

RESEARCH ARTICLE

Climate change is predicted to cause population collapse in a cooperative breeder

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Abstract

It has been suggested that animals may have evolved cooperative breeding strategies in response to extreme climatic conditions. Climate change, however, may push species beyond their ability to cope with extreme climates, and reduce the group sizes in cooperatively breeding species to a point where populations are no longer viable. Predicting the impact of future climates on these species is challenging as modelling the impact of climate change on their population dynamics requires information on both group- and individual-level responses to climatic conditions. Using a single-sex individual-based model incorporating demographic responses to ambient temperature in an endangered species, the African wild dog *Lycaon pictus*, we show that there is a threshold temperature above which populations of the species are predicted to collapse. For simulated populations with carrying capacities equivalent to the median size of real-world populations (nine packs), extinction risk increases once temperatures exceed those predicted in the best-case climate warming scenario (Representative Concentration Pathway [RCP] 2.6). The threshold is higher (between RCP 4.5 and RCP 6.0) for larger simulated populations (30 packs), but 84% of real-world populations number <30 packs. Simulated populations collapsed because, at high ambient temperatures, juvenile survival was so low that packs were no longer recruiting enough individuals to persist, leading them to die out. This work highlights the importance of social dynamics in determining impacts of climatic variables on social species, and the critical role that recruitment can play in driving population-level impacts of climate change. Population models parameterised on long-term data are essential for predicting future population viability under climate change.

KEYWORDS

climate change, demography, individual-based model, *Lycaon pictus*, mammal, populations, social species, temperature

1 | INTRODUCTION

Despite the identification of climate change as a causal factor in a number of contemporary extinctions of both populations (Cahill

et al., 2012) and species (Waller et al., 2017), predicting the extinction risk of species under future climate regimes still proves challenging. Ultimately, climate driven extinction is a consequence of weather-related impacts on demographic rates, whether they be decreased

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survival or reproductive success, which are severe enough that the population declines to extinction. This can occur through either direct impacts of weather on species or indirectly through changes in habitat or food. The fact that extinction is ultimately driven by changes in demographic rates means that detailed population models, incorporating climate change impacts on all elements of species' populations, are helpful to predict species' likelihood of persistence under climate change. While earlier studies of the demographic impacts of high temperature tended to focus on ectothermic species in which the impacts of temperature on demography operate through a direct physiological mechanism (e.g., Hulin et al., 2009; Mitchell et al., 2010), there is growing evidence of demographic impacts of climate change on endotherms (Paniw et al., 2021). Climate change poses a particularly acute risk to large-bodied mammal species because their ability to shift their range is severely limited by habitat fragmentation, and their generation times are too long for genetic changes to keep pace with climate change (Hetem et al., 2014).

Predicting the impact of environmental change on social species is particularly challenging, because they require complex models to capture demographic feedbacks within and between social groups (Marescot et al., 2012). Reproductive success, survival, and dispersal probability are commonly impacted by group characteristics like group size and composition (Clutton-Brock & Sheldon, 2010; Marescot et al., 2012). These demographic variables also vary between group members depending on dominance status (Armitage, 1987; Rood, 1990), sex (Ewen et al., 2001; Kingma et al., 2017; Lawson Handley & Perrin, 2007) or age (Marjamäki et al., 2013; Woodroffe, O'Neill, & Rabaiotti, 2020). In some cooperatively breeding species, dominant individuals monopolise breeding completely, with subdominant individuals helping to raise the dominant individuals' offspring (Gaston, 2015). This behaviour means that the loss of a specific group member may have a different impact on group dynamics, and therefore rates of reproduction, depending on whether the individual is dominant or subdominant.

Long-term individual-based studies are essential to inform population models of social species, as they are the only way to obtain empirical data on the structure and dynamics of social groups (Clutton-Brock & Sheldon, 2010; Grimm et al., 2003). As there are few such long-term studies, models of environmental impacts on social species have been limited to a relatively small number of taxa, including meerkats (*Suricata suricatta*) (Bateman et al., 2012, 2013) and the Southern pied babbler (*Turdoides bicolor*) (Bourne et al., 2020; Ridley et al., 2021), for which long-term individual-level demographic data exist.

It has been suggested that cooperative breeding is a reproductive strategy that increases population viability under variable and extreme climatic conditions (Lukas & Clutton-Brock, 2016; Rubenstein & Lovette, 2007; Smaldino et al., 2015). Social species, in particular cooperative breeders, exhibit high levels of behavioural plasticity and social learning, which may facilitate survival in extreme climates (Komdeur & Ma, 2021). In addition to this, a loss of energy reserves for nonbreeding subdominant individuals has a lower impact on population recruitment than loss of energy reserves for a dominant

individual, and therefore the contribution to the persistence of the population by subdominants is limited (Komdeur & Ma, 2021). Thus, populations of cooperatively breeding species may be able to buffer climate induced food shortages by supporting dominant individuals with a higher reproductive output. Other studies, however, have failed to find evidence that sociality buffers the impact of adverse climatic conditions (Bourne et al., 2020; Guindre-Parker & Rubenstein, 2020), thus it would appear that this social buffering against climate variability is not universal across species.

Despite having lower reproductive outputs, or, in some cases, forgoing reproduction altogether, subdominant individuals play a key role in group-level reproductive output. Reproductive success is positively correlated with group sizes across a variety of species, including meerkats (Bateman et al., 2011, 2012), Arabian babblers (*Turdoides squamiceps*) (Keynan & Ridley, 2016) and African wild dogs (*Lycaon pictus*) (Woodroffe et al., 2017). Similarly, individuals in larger groups of many cooperatively breeding species have been found to have higher survival rates (Brown & Brown, 2004; Clutton-Brock et al., 2001; Rabaiotti et al., 2021; Robinette et al., 1995). This has led to the prediction that smaller groups of cooperatively breeding species are less likely to persist, and therefore populations consisting of smaller groups will have lower growth rates and higher extinction risk (Angulo et al., 2013; Courchamp et al., 2000). If this prediction were upheld, environmental changes resulting in higher mortality, lower reproduction or increased dispersal might lead social group sizes to decrease to a point where there are not enough subdominant individuals to assist in activities on which group persistence is dependent, such as defence against predators, foraging, or raising offspring. Alternatively, smaller group sizes may reduce numbers of dispersing individuals to a point where there are not enough dispersers to replace groups that die out. These processes would eventually, once conditions became extreme enough, lead to population collapse.

The demographic responses of cooperatively breeding species to climatic conditions have been found to be variable, and dependent on both group composition and size (Bateman et al., 2013; Koenig et al., 2011; Paniw et al., 2019). Assessing the impact of climatic variables on both group- and individual-level processes is therefore key to predicting the impact of climate change on populations of social species. Larger bodied species are less able to select favourable microclimates by burrowing, building nests, or using damp soil or shade, simply due to their larger body size. As a result, understanding the impact of climatic conditions on shorter term population trends is essential in providing insight into how these species will respond to rising temperatures in the future. Despite the unparalleled understanding into social species' climate change resilience such studies would provide, no research to date has integrated the impact of climatic conditions on multiple aspects of social species' population dynamics into projections of population viability under climate change.

One social species that experiences multiple demographic impacts of high ambient temperature is the African wild dog, a cooperatively breeding canid historically found throughout most of

sub-Saharan Africa. The species has a coat pattern that is unique to each individual, meaning that long-term studies across multiple sites have been able to monitor individuals throughout their lifetime (Creel & Creel, 2002; Woodroffe et al., 2017). Using such data, researchers have been able to estimate rates of recruitment (Abrahms et al., 2022; Woodroffe et al., 2017), survival (Rabaiotti et al., 2021; Woodroffe, 2011a; Woodroffe et al., 2007) and dispersal (Behr et al., 2020; Woodroffe, O'Neill, & Rabaiotti, 2020; Woodroffe, Rabaiotti, et al., 2020). Studies have shown that African wild dog vital rates are impacted by high ambient temperatures across a number of populations, with lower adult survival (Rabaiotti et al., 2021) and recruitment (Abrahms et al., 2022; Woodroffe et al., 2017) at higher temperatures. The time between one litter and the next (the inter-birth interval) is also longer at higher ambient temperatures at a site with aseasonal breeding (Woodroffe et al., 2017).

