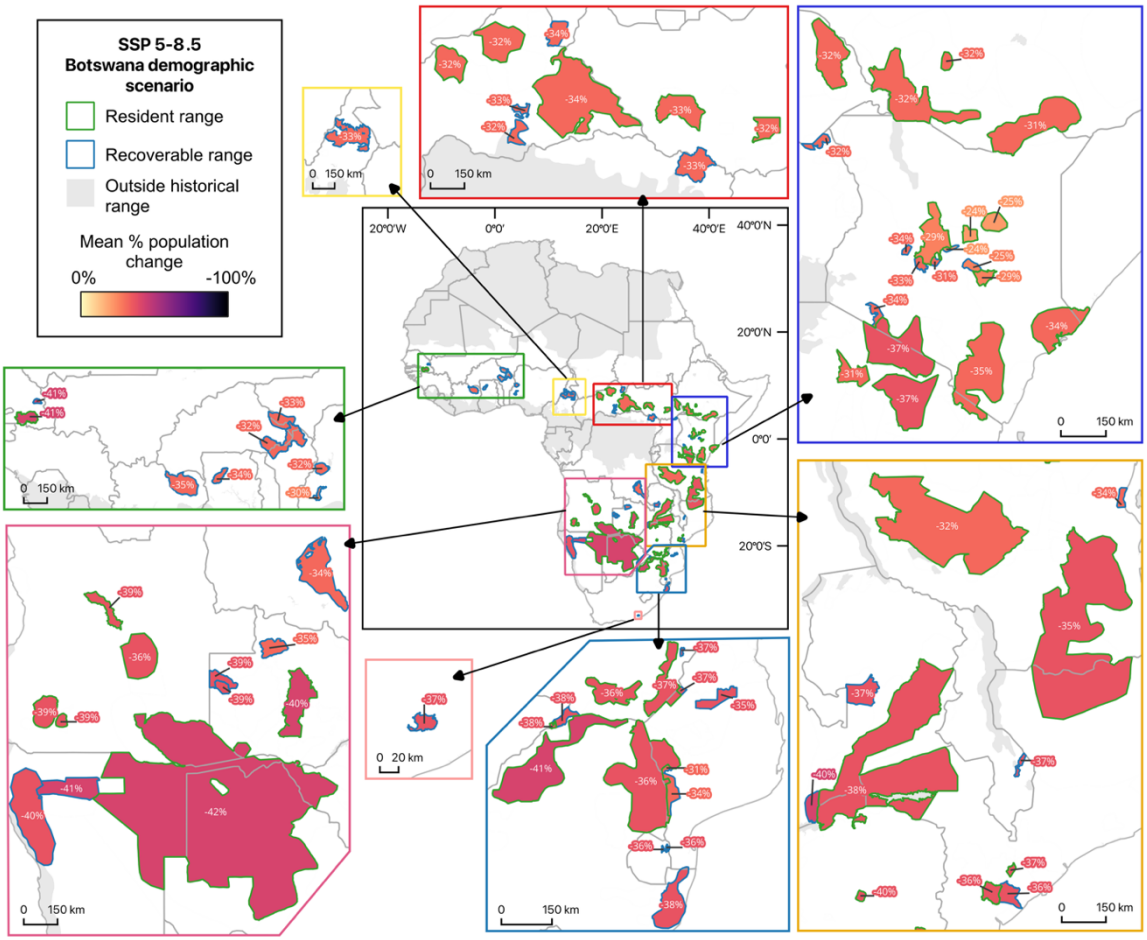


Figure S5.6. Mean predicted African wild dog population change under SSP 5-8.5 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Botswana site.

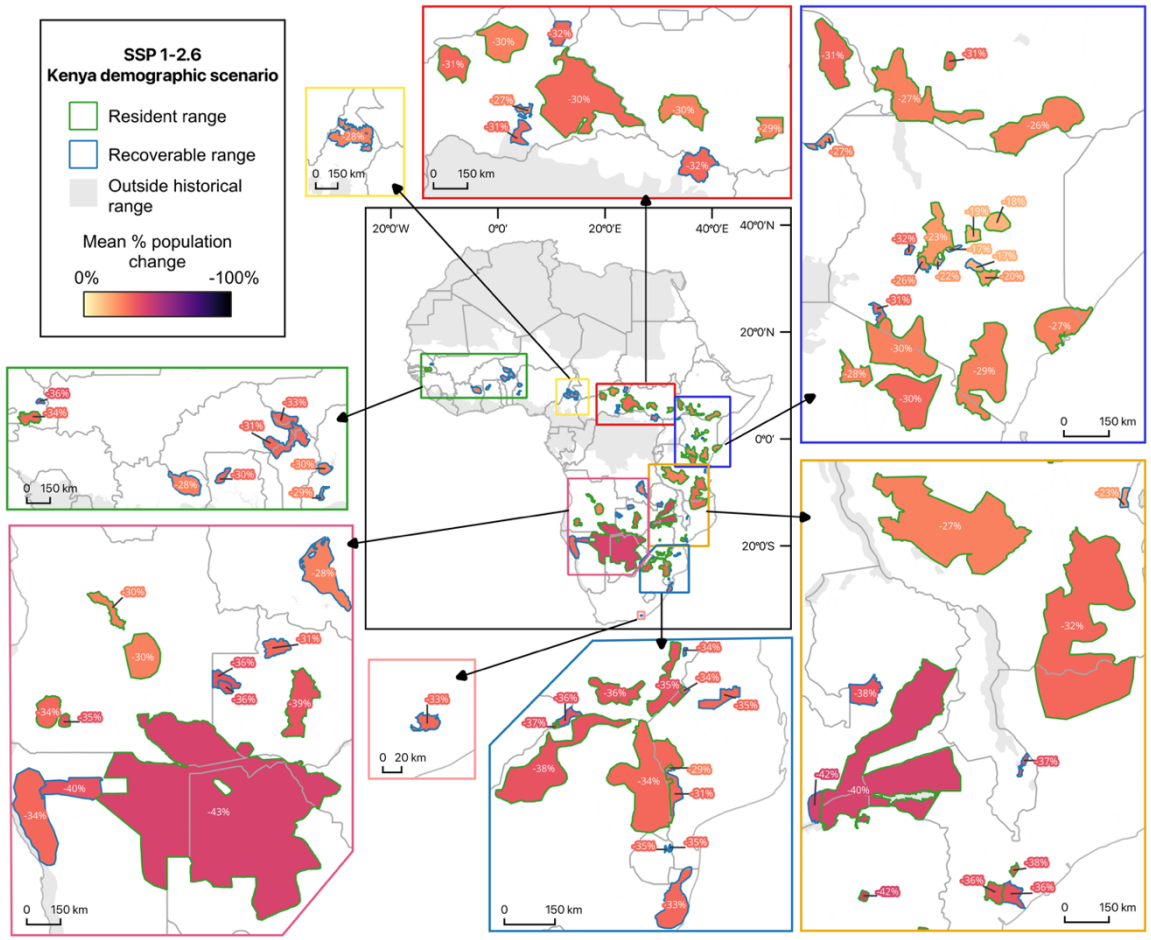


Figure S5.7. Mean predicted African wild dog population change under SSP 1-2.6 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Kenya site.