Here we use a novel individual-based population model of African wild dogs, parameterised using long-term field data, to investigate how the effects of ambient temperature on both recruitment rate and adult survival may impact population dynamics and persistence under future climate change scenarios.

2 | MATERIALS AND METHODS

2.1 | African wild dog life history

The African wild dog is an obligate cooperative breeder. Packs consist of a dominant breeding pair, known as alphas, and between two and 28 subdominant individuals that assist in raising their offspring (Creel & Creel, 2002; Malcolm & Marten, 1982). Across most of their geographic range, African wild dogs breed seasonally at the coolest time of the year, but they breed aseasonally near the equator (McNutt et al., 2019). African wild dogs typically raise litters of between 2 and 18 pups (Creel & Creel, 2002). Single-sex dispersal groups leave established packs and search for unrelated mates and new territories (McNutt, 1996). Those that successfully find another dispersal group will then go on to form a new pack (Behr et al., 2020; Woodroffe, O'Neill, & Rabaiotti, 2020; Woodroffe, Rabaiotti, et al., 2020). Reproduction, mortality risk and dispersal dynamics are all linked to pack composition (Rabaiotti et al., 2021; Woodroffe et al., 2017; Woodroffe, Rabaiotti, et al., 2020).

The life history parameters used in the study were obtained from long-term demographic data collected by the Samburu-Laikipia Wild Dog Project, in a study area which covers Laikipia County, Kenya and parts of the neighbouring counties of Samburu, Isiolo, and Baringo. African wild dogs were monitored between the years 2001 and 2017 using GPS collars, radio collars, and visual observation (Woodroffe, 2011b). The number of adults (individuals aged ≥ 12 months) and juveniles (individuals aged < 12 months) in each pack, litter sizes, births, deaths, and dispersal events were recorded by researchers throughout the course of the project. Dry bulb daily maximum air temperature data from a weather station at Mpala Research Centre (37°2' E, 0°6' N), within the study area (Caylor et al.,

2017) were used to investigate how temperature correlated with recruitment, survival, and dispersal.

Litter size, inter-birth interval, juvenile survival, adult survival, and dispersal parameters were obtained through re-analysing data from published papers using a monthly timestep (Rabaiotti et al., 2021; Woodroffe et al., 2017; Woodroffe, Rabaiotti, et al., 2020). Full details of these datasets and the models used to estimate the demographic parameters can be found in Appendix S1.

2.2 | Individual-based model

2.2.1 | State variables and scales

Four hierarchical levels make up the individual-based model: Individual, territory, population, and environment. Individuals are characterised by their dominance status—dominant or subdominant, and their age—adult (*a*) or juvenile (*j*). Within the model, juveniles are defined as individuals between 3 and 12 months. Juvenile classification begins at 3 months as opposed to zero as this is the age at which pups can be reliably counted (Woodroffe, 2011b). Litter size refers to the number of pups leaving the den at 3 months of age. Adult and juvenile wild dogs are modelled using separate age categories due to differences in survival rates and temperature impacts (Rabaiotti et al., 2021; Woodroffe et al., 2017). Due to the social dynamics of the species, in which only the dominant pair breeds and the pack dynamics are strongly influenced by survival of dominant individuals (Woodroffe, O'Neill, & Rabaiotti, 2020), breeding individuals are built into the model as a separate dominance category. The model is female only, therefore the dominant category contains a single individual, and no individuals move into this category unless the existing dominant individual has died.

A territory can be occupied by one pack of wild dogs, which consists of one dominant female along with a number of subdominant adults, and any juveniles born to that pack that have not yet reached 12 months of age. A territory has the following characteristics associated with it: its identity number, the number of adult and juvenile females present, the time since the pack formed, the size of the last litter of the pack occupying the territory, and the time since the birth of the pack's last litter. Because the model is female only, pack size and the size of the last litter equate to the number of females. If there are no individuals in the territory it is classified as 'empty'.

The population is composed of multiple territories and a number of packs. For the purposes of this analysis, two different territory numbers are used: 30 territories, which is the maximum number of packs recorded at our study site, and nine territories, which is the median number of packs per population within the species' remaining range throughout Africa (Woodroffe & Sillero-Zubiri, 2012). Each population is characterised by its size (the number of adult and juvenile individuals), and the number of packs. Outside of this population (and not included in the total population size) there is a dispersal pool which comprises individuals that have dispersed from their packs but have not yet occupied a territory and formed a pack. Because

the model is female only, population size and the dispersal pool are also female only. When the number of packs in the population is 0 the population is classed as extinct.

Abiotic environment is the highest hierarchical level in the model. As African wild dog recruitment and survival are impacted by mean daily maximum temperature, this is how the abiotic environment is characterised. Temperature, in degrees Celsius, is centred on the mean throughout, therefore the average temperature is represented by 0. The temperature variable represents the mean daily maximum temperature during the timestep, in line with the empirical findings of Rabaiotti et al. (2021), Woodroffe, Rabaiotti, et al. (2020), and Woodroffe et al. (2017), which found that mean daily maximum air temperature influenced wild dog demography.

2.2.2 | Process overview and scheduling

The model proceeds in monthly timesteps. Within each timestep six phases occur in the following order: mortality, dispersal, ageing, births, pack fate (consisting of three levels: inheritance of dominance status [the dominant individual dies and is replaced], pack break up [the dominant individual dies and the pack breaks up and becomes dispersers], or pack continuity [the dominant individual survives]), re-colonisation of vacant territories.

2.2.3 | Design concepts

Emergence

Pack- and population-level dynamics emerge from individual behaviour in the model, the timing of breeding, and number of territories available. Individual life histories and behaviours within the model are defined by empirical rules describing ageing, as well as mortality

and dispersal probabilities. Adaptation and fitness seeking are not explicitly modelled. They should be partially captured by the model, however, particularly through the rules describing dispersal, as the higher probability of dispersing at higher pack sizes is thought to be driven by likelihood of reproduction, and therefore individual fitness (Woodroffe, O'Neill, & Rabaiotti, 2020).

Sensing

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

Interactions

The interactions modelled explicitly in the model are: adult survival and juvenile survival decrease at higher temperatures, the inter-birth interval is longer at higher temperatures (Woodroffe et al., 2017), adult survival increases with pack size (Rabaiotti et al., 2021; Woodroffe, O'Neill, & Rabaiotti, 2020), litter size increases with pack size (Woodroffe, Rabaiotti, et al., 2020), dispersal probability increases with pack size (Woodroffe, Rabaiotti, et al., 2020), the inter-birth interval increases with litter size (Woodroffe et al., 2017), and juvenile survival increases with litter size (Woodroffe et al., 2017). Explicit interactions are shown in Figure 1 and Figure S1. Interactions implicitly modelled, that is, emerging from the model through indirect impacts, without being explicitly parameterised, are: litter size and dispersal probability are both lower at higher temperatures. The indirect effects of temperature on both litter size and dispersal probability occur because high temperatures decrease adult and juvenile survival, which lowers pack sizes, leading to lower litter sizes and dispersal rates.