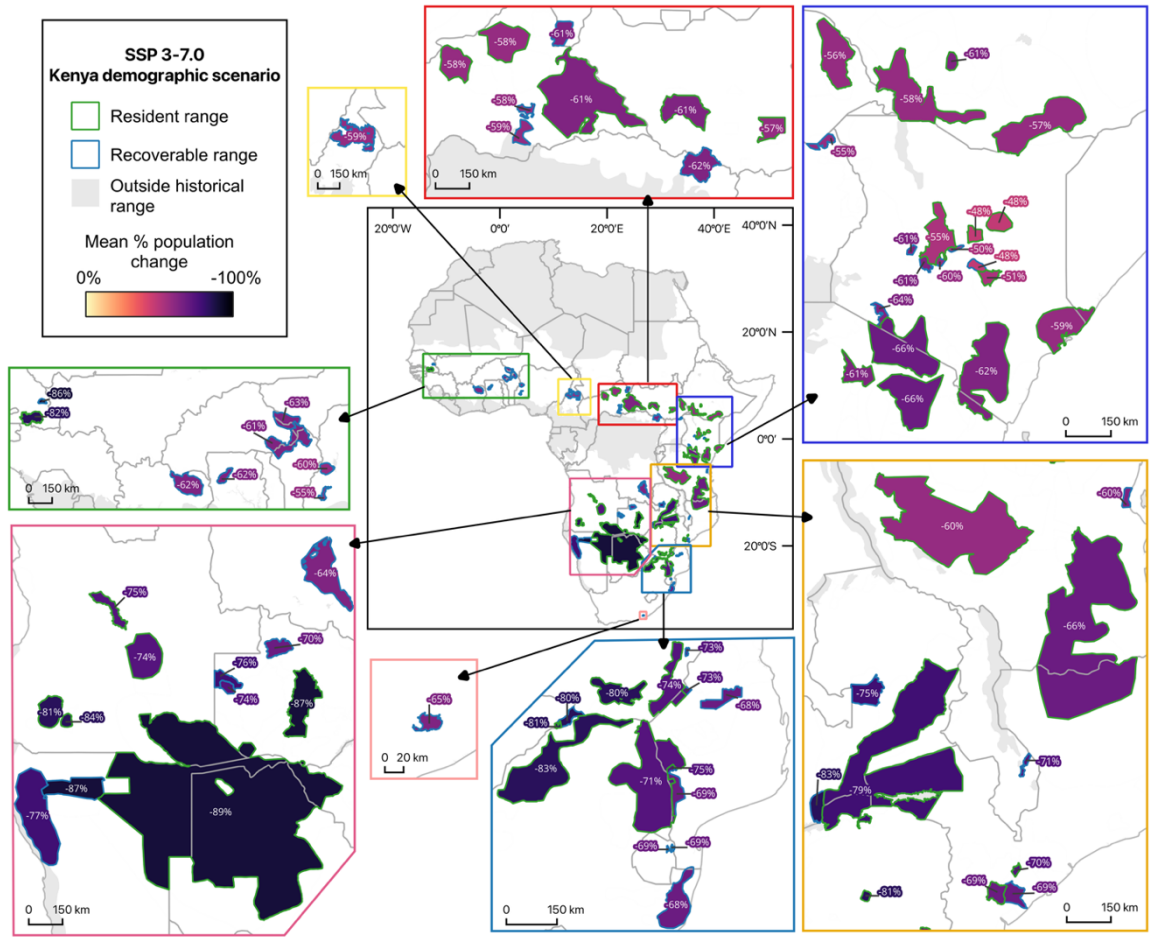


Figure S5.8. Mean predicted African wild dog population change under SSP 3-7.0 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Kenya site.

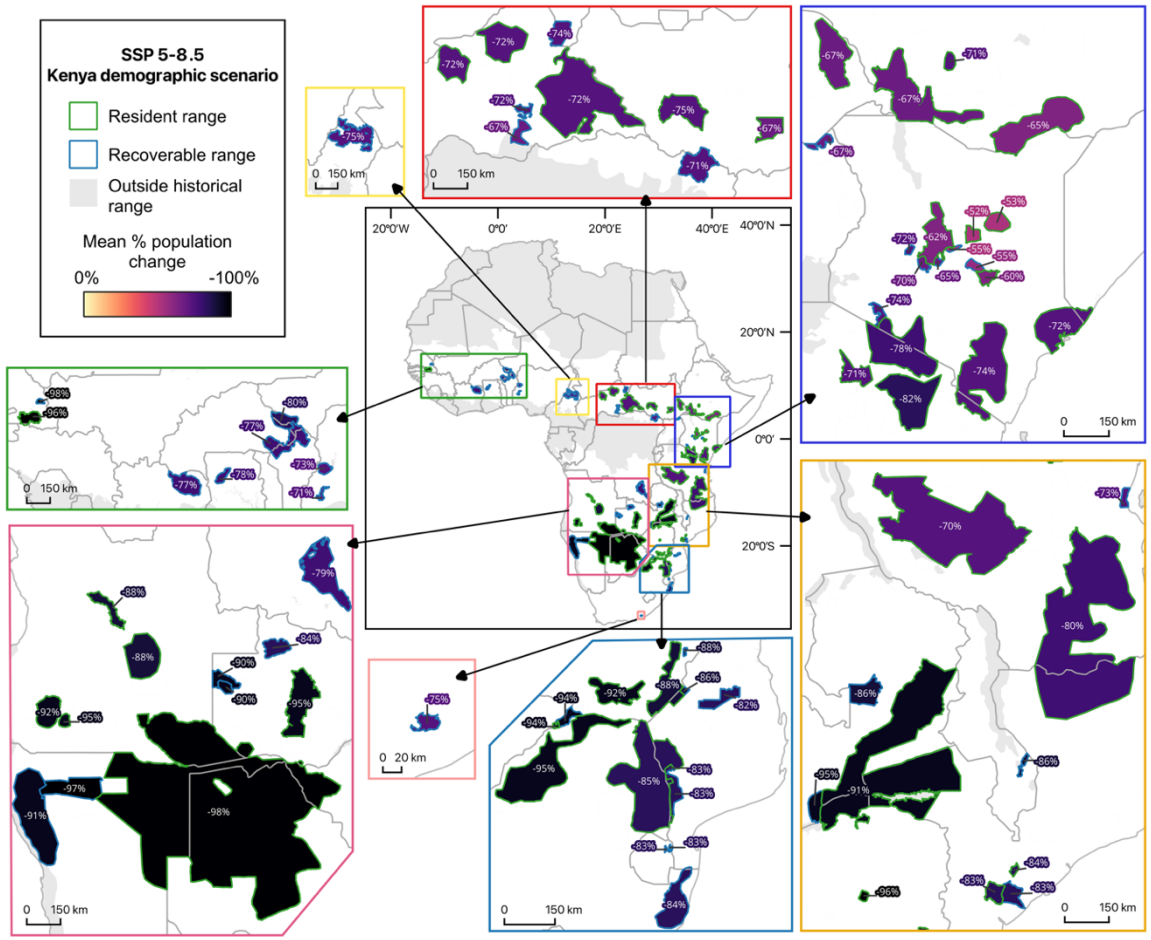


Figure S5.9. Mean predicted African wild dog population change under SSP 5-8.5 climate projections over 90 years within each resident and recoverable range polygon for simulated populations. To facilitate comparisons of the impacts of climatic conditions, carrying capacity was standardised as nine packs at each site. Parameterised using demographic data from the Kenya site.

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APPENDIX E – MANUSCRIPT IN PRESS: Refining the use of implanted biologgers in an endangered species

As accepted by *Journal of Applied Animal Ethics Research* on 27/03/2026

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Abstract

Research on endangered wildlife is vital to inform conservation, but may risk adverse welfare impacts. Following predictions that African wild dog (Lycaon pictus) populations could collapse as global temperatures rise, we initiated a thermal ecophysiology study to better understand weather impacts on this endangered species. Four institutional ethics committees approved our plan to surgically implant small (3.3g) thermal data loggers, using methods previously applied safely in similar species. One confirmed, and one unconfirmed, incident of adverse effects led us to refine our protocols and reduce target sample sizes. We experienced difficulties in detecting and responding to ill-effects, and our refined protocols approached the limit of what was possible with this wide-ranging species. Hence, any attempt to repeat our study would need to be carefully considered and strongly justified. Future projects performing novel invasive procedures on endangered species should recruit study animals gradually, using intensive post-surgery monitoring to inform recruitment decisions.

Key words: African wild dog; animal ethics; animal welfare; biologger; endangered species; implant; logger; Lycaon pictus

1. Introduction

Field research on endangered species is urgently needed to inform and improve their conservation. Nevertheless, where such research involves animals, there is a need to balance the benefits accrued from the knowledge generated, against the potential costs in terms of animal suffering and environmental damage (ASAB Ethical Committee/ABS Animal Care Committee, 2023; Putman, 1995; Simmons, 2023). The "3Rs" framework (Russell and Burch, 1959) is a widely-used approach helping researchers to design studies which minimise the "costs" side of this balancing process, by ***replacing*** animal subjects with alternatives where possible, ***reducing*** sample sizes to the minimum required to answer the research question, and ***refining*** methods to minimise animal suffering. Several other "Rs" have been proposed subsequently, including ***responsibility*** (Banks, 1995), to capture the scientific community's wider duty to actively pursue research and public discourse aimed at improving animal welfare, and ***refusal*** (Curzer et al, 2013), to highlight that research should not go forward where the welfare costs exceed the knowledge benefits.