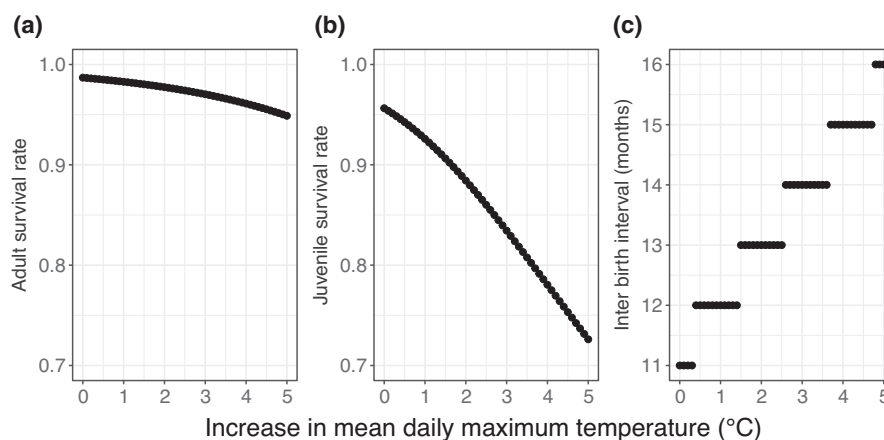


FIGURE 1 Relationships between temperature and submodel outputs. Panel (a) is the output from the submodel for adult survival, for a subdominant individual, at 12 months of age, in a pack size of 4. Panel (b) is the output from the submodel for juvenile survival, at a litter size of three. Panel (c) is the output from the model for inter-birth interval, at a litter size of three. Points denote 0.1°C temperature intervals. Inter-birth interval has a step pattern because the time is rounded to the nearest month so that it falls within a modelled timestep. All submodels had stochastic elements removed for the purposes of this figure, in order to more clearly demonstrate the explicitly modelled relationships with temperature.

Stochasticity

Mean daily maximum temperature for each month-long timestep is drawn from a normal distribution to mimic the stochastic variation in temperature observed in the field (Caylor et al., 2017). All demographic parameters (listed as input parameters in Table 1 and described in Table 2) are drawn from a normal distribution with μ equal to the estimated parameter mean and the standard deviation equal to that estimated during submodel parameterisation (Table 2; Appendix S1). This was done to account for uncertainty in the estimates of these parameters. To determine death, a random number is drawn from a uniform distribution between 1 and 0, and if the number is higher than the probability of survival the individual dies, if it is lower the individual survives. The same occurs for dispersal, but with dispersal probability as opposed to survival probability. When dominant females die, the fate of their surviving pack members is determined by drawing a random number from a uniform

distribution between 0 and 100 and if the number is over 40, dominant status is inherited by a subdominant pack member, and if it is less than or equal to 40, then all subdominant individuals leave the territory and enter the dispersal pool. A 40% probability is used as this is the percentage of pack break-up (as opposed to pack inheritance) observed in the field (Woodroffe, O'Neill, & Rabaiotti, 2020).

Observation

For the purposes of model testing each individual is observed throughout the model and all variables recorded. For model analysis, only pack- and population-level variables are recorded, namely: pack size, pack inter-birth interval, pack litter size, pack longevity (the period between a pack occupying a territory and breaking up or dying), number of dispersers (the total number of individuals in the dispersal pool in any one timestep), number of packs, population size, and time to population extinction.

TABLE 1 Symbols used in the models. Temperature refers to mean daily maximum temperature throughout.

Symbol	Variable	Unit
h	Individual identity	Individual identifier
i	Group identity	Group identifier
H	Number of territories in the model	n territories
N_t	Total number of individuals (adult and juvenile) at time t	n individuals
$N_{a,t}$	Number of adults (dominant and subdominant) in the population at time t	n individuals
$N_{h,t}$	Number of subdominant adults in the population at time t	n individuals
$N_{i,t}$	Number of individuals (adult and juvenile) in pack i at time t	n individuals
$N_{ia,t}$	Number of adults (dominant and subdominant) in pack i at time t	n individuals
$N_{D,t}$	Total number of dispersing individuals in the dispersal pool at time t	n individuals
$N_{iD,t}$	Number of dispersers leaving pack i at time t (n individuals)	n individuals
$N_{id,t}$	Number of adult deaths in pack i at time t (n individuals)	n individuals
$b_{i,t}$	Whether pack i has a litter at time t	Binary
$\alpha, \beta, \gamma, \delta, \epsilon, \zeta, \theta, \lambda, \mu, \xi, \sigma, \varphi, \nu, \omega$	Input parameters. Further details in Table 2	
r_i	Inter-birth interval for pack i	n timesteps
$i_{i,r-1}$	The timestep of the previous breeding attempt for pack i	n timesteps
$i_{i,r}$	The timestep of the next breeding attempt for pack i , calculated as $t_{i,r-1} + r_i$	n timesteps
$i_{i,r,t-1}$	The timestep prior to the previous breeding attempt	n timesteps
$l_{i,t}$	Litter size for pack i at time t	n individuals
$l_{i,tr-1}$	Litter size of pack i in the most recent breeding event	n individuals
T_t	Temperature at time t	°C (centred)
$T_{i,tr-1}$	Mean temperature across the three timesteps prior to the first count of 3-month-old juveniles in pack calculated as $\left(\frac{T_{i,t-2} + T_{i,t-1} + T_{i,t}}{3}\right)$ at time $t-1$	°C (centred)
$S_{j,t}$	Juvenile survival probability for an individual at time t	0–1
$S_{a,t}$	Adult survival probability for an individual at time t	0–1
m_t	Age of an individual (in months) at time t	n timesteps
v_t	Dominance status of an individual at time t : 0 for subdominant individuals and 1 for dominant individuals	Binary
$P_{D,t}$	Probability of dispersal of an individual at time t	0–1
$P_{ip,t}$	Probability that dispersal group i will occupy an empty territory at time t	0–1
x,y	Random numbers drawn from a uniform distribution between 1 and 0	0–1

Variable	Coefficient	Symbol	Value	SE
Inter-birth interval	Intercept	α	9.1045	0.6213
	Impact of temperature	β	0.9156	0.3349
	Impact of litter size	γ	0.5198	0.1645
Litter size	Intercept	δ	0.9751	0.1368
	Impact of pack size	ϵ	0.0457	0.0232
Juvenile survival	Intercept	ζ	-1.4871	0.6465
	Impact of temperature	θ	-0.7057	0.2937
	Impact of litter size	λ	0.5482	0.1565
Adult survival	Intercept	μ	0.0265	0.0002
	Impact of temperature	ξ	0.2718	0.0064
	Impact of pack size	σ	-0.1405	0.0222
	Impact of age	φ	0.0162	0.0011
	Impact of dominance	ν	0.3529	0.3529
Dispersal	Intercept	φ	0.0064	0.0002
	Impact of pack size	ω	0.1059	0.0239

TABLE 2 Mean values of the normal distributions the input parameters in the model were drawn from.

Initialisation

Each territory is initially occupied by one dominant female and a number of subdominants, determined by selecting a number from a Poisson distribution with a lambda of 3.24, and standard deviation of 2.08 (the mean number of subdominant females in a pack, and the standard deviation, from the field data (Woodroffe, Rabaiotti, et al., 2020). The time until the first litter leaves the den is determined by selecting a random number from a truncated normal distribution with a minimum value of 3, maximum value of 11, and a mean of 6, with a standard deviation of 1.62 (the rounded mean inter-birth interval (in months), and standard deviation, from the field data) (Woodroffe, O'Neill, & Rabaiotti, 2020). The model is then run for 100 months at a mean (centred) temperature of 0, after which the evaluation of the first run starts.

Inputs

Temperature is selected from a normal distribution with a mean of 0, representing the centred mean daily maximum temperature over a period of 30 days in °C, with variance (Ψ) matching temperature variance from the weather station at the study site. Seasons were not modelled as the study site is aseasonal due to its proximity to the equator.

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

2.2.4 | Submodels

Pack size, that is, the number of adult and juvenile female African wild dogs in each pack ($N_{i,t}$) in the model at timestep t (N_t) is a function of the number of individuals present in each pack in the previous timestep ($N_{i,t-1}$), the number of deaths in each pack during timestep t ($N_{id,t}$); the number of dispersals from that pack in timestep t ($N_{iD,t}$); and the number of births in each pack in that

timestep ($N_{ib,t}$). The population size (N_t) is the sum across all packs in the model.