Designing studies involving wildlife carries additional challenges (ASAB Ethical Committee/ABS Animal Care Committee, 2023; Cuthill, 1991; Putman, 1995; Zemanova, 2020). The relative difficulty of observing wild animals may demand more invasive methodologies than those used in captivity; for example, tracking collars are routinely deployed on free-ranging animals to help researchers locate and observe them, and may impact welfare (Barron et al, 2010; Forin-Wiart et al, 2019; Harvey-Carroll et al, 2025; White et al, 2013). Unfortunately, this challenge of observing wild animals also applies to the detection of adverse effects (Putman, 1995; Zemanova, 2020). Even if evidence of suffering is observed, responding with timely veterinary care may be challenging, and the associated capture and confinement may in themselves confer further suffering. Moreover, for some wildlife species, there may be few previous studies on the same (or a closely related) species available to inform risk assessments for specific procedures, or to help identify appropriate refinements.

Research involving endangered species adds a further dimension (Cooke, 2008). On the one hand, such research may inform conservation action, increasing its benefits. However, the risk of impairing survival or reproduction for an endangered species may undermine conservation efforts, adding an additional cost (ASAB Ethical Committee/ABS Animal Care Committee, 2023; Cuthill, 1991).

Under these circumstances, studies on endangered wildlife may need to adopt a flexible approach, proceeding on the basis of the best available evidence, but modifying study design as such evidence accumulates through experience. Reporting such experience – whether positive or

negative – is essential to informing the choice and design of future studies, consistent with the "***Responsibility***" principle (Banks, 1995). Within this context, we report our experience of designing and conducting a field study of conservation physiology, using implanted biologgers, in an endangered species, the African wild dog (*Lycaon pictus*).

2. The research question

Climate change is a growing existential threat to many wildlife species. Identifying appropriate conservation responses to this threat is complicated by the tendency for weather to impact species indirectly, through complex interactions with predators, prey, competitors, or pathogens (Ockendon et al, 2014). In contrast, weather impacts on African wild dogs appear relatively simple and direct (Rabaiotti and Woodroffe, 2019; Woodroffe et al, 2017), making this species a potentially valuable model for exploring the threat of climate change, and its conservation solutions.

African wild dogs are highly social, wide-ranging, coursing predators, reliant on high-speed chases to capture their prey (Frame et al, 1979). Evidence suggests that such chases demand both low ambient temperatures and sufficient light, constraining hunting to narrow time windows at dawn and dusk, and to nights with strong moonlight (Rabaiotti and Woodroffe, 2019; Woodroffe et al, 2017). Lower reproductive success (Woodroffe et al, 2017) and survival (Rabaiotti et al, 2021) at higher ambient temperatures show that the weather conditions which constrain hunting are also linked to harmful demographic consequences, sufficient to cause projected population collapse under climate change (Rabaiotti et al, 2023). Based on this evidence, we hypothesised that the risk of heat stress might curtail wild dog hunts at high ambient temperatures, limiting food intake and impacting survival: essentially, that wild dogs traded off under-eating against overheating.

Prior research suggested that another African large carnivore, the cheetah (*Acinonyx jubatus*), did not stop hunting as a consequence of high body temperatures (Hetem et al, 2013). However, cheetahs and African wild dogs are taxonomically and behaviourally dissimilar. In a closer relative, the domestic dog (Canis familiaris), intense exercise causes potentially dangerous hyperthermia (Carter and Hall, 2018; McNicholl et al, 2016; Phillips et al, 1981), and the same may be true for wild dogs (Taylor et al, 1971).

We hypothesised that thermal physiology, through its impacts on hunting behaviour, was the ultimate mechanism underlying African wild dogs' vulnerability to climate change, and therefore a key to identifying conservation solutions. To test this hypothesis, we designed a project to simultaneously monitor hunting behaviour and body temperature in free-ranging wild dogs.

Across multiple study sites representing a range of climatic conditions (Table 1), we planned to characterise hunting behaviour using collar-mounted accelerometers (Redcliffe et al, 2024), while monitoring body temperature using implanted biologgers.

3. Project timeline

3.1 The decision to use implanted biologgers

In designing our study, we considered several less invasive ***replacements*** for surgically implanted biologgers. Unfortunately, body surface temperature measured using infrared thermography has been shown to provide a poor surrogate for core body temperature, across a wide range of species (e.g., McFarland et al, 2020b; Russell et al, 2024; Szafranska et al, 2020). Moreover, for free-ranging African wild dogs, thermography would be possible only during the fraction of time when the animals could be visually monitored at close quarters, making measurements during the energy-intensive hunting periods essentially impossible. The use of ingestible biologgers (Friend et al, 2020; Signer et al, 2010) was discounted because free-ranging wild dogs are reluctant to consume food baits (Knobel et al, 2002), their rapid passage times (Davies-Mostert et al, 2010) would likely constrain temperature monitoring to very few days (possibly hours), and their wide-ranging behaviour (Pomilia et al, 2015; Woodroffe, 2011) would make logger retrieval almost impossible. In contrast, surgically-implanted temperature loggers have been shown to accurately and precisely measure core body temperature, at frequent and regular intervals, over periods of many months, irrespective of whether the animals were accessible for visual observation (e.g., Forin-Wiart et al, 2019; Trethowan et al, 2016; Williams and Hindle, 2021).

Having recognised the benefits of using implanted loggers, we carefully evaluated the potential risks. We were aware that implanted devices had been recorded to cause harm (Arnemo et al, 2018; Barron et al, 2010), although in birds this impact was reported to be smaller than that caused by externally attached devices (Forin-Wiart et al, 2019; White et al, 2013). In addition to the general risks of causing physical harm during surgery, and of introducing infection, we also noted potential species-specific risks, during the post-surgery recovery period, of impeding wild dogs' ability to chase and subdue large prey, or to escape from larger competitors. Additionally, we noted a potential risk of other group members licking or biting at surgical wounds during social interaction. Importantly, we recognised that, as data could be obtained from the loggers only by retrieving them, each animal would require two surgical procedures, one to implant a logger, and another to explant it. Although we found no publications measuring the impacts of explant surgery (studies tend to focus on implant surgery, or living with an implant, e.g., Arnemo et al, 2018; Barron et al, 2010; White et al, 2013) we were reassured that members of our team had, at the time,

observed no harmful effects from implanting or explanting similar loggers in 233 animals belong to 16 other wildlife species (Table S1), including animals which, like wild dogs, hunt large prey (cheetahs, lions *Panthera leo*), need to evade large carnivores (multiple antelope species), or engage in social grooming (vervet monkeys, *Chlorocebus pygerythrus*; Table S1).

Through these prior studies, the team had developed a number of ***refinements***, which we adopted in this study (Table 2). We chose a retroperitoneal implant site, which had been shown to provide temperature readings closely approximating core body temperature, without the need to open the abdominal cavity (Torrao et al, 2011). Additionally, we took advantage of a newly-developed cylindrical logger (DST-micro-T with extended memory; Star-Oddi, Gardabaer, Iceland) which, at 25mm x 8mm x 8mm and 3.3g, was smaller than many of those used previously, while still being capable of recording temperature every 5 minutes for 455 days.

From this evidence, we concluded that the use of surgically implanted biologgers was unlikely to cause lasting harm, and therefore that the benefits of the planned research outweighed the risks. Our proposed study design entailed deploying biologgers in 35 free-ranging African wild dogs, at six study sites representing a range of ambient temperature and rainfall patterns (Table 1). All six sites had wild dog monitoring in place, for ongoing research and/or conservation projects (Davies-Mostert et al, 2015; Groom et al, 2017; Woodroffe et al, 2017). Sample size was informed by power calculations, with the intention of capturing individual variation within and between study sites, and to allow for some logger loss due to natural mortality and dispersal. Based on the available evidence, the study was approved by four ethics committees, and also permitted by two national governments (Kenya and Zimbabwe) and four provincial governments within South Africa (Table 1).