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

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

Model parameters (Table 2) were estimated from empirical data (as described in Appendix S1), and functions determining the variables within the individual-based model took the same form as the statistical models from which the parameter estimates were derived: Cox proportional hazard models (adult survival [S_a], and probability of dispersal [P_D]), a generalised linear model with a Poisson distribution (litter size [l]), a generalised linear model with a binomial distribution (juvenile survival [S_j]), and a generalised linear model with a Gaussian distribution (inter-birth interval [r_i]). Full details of model parameter estimation can be found in Appendix S1.

Reproduction

The number of offspring produced by a pack (b_i) at timestep t is dependent on the timing of the previous breeding attempt (t_{ir-1}) and the inter-birth interval (r_i):

$$b_{i,t} = \begin{cases} l_i, & \text{if } t = t_{ir-1} + r_i \\ 0, & \text{otherwise} \end{cases}$$

If offspring are produced by a pack (if $t = t_{ir-1} + r_i$ in the equation above) litter size ($l_{i,t}$) in this model, representing the number of juveniles at 3 months of age, is determined by the number of adults in the

pack at the time ($N_{i,t}$). Litter size is drawn from a truncated Poisson distribution with a minimum of 1, maximum of 8 and a mean of $e^{\delta+\epsilon N_{i,t}}$.

The formula used to calculate the mean litter size is below, and symbol definitions can be found in Table 1:

$$l_{i,t} \sim TP(e^{\delta+\epsilon N_{i,t}}, 0, 8)$$

The inter-birth interval is dependent on the temperature during the previous denning period ($T_{i,r-1}$) (Figure 1) and the size of that previous litter ($l_{i,r-1}$), where $t_{i,r-1}$ is the timestep when the previous litter was 3 months old. Temperature during the previous denning period ($T_{i,r-1}$) was calculated from the temperature over the 3 months prior to the previous litter leaving the den at $t_{i,r-1}$

$$T_{i,r-1} = \left(\frac{T_{i,rt-2} + T_{i,rt-1} + T_{i,rt}}{3} \right)$$

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

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

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

Number of deaths

Number of deaths (N_{dt}) is dependent on the survival probability in both adults (S_a) and juveniles (S_j), characterised together as S :

$$N_{dt} = \sum_{h=1}^{N_{h,t-1}} \left[\begin{array}{l} 1 \text{ if } y \sim U(0, 1) < S \\ 0 \text{ otherwise} \end{array} \right]$$

The probability of an individual juvenile's survival at each timestep ($S_{j,t}$) is dependent on the size of that individual's birth litter at the time they permanently left the den ($l_{i,tr-1}$) and the mean daily maximum temperature when that individual was in the den ($T_{i,tr-1}$) (Figure 1). As the data from which the survival rate was estimated only contained the number of juveniles at 3 and 12 months of age, the ninth root was taken to obtain monthly survival rates.

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

ζ , θ and λ are constants defined by the binomial generalised linear model describing juvenile survival (Table 2).

The probability of adult wild dog survival, at timestep t ($S_{a,t}$) is dependent on pack size ($N_{i,t}$) and dominance (v_t) at the time, and average temperature over the three previous timesteps $\frac{T_t + T_{t-1} + T_{t-2}}{3}$ (Figure 1). For dominant individuals, survival is also dependent on age (m_t). The formula used to calculate the probability of survival for each individual adult is below:

$$S_{a,t} = 1 - \mu (e^{\xi T_t + \sigma N_{i,t} + v + v \phi m_t})$$

μ , ξ , σ , v and ϕ are constants defined by the Cox proportional hazards model of adult survival (Table 2; Appendix S1).

Dispersal

Within the model, only subdominant adults could disperse, as this is what is observed in the field (Woodroffe, Rabaiotti, et al., 2020). Number of dispersers (N_D) was dependent on the probability of dispersal (P_D):

$$\sum_{h=1}^{N_{h,t-1}} \left[\begin{array}{l} 1 \text{ if } x \sim U(0, 1) < P_D \\ 0 \text{ otherwise} \end{array} \right]$$

Individual dispersal probability at each timestep ($P_{D,t}$) was dependent on pack size in that timestep ($N_{i,t}$). The formula for individual dispersal probability is shown below, and symbol definitions can be found in Tables 1 and 2:

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

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

All individuals, in the same pack, that disperse at the same timestep form a dispersal group and enter a dispersal pool. Individuals in the dispersal pool are lost from the model after two timesteps (equivalent to 2 months). This time period was chosen because, while empirical data indicate that wild dogs dispersed for a mean time of 19.4 days (range 3–68 days) (Woodroffe, Rabaiotti, et al., 2020), this mean is likely to under-represent longer dispersals as, the longer an individual disperses for, the more likely it is to be lost to monitoring, and individuals have reappeared in the study population after much longer periods of time (Woodroffe, Rabaiotti, et al., 2020). In the model, individuals also disperse if the pack breaks up after the dominant individual's death. When this happens all juveniles in the pack die.

Territory inheritance

If any of the packs within the model break up or all individuals in a pack die, leaving an empty territory, a dispersal group can then occupy that territory, starting a new pack. The probability of a group occupying a territory was directly proportional to group size. This rule was based upon empirical evidence that larger dispersal groups were more likely to form new packs (Appendix S1). If an empty territory is available at time t , the formula for the probability that a dispersal group would occupy it ($P_{p,t}$) is shown below, with $N_{ID,t}$ representing dispersal group size (Table 1):

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

If there is more than one empty territory the process is repeated until all territories are filled, or there are no more dispersal groups left in the dispersal pool. A diagram of the positive and negative relationships between the parameters and demographic variables is shown in Figure S4.

2.2.5 | Assessing model performance

Before projecting the impact of future climate change on the simulated population, model outputs were visually compared with the empirical data collected over 16 years by the Samburu–Laikipia Wild Dog Project, equating to 38 group years, to assess fit (Figure 2; Table S1). For assessment purposes, we recalculated the input parameters excluding data from the two consecutive years with the highest mean maximum temperatures, and for the two consecutive years for the lowest mean maximum temperatures. The model was run 1000 times at the mean maximum temperature during the hottest years, and 1000 times at the mean maximum temperature during the coldest years, for 100,000 timesteps. Pack size, dispersal group size, inter-birth interval and litter size predicted from the model were compared with the empirical data from the two excluded years. We also performed sensitivity and elasticity testing on the model to explore which demographic parameters and inputs most impacted population dynamics (detailed in Appendices S2 and S3).

The model predictions matched the field data adequately, with the predicted distributions of pack size, inter-birth interval, dispersal group size, and the size of the pack at formation approximately matching the distribution of the data (Figure 2). Short-lived packs were over-represented in the model predictions due to the fact the model was single sex and therefore small dispersal groups

were assumed to form small packs, whereas in reality small female groups may bond with large male groups, and vice versa (Woodroffe, O'Neill, & Rabaiotti, 2020). When used to predict the pack dynamics under conditions of the hottest and coldest years, the outputs from the model matched the data well, with small differences in observed and predicted values (Figure 3).