3.2 Commencing implant surgery

Implant surgery began at Site 1 in the early morning of 23 March 2021. Following the procedures agreed with the ethics committees, three wild dogs within a single free-ranging pack were darted using tiletamine-zolazepam (20mg, equivalent to 0.57-0.92 mg/kg) and medetomidine (2mg, equivalent to 0.057-0.092 mg/kg), by a team of wildlife veterinarians experienced in logger implant surgery. Animals were transported <100m to a mobile surgical station where they were maintained on isoflurane inhalation anaesthesia (Figure 1). Each animal was given a long-acting antibiotic, as well as a non-steroidal anti-inflammatory injection. Heart rates, respiratory rates, rectal temperature, SpO_2, mucous membrane colour, capillary refill time, and reflexes were monitored throughout the procedure. Each wild dog was placed in dorsal recumbency, and an area surrounding the surgical site was aseptically prepared by clipping the fur, cleaning with antiseptic

soap, cleaning with antiseptic alcohol swabs, and then spraying with a solution of chlorhexidine and alcohol. Subcutaneous lignocaine was injected along the incision site, and then a 30mm incision was made into the ventral midline through the skin and *linea alba* (Figure 1). Underlying tissue was bluntly dissected to visualise the external parietal peritoneum and to make a pocket between the peritoneum and the abdominal wall. The data logger (coated in inert wax, dry sterilised in formaldehyde gas, and then rinsed with sterile water) was placed in this pocket; the intention was to place the logger just outside the peritoneum, without entering the abdominal cavity. The abdominal wall was then closed with simple interrupted sutures, using a coated vicryl suture material, using the *linea alba* as an anchor. The skin was then closed, first with intradermal sutures, and then with simple interrupted sutures, both using coated vicryl. Externally, the wound was treated with an antiparasitic petroleum-based ointment (Tick Grease, Kyron Laboratories, South Africa) and antibacterial spray (Necrospray, Bayer, Animal Health Division). Finally, each animal was fitted with a 300g custom-built tracking collar containing a "Daily Diary" accelerometer/magnetometer (Wilson et al, 2008), VHF transmitter, and GPS logger.

Animals were allowed to recover from anaesthesia together (mean time from reversal to walking 10 mins, range 3-41 mins), and to return to the rest of their pack which was waiting nearby. Tracking collars were used to locate the pack later the same day, during its normal evening active period. Although thick vegetation limited observation, the implanted animals were observed on the road, moving freely and interacting with other pack members in a normal manner, apparently participating in the regular evening hunt. Normal behaviour (morning and evening hunts, interspersed with midday and night-time rest periods, observed through telemetry and twice-daily visual checks, Woodroffe et al, 2017) continued to be observed and recorded over the subsequent two days.

Based on this success, on 26 March 2021 three more wild dogs were implanted and collared using the same protocol. These animals were being held temporarily (anticipated to be a few weeks) in an enclosure (a "boma") ahead of a planned release, as part of population management (Davies-Mostert et al, 2015). Again, the animals showed no signs of ill-health, and were observed feeding, moving, and resting at the expected times (Woodroffe et al, 2017) in the days and weeks immediately post-surgery.

Following this success at Site 1, five animals were recruited to the study at Site 2 during the period 14-17 May 2021, and then another three animals were recruited at Site 3 on 14-15 Jun 2021 (Table S2). At all three sites, animals recovered rapidly and were repeatedly observed behaving normally in the days and weeks following surgery. Indeed, with the exception of one animal killed by

conspecifics on Day 98 post-surgery, all ultimately survived >300 days, with some still alive over four years later (Table S2).

3.3. An incident of adverse effects following implant surgery

With 14 animals successfully implanted, on 16 Jun 2021 efforts commenced to deploy three more biologgers at Site 2, in Zimbabwe. Restrictions on South African veterinarians practising in Zimbabwe required the use of a different surgical team (including experienced clinical veterinarians with substantial wildlife expertise), but otherwise the same protocol was used to implant two animals within the "Gentlemen Pack" (Table S2). The following day, these animals were located using their tracking collars, but could not be observed visually due to dense vegetation. The surgical team then located a different pack and successfully implanted the third and final logger designated for Site 2.

On 18 Jun 21, the monitoring team were able to visually observe the Gentlemen Pack, and noted a mass protruding from the implant wound of one of the animals which had received a logger two days previously. The implanting veterinarian returned to the site, and on 19 Jun was able to dart the affected animal. It appeared that the sutures had been bitten at, exposing a loop of intestine which had been bitten in two. The veterinarian performed emergency restorative surgery, but the animal died the same night.

3.4 Responses to the adverse incident associated with logger implant

The project team responded to this death by (i) immediately pausing logger deployments; (ii) investigating why the death had occurred; (iii) reviewing procedures for recruiting, implanting, and monitoring animals within the study, to explore whether further ***refinements*** might reduce the risks of adverse effects; and (iv) formally considering (with overseeing ethics committees) alternative ways forward, combining potential ***refinements*** and ***reductions*** (Table 3).

Careful evaluation of events identified no clear explanation for the adverse effect. There was no evidence that the implanting veterinarian had made mistakes, or that the animal or pack had observable characteristics which made it high-risk. The animal did appear to be "hypersensitive", later biting at the site where a drip line had been inserted (and then removed) during emergency care, and at a small natural wound on its leg. The pack was not denning, so there was no possibility of the sutures being chewed by small pups. Recognising that previous experience of logger safety did not involve canids, we reviewed the outcomes of other types of abdominal surgery in wild canids, and found no evidence to suggest that they were especially sensitive to surgical procedures or prone to adverse effects (Table S3).

Our review identified no warning signs which might have flagged this particular animal as high-risk before surgery. However, it did note delays to both the detection of the adverse effect, and the affected animal then receiving veterinary care. These delays occurred because the pack had not been visible until two days post-surgery, by which time the veterinarian had left the site, and needed to return to provide treatment.

Our team identified several ***refinements*** which might potentially reduce the risk of adverse effects from any future implant surgeries (Table 2). Few improvements to surgical procedures could be identified, and these refinements applied primarily to pre- and post-surgery checks (Table 2). A key refinement was for veterinarians to be more closely involved with post-surgery monitoring, especially immediately after surgery, to minimise any delay to the provision of veterinary care in the event of adverse effects (Table 2).

In partnership with ethics committees, the team evaluated four potential ways forward, ranging from halting all surgeries (a form of the "***refuse***" proposed by Curzer et al, 2013), to proceeding with the original sample size but with refined procedures ("***refine*** only"; Table 3). The consensus was that the conservation value of the research justified continuing. However, while proposed ***refinements*** might reduce the risks of implant surgery, the unpredictability of adverse effects also justified ***reduction*** in the number of animals implanted. The ethics committees therefore agreed an option (Option 4 in Table 3) which combined both refinement and reduction, with further implants prioritising hot and dry sites, which would be most informative for the research questions. As a result of this decision, the proposed sample size was reduced, with no biologgers deployed at Sites 5 or 6 (Table 1).

3.5 Completing the implant surgeries

Implant surgeries recommenced on 29 Sep 2021, when three animals were implanted at Site 4, in the South African Kalahari, using the refinements listed in Table S2). All three animals were seen with the pack on the following day, and again on Day 5, behaving normally and with their implant sites visibly intact. On days 2-4, the pack was ranging in very dense bush, where it could not be seen, but tracking collars indicated normal ranging behaviour. No adverse effects were observed with any of these animals (indeed, they ultimately all survived well over 12 months; Table S2).

Following this success, the ethics committees approved implantation of three more animals at Site 1, to achieve replication across more than one pack at this site, after one of the original six animals died in a fight with other wild dogs, and three others were released elsewhere for management

reasons (Table S3). No ill effects were observed (Table S2), and these three implants completed the revised sample size for biologgers deployment (Table 1).

3.6 Commencing explant surgeries

The first explant surgeries were conducted at Site 1 on 23 Mar 2022, exactly a year after loggers were first implanted (Table S2). As part of routine metapopulation management in South Africa, the two instrumented animals had been removed from the wild on 14 Dec 2021 and were being held in a boma, where they were being introduced to new females. Explant surgery, which followed the same protocol as that used for implant, except that loggers were removed rather than added, revealed that both loggers had migrated from their retroperitoneal implant site into the abdominal cavity. Although this migration required explant surgery to be more invasive than intended, the loggers were located easily, and the surgeries were completed successfully. Both animals were observed daily by local monitoring teams, feeding and moving around the boma, until four days post-explant.

3.7 A death following explant surgery

Six days post-surgery, one of the explanted animals ("Two Tears") was found dead in the boma (Table S2; Annex S1). He was estimated to have died late on Day 4 or early on Day 5, but necropsy (by the park veterinarian; Annex S1) concluded that decomposition, advanced by hot weather and a refrigeration failure, had made it impossible to identify the cause of death (Annex S1). The surgical site was intact, and the other explanted animal showed no signs of ill health (indeed, he survived another 4.5 months, until he succumbed to a natural hunting injury; Table S2).

3.8 Responses to the death following logger explant

Although there was no confirmed link between explant surgery and the death of Two Tears, the team took a precautionary approach and, as for implant surgery, responded by (i) immediately pausing explant surgeries; (ii) seeking to understand why Two Tears had died; (iii) reviewing procedures for explant and post-surgery monitoring, to explore whether further ***refinements*** might avoid potential adverse effects; and (iv) formally considering (with overseeing ethics committees) alternative ways forward, combining potential ***refinements*** and ***reductions*** (Tables 2 & 4).

Although cause of death could not be confirmed for Two Tears (Annex S1), two lines of evidence suggested that he had been in (undetected) poor health prior to surgery. First, there was evidence of stress and fighting within the pack. The males had recently been introduced to new females, a period sometimes linked to aggression within and between the sexes in this species (Marneweck et al, 2019; McCreery and Robbins, 2001). Two of the females had severe injuries from fighting,

and Two Tears had a minor injury on one of his legs. Second, data from Two Tears' temperature logger showed that (unlike his surviving pack-mate) he had experienced a fever two weeks before the explant (Figure S1). At the time, metapopulation managers were reviewing protocols for maintaining wild dogs' welfare inside bomas (which, unlike zoo enclosures, are designed to maintain animals' natural fear of people, making it more difficult, for example, to remove faeces and uneaten food, with potential hygiene and health consequences).

There was no direct evidence that explant surgery on Two Tears inadvertently caused infection. However, this possibility could not be ruled out. The location suggested by park staff for the mobile surgical station was, unexpectedly, frequented by monkeys habituated to human presence, and their activities in the trees above the surgical station led to instruments being potentially contaminated by falling leaves, despite efforts to prevent this.

In addition, post-surgery monitoring had been less intense than expected. The boma contained dense vegetation, and management protocols involved monitoring from a vehicle outside the fence. These protocols were designed to minimise stress to wild animals held in temporary captivity; however, they also constrained visibility and, hence, post-surgery health checks. The wild dogs' confinement in a boma therefore did not facilitate monitoring as expected, delaying detection of Two Tears' ill health and subsequent death.

Without a confirmed cause of death (Annex S1), it was impossible to determine whether surgery contributed at all to Two Tears' death (for example, he could have been killed through ongoing fighting), and hence to identify a specific action which could have prevented it. As a precaution, the team identified an additional series of refinements (Table 2), designed to reduce the risk of further surgeries. These refinements included avoiding surgery on animals in bomas, additional health checks before and after explant surgery, and adding a gazebo to the mobile surgical station, to minimise potential contamination from leaves and dust (Table 2; Figure 1).

In partnership with ethics committees, the team evaluated five potential ways forward, ranging from halting all explant surgeries, to conducting all planned explants with refined procedures (Table 4). This decision was more complex than the corresponding decision for implant surgery because, in addition to the potential risks of conducting further explant surgery, not conducting such surgery, i.e., leaving loggers inside animals indefinitely, also carried potential risks. The two recently-explanted loggers had both migrated into the abdominal cavity and, in other wild carnivores, prolonged deployment of abdominal radiotelemetry transmitters had occasionally been linked to complications, including battery leakage (brown bear Ursus arctos, Arnemo et al, 2018) and omental torsion (American badger Taxidea taxus, Quinn et al, 2010). Relative to

implanted radiotelemetry transmitters (Arnemo et al, 2018; Quinn et al, 2010), our thermal data loggers were much smaller (3g and 1.3cm3 vs 85-240g and 83-180cm3), with a different battery type (silver oxide vs lithium) and enclosed in durable material (epoxy potting covered with ceramic, vs plastic shell cylinder sealed with glue), reducing the risk of harm from prolonged deployment. Nevertheless, as this possibility was non-zero, none of the available options could completely avoid risks to animal welfare (Table 4).

Together with the ethics committees, we chose an option (Option 5 in Table 4) which entailed conducting explants (using refined protocols) gradually, in a staggered manner and with repeated focal observations (supported by tracking collars) to assess health before and after surgery (data sheet at Annex S2). This approach sought to facilitate rapid veterinary intervention, and a halt to further explants, if adverse effects were detected. However, it also expanded the project's duration and budget beyond the limits of its grant funding.

3.9 Recommencing explant surgeries

Explant surgeries recommenced on 13 Sep 2022, when a single animal was explanted at Site 4 and fitted with a mortality-sensing satellite-linked GPS collar (350g; Vertex Lite, Vectronic Aerospace GmbH, Berlin, Germany) programmed to record locations hourly and report every four hours. Intensive monitoring by visual observation (Annex S2) and high-resolution GPS tracking indicated a rapid and successful recovery (Figure 1F). These encouraging results justified additional explants, which were conducted 13 and 15 days later using the same protocols (Table S2). Eight further explant surgeries were conducted in Nov-Dec 2022 (Table S2). In all cases, the retriperitoneal loggers had migrated through the peritoneum into the abdominal cavity. In one case, the logger could not be readily located, and the veterinary team performing the surgery took a decision not to proceed further; this logger was later retrieved after the animal died (Table S2). In addition to Two Tears, two animals died within a month of explant surgery, one killed by poachers (after 17 days) and the other (after 26 days) from causes which were unknown because a collar malfunction delayed detection of the death (although intraspecific fighting had been observed shortly before the death; Table S2).

Six loggers were ultimately not explanted, after animals were moved for management reasons and were either lost to monitoring, or were moved outside the sites where permits were in place for explant surgery (Table S2).

4. Mortality rates

The survival of implanted animals was monitored (with mortality-sensing tracking collars, and visual observations) for a combined total of 15,103 days during and after the thermal physiology

study, during which 10 deaths were recorded due to all causes (Table S2). These data indicate an annual post-implant mortality rate of 21.5% (95% confidence interval (CI) 12.3-35.9%). The equivalent post-explant mortality rate was 34.0% (95% CI 17.3-59.6%; note wide confidence interval due to small sample size). For comparison, background mortality, in the absence of any surgery, was 25% (95% CI 12-36%) at Site 2 and 28% (95% CI 20-35%) at site 6 (Rabaiotti et al, 2021).

5. Discussion

Our study illustrates the challenges of conducting invasive research on endangered wildlife, and the consequent need to adapt to changing circumstances. Despite careful consideration of available evidence prior to commencing, including initial review and approval by four different institutional ethics committees, we twice re-evaluated our study design and refined our research methods in the light of emerging evidence (Table 2).

The challenge of monitoring wild dogs was central to the difficulties we faced. Because wild dogs range widely, and often rest in dense vegetation, visual monitoring was difficult, and could not always be conducted to a predetermined schedule. Our post-explant monitoring (Annex S2) detected no observable evidence of harm on days when it was possible to see our study animals. However, the fact that visual observation was often impossible means that nonlethal impacts could have been undetected. Indeed, this constraint hindered detection of the one post-implant injury, delaying veterinary treatment which might have been more successful had it been possible to implement it more quickly. For similar reasons, when one of the first explanted animals died, we could not confirm the cause of death and therefore could not be confident of which specific actions might prevent further deaths (indeed, we could not confirm that the death was related to explant surgery at all). Nevertheless, collar-based monitoring suggested that post-implant mortality of animals in the study was similar to baseline levels (although our decision to perform fewer surgeries constrained sample sizes and thus reduced our statistical power to detect mortality differences, especially post explant). More reassuringly, when an animal at Site 2 died 17 days post-explant, field monitoring showed that her death (which might otherwise have raised concerns about her recovery from surgery) was caused by poachers (Table S2).