2.2.6 | Future projections

To determine the levels of warming to be experienced by model populations in the future scenarios, we calculated how much the study site is predicted to warm between now and 2070. Raster layers of current (1975–2013) mean daily maximum temperature estimates from across the study site were obtained at a resolution of 30 arc seconds from the WorldClim climatic dataset (Hijmans et al., 2005). Raster layers of future mean daily maximum temperature projections (from the HADGEM-2-ES climate models) for 2070 under representative concentration pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 were also obtained from WorldClim (Hijmans et al., 2005) at the same resolution. RCP 2.6 assumes carbon dioxide emissions reach zero by 2100, keeping the increase in global temperatures by 2100 below 2°C. RCP 4.5 and 6.5 are in line with global temperature rises between 3°C and 4°C by 2100, however in RCP 4.5 emissions peak

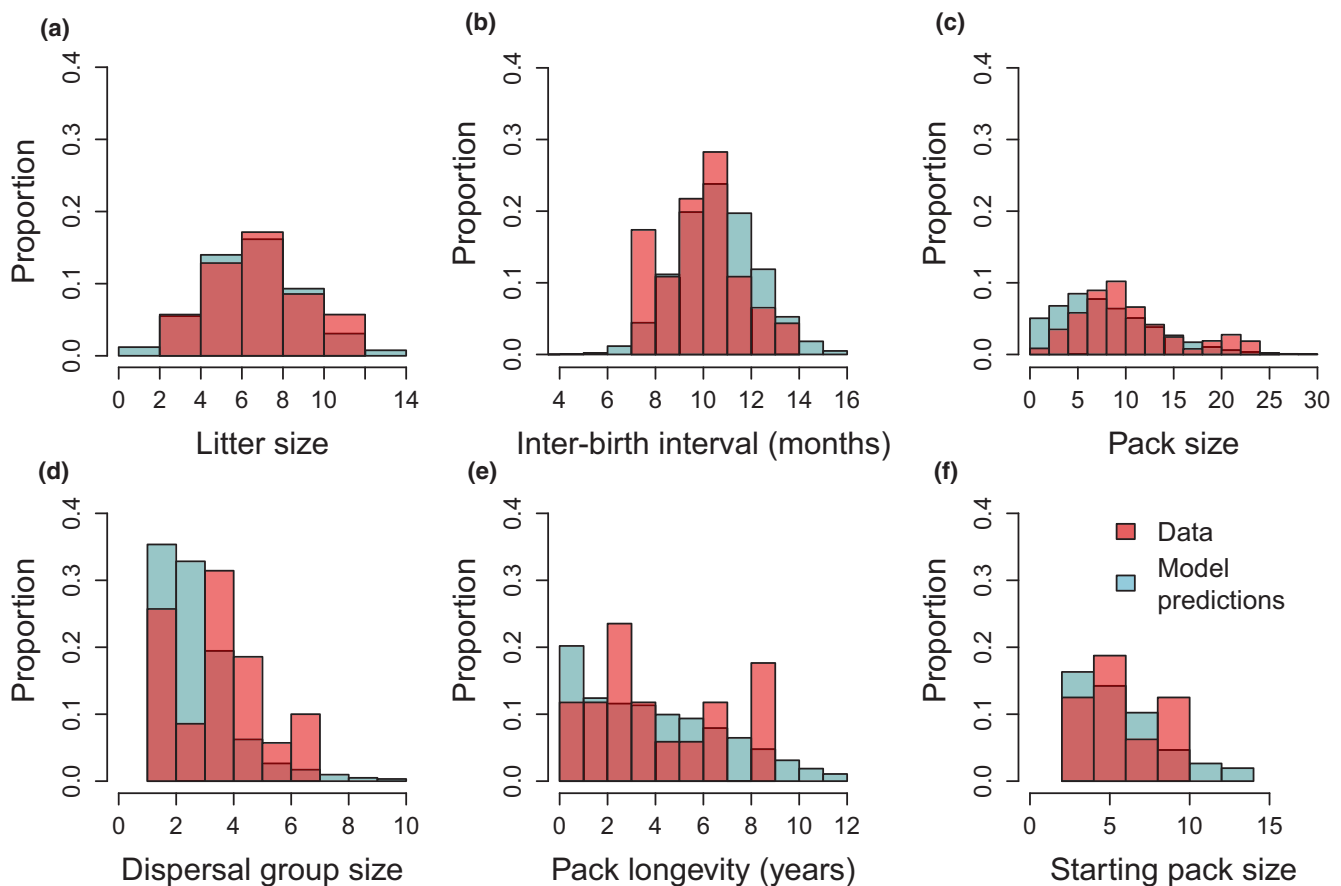


FIGURE 2 Histograms of empirical data and predictions from the population model. As the model is single sex, model predictions of litter size and pack size have been doubled.

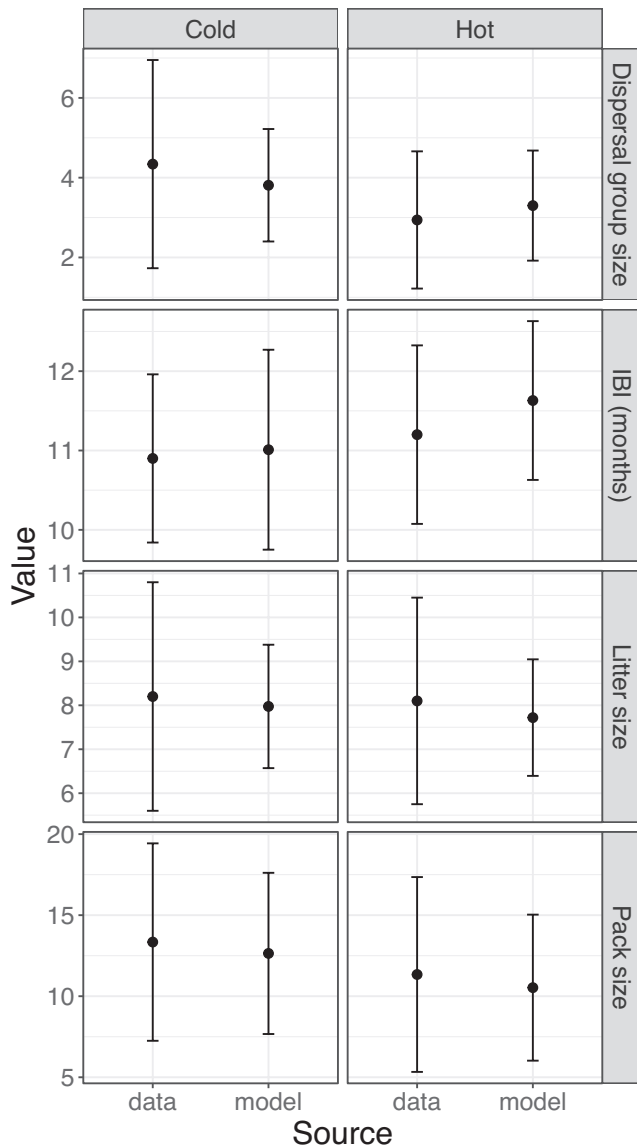


FIGURE 3 Comparison between data and model estimates for the two consecutive hottest and coldest years. IBI stands for inter-birth interval. Error bars represent the 95% confidence interval.

around 2045, compared to 2080 in RCP 6.0. RCP 8.5 is the worst-case scenario, and assumes emissions continue to rise throughout the 21st century, causing global temperature rises of around 4.3°C by 2100.

We defined the study area by drawing minimum convex polygons around locations obtained from GPS-collared individuals monitored by the Samburu Laikipia Wild Dog Project and merging them to generate a single polygon. We calculated mean projected future warming across the study site under each of the four emissions scenarios and used these as the temperature variable in the models. The variance was kept consistent. Mean daily maximum temperatures across the study site were projected to rise between 1.6°C and 3.9°C by 2070, depending on the RCP scenario.

We ran the model under warming of 0.5–5 degrees at 0.1 degree intervals, for the model constructed with 9 and 30 territories, to

investigate the effect of increased mean daily maximum temperature on the population. We estimated the population extinction risk within 600 timesteps (50 years, or approximately 10 generations (Woodroffe & Sillero-Zubiri, 2012)) at these temperatures, and ran the model for 6000 timesteps (approximately 100 generations) to estimate average population persistence time. To investigate the drivers behind changes in population dynamics at high temperatures we ran the model for 600 timesteps under warming of 0.5–5 degrees at 0.1 degree intervals with the impacts of temperature on adult survival, juvenile survival, and inter-birth interval removed sequentially. The model was run 1000 times for each temperature and pack size described above to obtain all estimates of pack and population characteristics, extinction risks, and population persistence time.

3 | RESULTS

3.1 | The impact of warming on population dynamics

The model predicted that litter size, pack size, and pack longevity would all decrease at higher temperatures (Figure 4). The number of packs was predicted to remain approximately stable at warming scenarios below 2.5°C above current temperatures but, above this threshold, small increases in temperature were associated with large reductions in the predicted number of packs (Figure 4).

In the best-case scenario (RCP 2.6, equivalent to a 1.6°C increase in local mean daily maximum temperature), average pack size in the model was predicted to fall from 5.2 to 3.1 adult females relative to current climate conditions, with the average pack longevity falling from 4.15 to 2.25 years (Figure 4). Despite the average number of packs in the population remaining unchanged in the best-case climate scenario, the average population size was predicted to fall by 45% (Figure 4) reflecting the reduction in pack size. Average litter sizes were predicted to be 0.3 pups smaller, which is 8% lower than the litter size predicted under current temperatures, at temperatures predicted under the best-case climate scenario (Figure 4).

Under RCP 4.5 (equivalent to 2.5°C increase in local mean daily maximum temperature) the mean pack size was predicted to fall as low as two adult females per pack, with the population size reduced by 64% compared to predictions under current temperatures (Figure 4). However, the number of packs in the population was predicted to remain high (Figure 4). Under RCP 6.0 (2.8°C increase in local mean daily maximum temperature) average pack longevity was predicted to fall below 1 year, and average pack size to fall below two adult females (Figure 4). At this level of warming the mean predicted number of packs in the population across 600 timesteps began to fall (Figure 4). Under the worst-case scenario, RCP 8.5 (3.9°C increase in local mean daily maximum temperature), the average pack duration was predicted to be under 1 year, and inter-birth interval was predicted to be 13.5 months, causing breeding rates to collapse (Figure 4). The average litter size was predicted to fall to three female

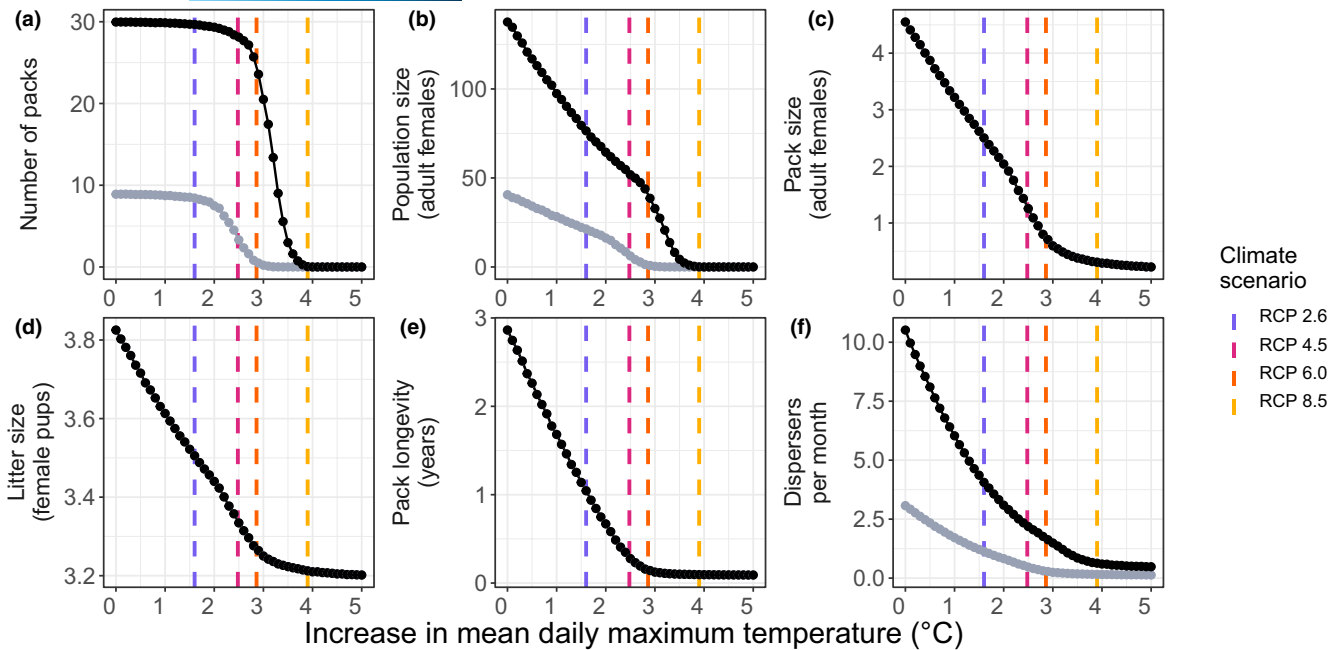


FIGURE 4 The impact of temperature increase ($^{\circ}\text{C}$) on estimated mean population and pack variables for a simulated population with a carrying capacity of 30 (black) and nine (grey) packs over 10 generations. Curves are splines through predictions made for 0.1 degree intervals of increase in temperature, depicted by the points. Predicted warming by 2070 at the study site under four representative concentration pathways are marked with vertical dashed lines.

juveniles, and the average number of both packs and individuals was predicted to be very low (Figure 4).

3.2 | The impact of warming on population persistence

Extinction risk (the proportion of the 1000 model runs in which the population went extinct within 10 generations) was predicted to remain at 0 for levels of warming below 1.8°C above current mean daily maximum temperatures for a population with nine available territories (Figure 5). Above these threshold levels of warming, small increases in temperature were associated with large increases in extinction risk. For populations occupying up to nine territories, a 1.4°C increase in warming (from 1.8°C to 3.2°C above current temperatures) was sufficient to transition the 10-generation extinction risk from 0 to 1. For populations occupying up to 30 territories, this transition was predicted to occur across just 1°C of warming (from 2.8°C to 3.8°C above current levels) (Figure 5). Patterns of predicted population persistence mirrored that of extinction risk, remaining at 100 generations (persistence until the end of the model runs) at temperature increases of up to 1.5°C in a population with nine territories available, before reducing to under five generations at 3.2°C of warming. The same pattern was predicted for a population of 30 available territories, but with the population persistence first falling at temperatures 2.5°C above current levels and reducing to five generations at 3.8°C of warming.

3.3 | Drivers of declines

Population collapse at high temperatures was driven primarily by falls in recruitment within packs (Figure 6). While the number of individuals dying and dispersing in each pack did fall at higher temperatures, this was due to a decrease in pack size (Figures 4 and 6). At higher temperatures, the number of individuals lost to packs through death and dispersal was predicted to become increasingly larger than the number of new adults recruited through birth and juvenile survival (Figure 6). The decrease in juvenile survival at high temperatures contributed more to the predicted fall in recruitment than the decreased number of births (Figure 6). This pattern is illustrated by the small fall in births at high temperatures, compared to the large fall in juvenile survival, and also by the finding that removing the impact of temperature on juvenile survival resulted in the largest reduction in climate driven extinction risk (Figure 6). Removing the impact of temperature on juvenile survival in the model increased the threshold for accelerating extinction risk from 1.8°C (in the model with all temperature impacts present) to 4°C (with effects on juvenile survival removed). Removing the impact of temperature on the inter-birth interval also had a relatively large impact on extinction risk, increasing the threshold at which extinction risk is predicted to rise from 1.8°C to 3°C (Figure 6). Removing the impact of temperature on adult survival had little impact on extinction risk, with the threshold at which extinction risk is predicted to rise only increasing by 0.2°C from 1.9 to 2.1°C above current temperatures (Figure 6).