An additional challenge to working with endangered wildlife was that some of our study animals were also under conservation management. Within South Africa's wild dog metapopulation, the movement of wild dogs in and out of captivity, and between sites, is an essential part of metapopulation management (Davies-Mostert et al, 2015). This management unexpectedly contributed to our research (e.g., it helped us to explore relationships between body temperature

and hunting, by comparing data from the same animals when free-ranging, and when prevented from hunting within a boma (Linden et al, in prep)). However, it also influenced where, and sometimes whether, surgery could be conducted, for example leading to six loggers not being retrieved (Table S2).

While 22 of 23 animals recovered fully from implant surgery (Table S2), with no ill-effects observed, the factors contributing to the one post-implant death remain uncertain. Neither the review conducted immediately after this event, nor subsequent experience, identified evidence which could have highlighted this animal as high risk before surgery commenced. While our subsequent refinements (Table 2) may have reduced the risks of further deaths, it is unlikely that such risks were eliminated completely. Indeed, while we continue to believe that our precautionary approach was appropriate, it is impossible to be sure whether our refinements helped to reduce suffering or to improve survival.

In our view, the ***refinements*** that we implemented (Table 2) approached the limit of what was possible with field surgery and monitoring of free-ranging African wild dogs. Likewise, the sample size ***reductions*** that we imposed (Table 1), especially when combined with failure of some of the tracking collars designed to collect data on hunting behaviour, approached the limit of what was informative. While the study was sufficient to answer the core research question (Linden et al, in prep), subsidiary questions (concerning variation between individuals and sites) could not be addressed. However, the data that we obtained may now be used to evaluate opportunities for future studies to ***replace*** wild dogs with domestic dogs, which can be studied less invasively using rectal thermometers (McNicholl et al, 2016; Phillips et al, 1981), or ingestible loggers (Friend et al, 2020), and may be an appropriate surrogate.

Our experience with this case leads us to three recommendations. First, we recommend that projects budget sufficient time and resources (including human resources) for intensive monitoring after both implant and explant surgery. Few veterinarians have the experience needed to dart, treat, and perform surgery on wildlife, placing their time at a premium and encouraging projects to minimise the investment of veterinary time that they request. Our decision to ask implanting veterinarians to become involved in post-surgery monitoring increased the cost, in terms of time and funding, of refined monitoring. Nevertheless, had such monitoring been in place earlier in the project, it could have accelerated the provision of veterinary care to the animal which was injured post-implant, and might have prevented that animal's death. Likewise, because we had expected explant surgery to be less invasive than implant, we had originally planned to remove tracking collars and cease monitoring at the time of explant, with the intention of minimising the

time that animals spent wearing collars (Table 2). Removal of collars at the end of a study is widely considered best practice due to the possibility of them causing harm (e.g., Soulsbury et al, 2020). However, tracking collars were ultimately essential to the refinements of post-surgery monitoring (Table 2). Importantly, although in principle it might be expected that bringing animals into temporary captivity might be a way to facilitate post-surgery monitoring (an approach adopted e.g., in several coyote *Canis latrans* studies; Table S3), in practice we found that temporary captivity did not adequately improve monitoring success, and also imposed additional welfare costs for this socially complex species.

Second, we recommend that researchers using an invasive procedure for the first time in an endangered species should adopt a staggered approach, starting with one animal (or very few animals), monitored intensively. It is important that such piloting should include the whole procedure (e.g., including explant as well as implant surgery); we note that studies comparing the impacts of implanted versus externally-attached devices have focused (as we did initially) on potential harms of deploying devices, rather than retrieving them (e.g., Barron et al, 2010; White et al, 2013). Sample size can then build up gradually as evidence of safety accumulates. Stopping rules, defining the circumstances under which procedures will halt, should be decided in advance. This approach closely resembles guidance on First-in-Human trials of pharmaceuticals (European Medicines Agency, 2017). Adopting this approach is likely to increase the time and resources which projects must budget for such research. Although we have highlighted this approach for endangered species, the same principle applies to any species which is potentially predisposed to adverse effects, for example through morphology (e.g., thin peritoneum) or behaviours (e.g., hunting large prey, intraspecific fighting).

Finally, we advise that any future plan to implant either retroperitoneal or abdominal biologgers in African wild dogs would need to be carefully considered and strongly justified. Although the overall post-implant mortality of our study animals was similar to the baseline, and post-explant deaths may have been unrelated to recent surgery, at least one animal died as a direct result of surgery. Moreover, all retroperitoneal loggers migrated into the abdominal cavity, making explant surgery more invasive than originally intended. Although risk-benefit analysis supported our original planned project, and we continue to expect our study to inform wild dog conservation (Linden et al, in prep), it is our view that the risks of collecting further body temperature data from African wild dogs currently outweigh the benefits. This conclusion might be altered in future if (i) further refinements are identified in surgical methods and/or post-surgical monitoring; or (ii) key conservation questions cannot be addressed (by our team or by collaborators) with the data collected to date.



Figure 1. Implant and explant of thermal data loggers in free-ranging African wild dogs. Wild dogs were immobilised by darting, and then maintained on inhalation anaesthesia (A), in a mobile surgical station (B), to which a gazebo with mesh walls was later added to reduce risks of contamination (C; Table 2). The incision was kept as small as possible (D). Panel E shows the first implanted wild dog immediately post-surgery. Panel F shows two wild dogs feeding from a carcass, respectively 22 and 35 days after explant surgery; note the satellite-linked GPS collars used to monitor health and survival post-surgery.

Table 1 Planned and realised deployment of thermal data loggers at six study sites. The fates of individual animals are documented in Table S2. RSA= Republic of South Africa. T_{max}= mean daily maximum ambient temperature (°C) in the listed month; Rain=mean annual rainfall in mm.

	T_{max} (°C)		Rain	Numbers of thermal data loggers			
Site	*Dec*	*Jun*	*mm*	*planned*	*implanted*	*explanted*	*retrieved*
1: KwaZulu-Natal, RSA	29.6	24.2	848	8	9	2	3
2: Zimbabwe	31.3	24.5	712	8	8	5	6
3: Northern Cape, RSA	35.7	20.7	225	3	3	2	2
4: North West, RSA	35.0	23.7	311	5	3	3	3
5: Limpopo, RSA	32.5	24.4	316	3	0	NA	NA
6: Kenya	27.5	27.5	635	8	0	NA	NA
			Total:	35	23	12	14

Table 2 Key ***refinements*** to procedures for biologger implant and explant surgery, which were either in place at the start of the study, or added in response to confirmed or potential adverse effects involving implanted and explanted animals.