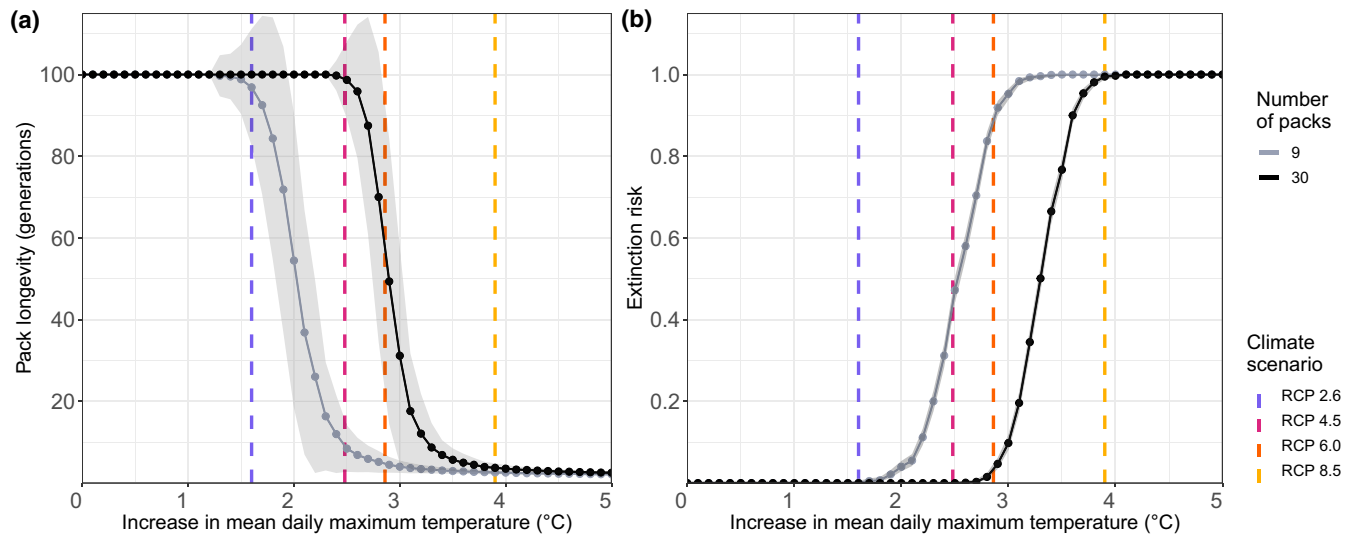


FIGURE 5 The impact of temperature increase (°C) on (a) estimated pack longevity over 100 generations, with confidence intervals derived from the standard deviation of the final timestep where there were packs in the model and (b) Extinction risk over 10 generations. Curves are splines through predictions made for 0.1 degree intervals of increase in temperature, indicated by points. Predicted warming by 2070 at the study site under the four representative concentration pathways are marked with vertical dashed lines.

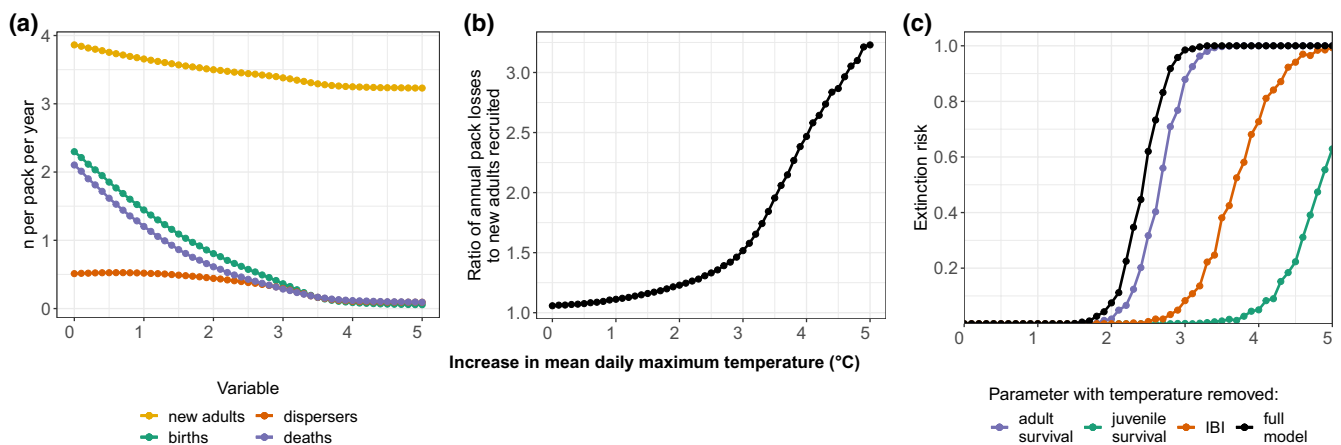


FIGURE 6 Underlying drivers of population trends as temperatures rise. (a) The simulated number of births, new adults, dispersals, and deaths per pack, per year, at 0.1 degree interval increases in temperature, indicated by points. Curves are splines through the predictions. (b) The ratio of pack losses to new adults recruited to the pack at 0.1 degree interval increases in temperature and (c) extinction risk of a population of nine packs at 0.1 degree interval increases in temperature with the impact of temperature on different demographic variables removed. Curves further to the right indicate a larger reduction in extinction risk. IBI stands for inter-birth interval.

4 | DISCUSSION

Our model predicts extreme sensitivity of African wild dog populations to climate change. Temperature rises in line with the middle case climate scenarios (RCP 4.5 and 6.0) were predicted to cause a population of nine packs to go extinct within 100 generations in over 50% of simulations. At temperatures predicted in the worst-case climate scenario (RCP 8.5), larger populations of 30 packs were predicted to go extinct within 100 generations 100% of the time. At both simulated population sizes, extinction risk within 100 generations rapidly increased under further warming once a threshold temperature was reached. These threshold effects are

cause for concern because population collapse would be likely to occur too fast for conservation action to prevent extinction. Without long term studies revealing the demographic impact of high temperatures there would be little warning of the resulting population declines. Knowing that such threshold effects can occur may be essential for the conservation of other, less well-studied, species.

While there was no detectable increase in temperature over the course of data collection at the Kenya study site (Figure S6), we have shown that mean daily maximum temperature during the breeding season increased by an average of 0.134°C per year from 1989 to 2012 at a site in Botswana (Woodroffe et al., 2017). At this rate,

a 1°C increase in daily maximum temperature during the breeding season, would occur over approximately 8 years. Increases in local mean maximum temperature across most of the African continent are predicted to be greater than increases in the global mean temperature used to characterise climate change in policy settings (Barros et al., 2014). As a result, an additional 1°C increase in the mean maximum temperature during African wild dog breeding season across most of their remaining range reflects a smaller increase in global temperatures. Thus, even temperature rises in line in RCP 4.5, which represents a 2.5°C rise in global temperatures by 2100, may cause increases in population extinction risk across much of the species' range.

A high number of territories within a population was predicted to buffer the impact of high temperatures, increasing the temperature at which the population collapsed by nearly a degree of warming. This required a 230% increase in carrying capacity of a population (from nine to 30 packs), however, and only the five largest remaining African wild dog populations contain 30 or more packs. The predicted buffering effect of larger number of territories implies that the largest populations, with over 100 packs, such as those in the KAZA and Selous, will benefit from considerable buffering against climate change. Increasing connectivity between African wild dog populations is therefore likely to increase resilience in the face of rising temperatures.

In contrast to the prediction that reduced group sizes due to environmental change would cause lower population resilience and increased risk of population extinction (Courchamp et al., 2000), at 2°C warming there is predicted to be little to no increase in extinction risk in the population despite a 50% reduction in pack size. The species' social structure buffers impacts of rising temperatures on extinction risk under low levels of warming in the model by maintaining the number of packs, and therefore breeding individuals, in the population. The rise in extinction risk at temperatures above a specific threshold is, rather than being driven by group size, driven by temperatures reaching a threshold above which juvenile survival is so low it causes an increase in extinction risk. Above this threshold packs are no longer recruiting subdominant individuals and there are not enough dispersers to replace dominant pairs. When there is no breeding pair to replace those that are lost, reproduction ceases and the population rapidly collapses.