	Refinements in place at project start	**Refinements added to implant protocol**	**Refinements added to explant protocol**
Pre-surgery checks	Animals with signs of ill health are not candidates for surgery	Formally record visual health check of immobilised animal, before proceeding with surgery Encourage team mindset to avoid any explicit or implicit pressure on veterinarians to proceed with surgery on possibly unhealthy animals	No surgery on animals held in bomas Focal observations (Annex S2) for visual health check of target animal before darting Small blood sample for health screening using EPOC Blood analyser before surgery Surgeries staggered to build evidence of safety
Surgery	Performed only by veterinarians with extensive experience of field surgery on wildlife Mobile surgical station set up on the back of a vehicle to avoid transporting animals Retroperitoneal logger placement avoids need to enter abdominal cavity Smallest available logger Smallest incision needed to admit the logger Long-acting antibiotic and non-steroidal anti-inflammatory	Performed only by veterinarians trained in person to do these implants	Surgery conducted under a covered mesh gazebo to minimise contamination (without restricting light and airflow) while maintaining ability to rapidly set up surgical station in the field, and avoiding need to transport animals from remote field locations to indoor surgical stations
Wound treatment	Antibacterial spray and antiparasitic ointment*	Also apply bitter wound spray** to discourage licking of the surgical wound	
Post-surgery monitoring	All implanted animals fitted with tracking collars, which facilitate visual monitoring Daily visual checks attempted for the first seven days post-surgery, or until there is clear evidence that the wound has healed Tracking collars removed at explant	First visual check should be conducted by the veterinary team, to facilitate immediate intervention in the case of adverse effects	Explanted animals fitted with tracking collars to facilitate post-surgery monitoring Focal observations (Annex S2), conducted by veterinarian, morning and evening for first three days post surgery, and daily for the first week

* "Tick grease", Kyron Laboratories, South Africa; **"Avert", Kyron Laboratories, South Africa

Option	**Advantages**	**Disadvantages**
*1 **Refuse**: a permanent halt to all surgery*	No further risk from implant or explant surgery	No body temperature data obtained, making 16 completed implant surgeries pointless Small risk of harm from prolonged logger use
*2 **Reduce**: proceed with explant surgery only (i.e. retrieve existing implants but fit no more)*	Yields some temperature data May be low risk if tendency to adverse effects is individual-specific, as explant surgery would exclusively target animals which have undergone successful implant surgery Avoids risk of harm from prolonged logger use	Adverse effects of explant surgery cannot be ruled out Lower sample size, especially from hot and dry environments, limits statistical power
*3 **Refine only**: Proceed with the planned sample size, using refinements from Table 2*	Maximises benefits by allowing the full range of (conservation-relevant) questions to be addressed, following the original calculations of statistical power	Potential remains for additional implant surgeries to cause further adverse effects
*4 **Refine** and **reduce**: Proceed with explants and a very small number of further implants at key sites using refinements from Table 2*	Allows key (conservation-relevant) questions to be addressed while reducing the risks of further harm through reduced sample size and refined procedures. Greatly reduces the risk of further harm by reducing the number of additional implant (and explant) surgeries	Further adverse effects cannot be ruled out Statistical power would be reduced, limiting the scope of the analyses which can be performed

Table 3 Potential ways forward considered in response to an incident of adverse effects of biologger ***implant***

Option	Advantages	Disadvantages
1 ***Refuse****: No further explant surgery*	No further risk from surgery	No body temperature data, making all previous surgeries pointless Small risk of harm from prolonged logger use in animals not explanted
2 Modified ***reduce****: Re-collar all implanted wild dogs with mortality-sensing satellite collars, and retrieve loggers when they die naturally*	No further risk from surgery May salvage some body temperature data, albeit over several years and with a risk of not retrieving carcasses	Small risk of harm from prolonged logger use in animals not explanted Loggers may be lost or consumed by scavengers before they can be recovered, reducing sample size Repeated collar changes may be needed, with associated costs, including risks from repeated immobilisation
3 ***Refine only***: Continue with logger explants using refined methodology	Maximises scientific outcomes from project Minimises risk of harm from prolonged logger use	Surgery may be more invasive surgery than originally envisaged if loggers have migrated from the retroperitoneal location, hence risks of post-operative complications may be increased
4 ***Reduce*** and ***Refine*** 1: Using refined methodology, explant only loggers palpable from the outside, indicating that they have not migrated inside the abdomen	Reduces severe infection risks by avoiding opening the abdominal cavity May reduce number of animals at risk of harm from prolonged logger use in animals not explanted May provide some body temperature data	Thin wild dog peritoneum means that there may be no animals not requiring abdominal surgery Demands that a trained veterinarian is present, prepared, and licensed for surgery, when no surgery may take place May substantially reduce the data generated by the project Small risk of harm from prolonged logger use in animals not explanted
5 ***Reduce*** and ***Refine*** 2 Explant loggers from free-ranging animals, in a staggered pattern, with intense post-surgery monitoring, avoiding or delaying surgery on animals in bomas	Maximises priority data from free-ranging animals Avoids surgery on animals potentially most stressed and least able to tolerate explant Reduces risk of harm from prolonged logger use	Increases costs and time needed to complete explants, beyond available funding Link between bomas and adverse outcomes of surgery is uncertain, so avoiding bomas may not reduce risks Pre- and post-surgery monitoring may be more difficult for free-ranging animals Small risk of harm from prolonged logger use in animals not explanted

Table 4 Potential ways forward considered in response to a death following (but not confirmed to be caused by) biologger ***explant***

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Appendix E Supporting Information

Table S1 – Published accounts of free-living mammals implanted with thermal data loggers by our research team

Species	Numbers of animals		Reference
	surgeries	*complications*	
Lion (*Panthera leo*)	18	0	[1]
Cheetah (*Acinonyx jubatus*)	5	0	[2]
Vervet (*Chlorocebus pygerythrus*)	19	0	[3]
Aardvark (*Orycteropus afer*)	12	0	[4]
Cape ground squirrel (*Xerus inauris*)	8	0	[5]
Wildebeest (*Connochaetes taurinus*)	26	0	[6-8]
Black wildebeest (*Connochaetes gnu*)	8	0	[6]
Impala (*Aepyceros melampus*)	49	0	[7, 9, 10]
Springbok (*Antidorcas marsupialis*)	25	0	[11, 12]
Sand gazelle (*Gazella subgutturosa*)	6	0	[13]
Blesbok (*Damaliscus pygargus*)	12	0	[14]
Eland (*Taurotragus oryx*)	12	0	[7, 15]
Kudu (*Tragelaphus strepsiceros*)	7	0	[16]
Gemsbok (*Oryx gazella*)	12	0	[8, 17]
Arabian oryx (*Oryx leucoryx*)	5	0	[13]
Grey kangaroo (*Macropus fuliginosus*)	9	0	[18]
Total	233	0	

Table S2 Histories of individual African wild dogs implanted with thermal data loggers. For comparison, the mean survival time of 80 wild dogs from collaring (but not implanting) to death at site 6 was 624 days (range 3-2,647 days).

ID	Site	Pack	Date implanted	Days survived post-implant	Date explanted	Days survived post-explant	Logger retrieved	Notes
Baboon Hand	1	Mbhulungu	23 Mar 2021	501	23 Mar 2022	136	23 Mar 2022	Killed by impala horn 6 Aug 2022
Two Tears	1	Mbhulungu	23 Mar 2021	369	23 Mar 2022	4	23 Mar 2022	Died 27 Mar 2022, cause of death uncertain
Hlokohloko	1	Mbhulungu	23 Mar 2021	98	NA	NA	29 Jun 2021	Died in a fight; logger retrieved at necropsy
DD9	1	In boma	26 Mar 2021	≥462	NA	NA	NA	Relocated to Site 5, last seen Jul 2022
DD10	1	In boma	26 Mar 2021	≥462	NA	NA	NA	Relocated to Site 5, last seen Jul 2022
DD11	1	In boma	26 Mar 2021	≥462	NA	NA	NA	Relocated to Site 5, last seen Jul 2022
Johnnie	2	Nova	14 May 2021	578	26 Nov 2022	17	26 Nov 2022	Killed by poachers 13 Dec 2022
Zulu	2	Nova	14 May 2021	>1,367	26 Nov 2022	>806	26 Nov 2022	Still alive 09 Feb 25
Canine	2	Chapungu	15 May 2021	>1,366	30 Nov 2022	>802	30 Nov 2022	Still alive 09 Feb 25
Nora	2	Festive	17 May 2021	467	NA	NA	Not retrieved	Died from snare 27 Aug 2022 before explant
Beebee	2	Chapungu	17 May 2021	1,041	30 Nov 2022	479	30 Nov 2022	Died 23 Mar 2024
Limpy	3	Korannaberg	14 Jun 2021	>1,550	15 Dec 2022	>1,001	15 Dec 2022	Still alive 11 Sep 2025
Bowling Pin	3	Korannaberg	15 Jun 2021	>1,549	15 Dec 2022	>1,000	15 Dec 2022	Still alive 11 Sep 2025
Dark Hound	3	Korannaberg	15 Jun 2021	~320	NA	NA	NA	Disappeared May 2022, presumed dead
Infinity	2	Gentlemen	16 Jun 2021	554	23 Nov 2022	26	19 Dec 2022	Logger not located at explant surgery, subsequently died 19 Dec 2022. Due to collar malfunction mortality alert only received 21 Dec and carcass located 22 Dec 2022, too decomposed to determine cause of death, although intra-pack fighting had been observed
Lycaon	2	Gentlemen	16 Jun 2021	3	NA	NA	NA	Died from presumed self-injury following implant surgery
Pug	2	Chapungu	17 Jun 2021	888	20 Nov 2022	367	20 Nov 2022	Died 22 Nov 2023
K21	4	North	29 Sep 2021	>657	26 Sep 2022	>295	26 Sep 2022	Tracking collar expired 18 Jul 2023
K23	4	North	29 Sep 2021	>559	13 Sep 2022	>210	13 Sep 2022	Tracking collar expired 11 Apr 2023
M28	4	North	29 Sep 2021	>494	28 Sep 2022	>130	28 Sep 2022	Tracking collar expired 05 Feb 2023
Duma	1	Siyavikela	24 Mar 2022	>453	NA	NA	NA	Relocated 20 Jun 2023
Kumela	1	Siyavikela	24 Mar 2022	>453	NA	NA	NA	Relocated 20 Jun 2023
Zobuhle	1	Siyavikela	24 Mar 2022	>189	NA	NA	NA	Relocated 29 Sep 2022