Removing impacts of temperature on juvenile survival virtually eliminated predicted rises in extinction risk under future climate change. The fact that juvenile survival is the driver behind the predicted population declines has implications for studies of the impacts of environmental change on bird and mammals more widely. It is broadly accepted that proportional changes in juvenile survival have a smaller effect on population growth rates in long-lived, iteroparous, species than the same change in adult survival (Gaillard et al., 2000; McKnight et al., 2018; Morris & Doak, 2004). Vital rates that have a bigger impact on population dynamics, particularly adult survival, show lower variation and are less sensitive to environmental factors (Gaillard & Yoccoz, 2003; Hilde et al., 2020). This has been found across a variety of mammal, bird and plant species, and is

theorised to be an adaptation to maintain population stability in the face of sub-optimal environmental conditions (Forcada et al., 2008; Gaillard & Yoccoz, 2003; Pfister, 1998). Breeding individuals sacrifice parental care and provisioning, lowering offspring survival rates, and increase their own survival probability to increase their probability of reproducing successfully in the next breeding attempt (Gaillard & Yoccoz, 2003). This adaptation is hypothesised to buffer populations against environmental change (Gaillard & Yoccoz, 2003; Hilde et al., 2020).

While cooperative breeders are less sensitive to adult survival than other species because the loss of subordinate individuals has a low impact on population recruitment, our findings suggest that this may be a 'trade-off', at the expense of higher sensitivity of population growth rates to juveniles' survival. Multiple cooperatively breeding species have been shown to experience negative impacts of high temperatures when they negatively impact foraging success, leading to changes to offspring provisioning and a subsequent reduction in offspring survival. Meerkat (*Suricata suricatta*) pups gain less body mass on hot days, and experience lower survival to adulthood at high temperatures (Van de Ven et al., 2020). In the Southern pied babbler lower food provisioning at high temperatures leads to lower chick body mass, and subsequently lower survival (Ridley et al., 2021). In African wild dogs high temperatures in the first 3 months of life lead to falls in juvenile survival (Woodroffe et al., 2017), likely due to decreases in time spent hunting in hot weather (Rabaiotti & Woodroffe, 2019). This raises concerns that other cooperatively breeding species are likely to exhibit similar population collapses in response to climate induced falls in recruitment.

Even in non-cooperatively breeding species, while demographic buffering can shield populations from the impacts of short-term periods of adverse environmental conditions, ongoing global change will lead to increases in the frequency and duration of these adverse environmental conditions. Should periods become so long, extreme or frequent that they span multiple breeding periods, this leads to a collapse in juvenile survival and a precipitous decline in recruitment, as has been found in multiple other species, including tortoises (*Testudo graeca*) (Rodríguez-Caro et al., 2021), tree swallows (*Tachycineta bicolor*) (Cox et al., 2020) and prairie dogs (*Cynomys ludovicianus*) (Facka et al., 2010). Low recruitment across an extended time period spanning multiple breeding seasons will ultimately lead to population declines, and even collapse (Facka et al., 2010; McLennan et al., 1996). The threshold at which this demographic buffering fails, and if that threshold is crossed under future environmental conditions, will be key in determining population persistence across long-lived species, and it is critical that this is explored using models that incorporate species' demographic responses to global change.

We modelled the population using a single-sex model to avoid introducing unnecessary model complexity. This was appropriate in this case because population growth rate in this population is not limited by the number of males available, and African wild dog males do not contribute to population growth rates beyond mating with the dominant female and acting as additional helpers (Woodroffe, O'Neill, & Rabaiotti, 2020). Modelling the population as female only

therefore has little impact on predicted population growth rates (Schindler et al., 2013). As our model represents females only, the predicted impacts of high temperatures on the population are likely to be conservative, as the presence of male dispersers with which the females could start new packs was assumed. In reality, an unrelated group of males is often not present in the population at the time that females disperse, potentially preventing pack formation. Inbreeding avoidance is very strong in wild dogs, and packs have been observed to cease breeding if there are no unrelated mates (Becker et al., 2012). The model also ignores the impact that the death of the dominant male may have on a pack; packs within a real population would be expected to break up when the dominant male dies if there were no males unrelated to the dominant female to take over. The female only dynamic led to an over-representation of short-lived packs within the model, as even a single female could occupy a vacant territory, and that packs' survival in the first 12 months was reliant on a single individual. This is a similar dynamic to that observed in transient, non-resident packs (Woodroffe, O'Neill, & Rabaiotti, 2020).

The model structure means the simulated populations are more stable than real African wild dog populations, as evidenced by the 0% extinction risk predicted at current temperatures for populations with carrying capacities of both nine and 30 packs. In reality multiple wild dog population extinctions have been documented in the past 30 years—for example in the Serengeti, North Cameroon, Liuwa, the W-Arly-Pendjari Complex and even in Laikipia itself, where wild dogs were extinct until 2000, when they recolonised (Woodroffe, 2011a; Woodroffe & Sillero-Zubiri, 2012). Other threats to wild dogs are likely to be exacerbated by the year 2070, including habitat loss (Williams et al., 2020), disease (Carlson et al., 2022), changes in prey (Milán-García et al., 2021), and conflict with people due to human encroachment into natural habitat in response to changing climatic conditions, none of which are explicitly incorporated into the model, but may be reflected in the number of available territories. As a result, our model predictions are likely to under-estimate population extinction risk, both now and under future climatic conditions. Future models should model dispersal dynamics and additional threats more explicitly to ensure that they better reflect both group dynamics and population pressures.

The way that temperature was modelled, using only the predicted future temperatures in 2070, does not incorporate expected temperature increases beyond that point. The RCP models only give a temperature prediction for that point in time, but warming is anticipated to increase beyond that point (Barros et al., 2014). Particularly for extinction risk estimates, which were modelled across 50 years, this means that the estimates are conservative, and there is likely to be an increase in both temperature and other threats beyond the 2070 time-point. In contrast to this, the population collapses are predicted to occur over fewer timesteps than we would expect in a real population experiencing increasing temperatures because the temperature change is abrupt, occurring across one timestep, as opposed to occurring gradually over 50 years. It will be important for any future models seeking to inform conservation action to

investigate the impact of this gradual warming on the time to this deterministic climate-induced population collapse.

The model is parameterised using data from a single study population in Kenya. Hence, exploring the consequences of using parameters from other populations will be an important next step in evaluating the generality of our findings. While temperature has been found to impact recruitment at all sites where it has been studied (Abrahms et al., 2022; Woodroffe et al., 2017), the age at which these impacts have been found to occur varies both within and between studies (Abrahms et al., 2022; Woodroffe et al., 2017). Temperature impacts on adult survival have not been detected at other sites (Rabaiotti et al., 2021). Unlike the Kenyan site, Southern African sites show strong seasonal variation in temperature and rainfall, and, consequently, seasonal wild dog reproduction (McNutt et al., 2019); these patterns complicate the association between temperature and wild dog demography. As seasonality is expected to increase across most of Africa (Hijmans et al., 2005) insight into the interaction between seasonality and temperature impacts will be important for understanding population responses to climate change into the future. The relationship between pack size and mortality may also vary between sites (Creel & Creel, 2002; Rabaiotti et al., 2021). Although our model was parameterised using data from a single population of African wild dogs, impacts of temperature on wild dog demographic rates have been found in two other populations (Rabaiotti et al., 2021; Woodroffe et al., 2017).

This work demonstrates the crucial role of long-term field data in parameterising models that predict the impact of environmental change on social species. Population models such as these can be used to identify how much environmental change a species is resilient to, determining 'tipping points' after which populations are likely to go extinct. The findings of this study highlight the importance of taking into account individual and group characteristics when predicting the impact of climatic conditions on social species, information which is often only derived through long-term study. This work also highlights the extent to which relatively simple mechanistic population models, when parameterised on detailed population information, can be used to predict the impacts of climate change on population viability. Our findings raise concerns about declines in long-term field-based studies across conservation biology as a whole (Hughes et al., 2017) as, without long-term monitoring across a range of weather conditions, predictions such as these are not possible. In cases where long-term field data are available, individual-based population models can shed new light on climate change threats, and enable predictions of future population trends of species.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study is available at <https://osf.io/st9w2/>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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