Table S3 – Reported outcomes of surgery in free-ranging canids. There was no evidence that wild canids were especially prone to adverse reactions.

		Number of animals		Source
Species	**Surgery type**	*surgeries*	*complications*	
Eastern wolf (*Canis lycaon*)	Transmitter implant	53	0	[19]
Red wolf (*Canis rufus*)	Transmitter implant	4	0	[20]
Coyote (*Canis latrans*)	Tubal ligation (& sham surgery)	13*	0	[21]
Coyote (*Canis latrans*)	Vasectomy (& sham surgery)	17*	0	[21]
Coyote (*Canis latrans*)	Tubal ligation (& sham surgery)	15*	0	[22]
Coyote (*Canis latrans*)	Vasectomy (& sham surgery)	30*	0	[22]
Coyote (*Canis latrans*)	Tubal ligation (& some spay)	66*	0	[23]
Coyote (*Canis latrans*)	Vasectomy (& some castration)	59*	0	[23]
Coyote/red wolf hybrid	Tubal ligation (& some spays)	26*	0	[23]
Coyote/red wolf hybrid	Vasectomy (& some castration)	31*	0	[23]
Coyote or hybrid	Sterilisation (not specified)	36*	0	[23]
Grey wolf (*Canis lupus*)	Tubal ligation	7	1 possibly	[24]
Grey wolf (*Canis lupus*)	Vasectomy	6	0	[24]
		363	1 possibly	

*kept overnight for observation

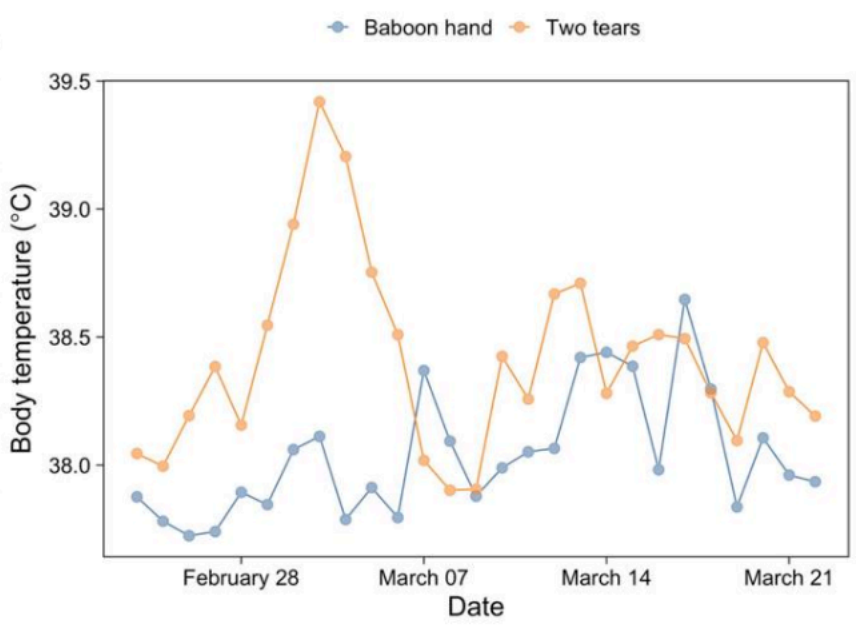


Figure S1 Mean daily body temperature recorded by thermal data loggers implanted in two African wild dogs in the same pack at Site 1, in the four weeks before the loggers were explanted. Two Tears (orange line) experienced a fever from 1-6 March while Baboon Hand (blue line) did not. The fever pattern was confirmed by inspecting the daily minimum and maximum body temperatures; both were elevated by at least 0.5°C, indicating an elevation in the body temperature set-point as occurs with fever [25]. Such fever is typically an indication of infection (rather than, for example, stress hyperthermia). This evidence suggests that undiagnosed ill health could have contributed to Two Tears' death, either directly or by compromising his ability to recover from surgery.

Annex S1 Necropsy report on "Two Tears", an African wild dog which died following explant surgery, which was conducted on 23 Mar 2022.

EZEMVELO KZN WILDLIFE
Conservation, Partnerships & Ecotourism

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NECROPSY REPORT

I, Dr Marelize Clasen (ID: 960401 0108 082), confirm that I am a veterinarian (SAVC registration: CS22/15967) employed by EKZN Wildlife and have been in this capacity since 1 March 2022.

On the afternoon of 29 March 2022, I was informed that one of the wild dogs in the holding facility, died. It was assumed to have died between Monday morning and Tuesday afternoon. The animals are monitored frequently in the holding facility and after speaking to the monitors, it was confirmed that this animal was seen on Sunday afternoon, and it was eating.

Photos that were taken of the carcass showed bloating of the abdomen and blood tinged fluid coming from the nostrils. The carcass was kept in a fridge-freezer to stop decomposition, since I could only conduct the necropsy the next afternoon (30/03/22).

Arriving at the carcass, it was covered in maggots and had a putrid smell. I assumed that the fridge-freezer it was kept in, did not actually work, or did not work well enough. After removing the bags the dog was kept in, it could be seen that the carcass was severely autolysed – the skin was sloughing, large amount of maggots present and the colour of the skin was a green-black mixture.

It was impossible to discern between ante- and post-mortem lesions. All organs were severely autolysed and no distinction could be made between different organs. Close inspection of the surgical site (surgery done 23/03/22) showed it was still intact, no adhesions to the site and no other abnormalities. No other conclusions could be made with the carcass in such a state.

Yours respectfully

Dr. Marelize Clasen

05/04/2022

Annex S2 Data sheet used for focal observations before and after explant surgery.

African Wild Dog Pre/Post-surgery Monitoring

Focal animal: **Pack:** **Date:** **Observers:**

Site name: **GPS location:** **Overseeing vet:**

Animal type (please circle)
pre-surgery / post-surgery / no surgery (for comparison) **Date of surgery:**

Focal start time: **Focal end time:** **Time shared with vet:**

Evidence of injuries (not including surgical site)

Please tick

	observed with injury		***observed without injury***		***not observed***	
Part of body	*left*	*right*	*left*	*right*	*left*	*right*
Head						
Neck						
Foreleg						
Hindleg						
Side						
Belly						
Rump						
Tail						

Describe any injuries (location, size, degree of healing)

Behaviour

Lying alone / with other lying dogs / with other dogs not lying / not seen lying

Walking alone / with other dogs / trailing behind other dogs / not seen walking
limping / not limping / not observed well enough to be sure

Running alone / with other dogs / trailing behind other dogs / not seen running
limping / not limping / not observed well enough to be sure

Feeding feeding alone / feeding with other dogs / not feeding when other dogs feed / no feeding behaviour observed

Any neurological signs?

Describe any unusual behaviour:

Surgical site (strike through if not relevant)

Surgical site observed? yes / no **Surgical site photographed?** yes / no

Response to surgical site licking self / biting self / others licking / others biting / no observed response

Describe condition of surgical site & animals' response to it (please take photos):

Other Comments

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