

Higher temperature extremes exacerbate negative disease effects in a social mammal

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Abstract

*One important but understudied way in which climate change may impact the fitness of individuals and populations is by altering the prevalence of infectious disease outbreaks. This is especially true in social species where endemic diseases are widespread. Here we use 22 years of demographic data from wild meerkats (*Suricata suricatta*) in the Kalahari, where temperatures have risen steadily, to project group persistence under interactions between weather extremes and fatal tuberculosis outbreaks caused by infection with *Mycobacterium suricattae*. We show that higher temperature extremes increase the risk of outbreaks within groups by increasing physiological stress as well as the dispersal of males, which are important carriers of tuberculosis. Explicitly accounting for negative effects of tuberculosis outbreaks on survival and reproduction in groups more than doubles group extinction risk in 12 years under projected temperature increases. Synergistic climate–disease effects on demographic rates may therefore rapidly intensify climate-change impacts in natural populations.*

There is now extensive evidence that climate change negatively affects the survival and reproduction, and therefore the local persistence, of animal populations¹. Most often, climate-change effects on demographic rates are associated with physiological stress under higher temperature extremes^{2,3} and decreases in resource availability^{1,4}. Another key way in which climate change can affect natural populations is by altering disease dynamics and interactions between hosts and parasites⁵. For instance, increases in thermal stress have been linked to a higher susceptibility to fatal bacterial infection⁶, and more severe droughts can increase the spread of pathogens among interacting species⁷. However, although infectious disease outbreaks under climate change have been linked to extinctions of local populations and are likely to increase in a warmer future⁸, the mechanisms through which climate change may affect the prevalence and consequences of disease outbreaks remain little understood^{8–10}.

Animals living in social groups may be particularly susceptible to increases in infectious disease outbreaks. Group living can raise the survival and reproductive success of group members^{11,12} and mitigate adverse effects of climate change on food availability through resource sharing and more efficient foraging¹³, but it may also increase the rates of infection by parasites and endemic diseases^{14–16}. Disease outbreaks can directly cause mass mortality

in social groups^{16,17}, or they may decrease group size by reducing individual survival and fecundity, and thus make groups more vulnerable to adverse climatic conditions^{18,19}. Assessing these complex pathways through which climate change may affect groups therefore requires quantifying the demographic responses (for example, survival, reproduction, dispersal) to climate–disease interactions²⁰. Here we use 22 years of detailed individual growth and life-history data from 85 groups of meerkats (*Suricata suricatta*)²¹, a common species in the Kalahari, to quantify how variation in climate interacts with disease dynamics to affect individual traits, demography and, ultimately, group persistence.

Recent climate change and tuberculosis outbreaks in meerkats

Kalahari meerkats are cooperative breeders that live in groups of 2–50 individuals²¹. Groups include a dominant female that has usually been born into the group, one or more unrelated immigrant males, one of which monopolizes reproduction with the dominant female, as well as a variable number of subordinates of both sexes that help to feed and protect their offspring, and occasionally attempt to breed²¹. A type of tuberculosis (TB), caused by infection with the species *Mycobacterium suricattae*, is endemic and widespread in meerkats^{22–24}. TB is a terminal disease for meerkats, and in the later stages of infection (henceforth, clinical TB), adult meerkats commonly develop pronounced submandibular lymph node swellings that grow in size and eventually burst. Individuals then die within approximately 6 months, causing an additional 6% deaths of the total adult population per year^{24,25}. Outbreaks of TB are the main cause of extinctions of established groups; 63% of groups that were monitored until failure (54 groups in total) failed due to TB, and this rate increased to 100% in groups that had persisted for >8 years and subsequently failed²⁴.

Over the past 22 years, the prevalence of clinical TB has increased in the study population, the increase corresponding with marked changes in weather (Fig. 1). At the study site, annual as well as seasonal maximum temperatures have increased by >1.5 °C since 1979 (Fig. 1 and Supplementary Fig. 3.3). This trend is consistent with current trends detected for the wider Kalahari desert²⁶ and with IPCC climate-change projections, which suggest increases of summer average maximum temperatures of >4 °C by 2090 under the ‘business as usual’ scenario²⁷. On the other hand, while rainfall is highly variable within and between years, there is no clear trend in past or projected future rainfall changes in the Kalahari²⁸ (Extended Data Fig. 1 and Supplementary Fig. 3.4). Increases in temperatures have been shown to negatively affect arid-environment species^{27,29} and are associated with reductions in body mass, survival, recruitment and group size in meerkats, especially in combination with lower rainfall^{13,30}. However, synergistic effects of changes in weather extremes and TB on group persistence have thus far not been explored, and such effects are probably complex, operating via phenotypic traits and demographic mechanisms (Fig. 2). Filling these knowledge gaps is relevant beyond the study system as several pathogenic *Mycobacterium* species cause chronic diseases in wildlife and domestic animals globally (the most prominent case being bovine TB due to infection with *M. bovis*)³¹ as well as in humans, and changes in TB disease patterns under climate change may have wide-reaching implications.

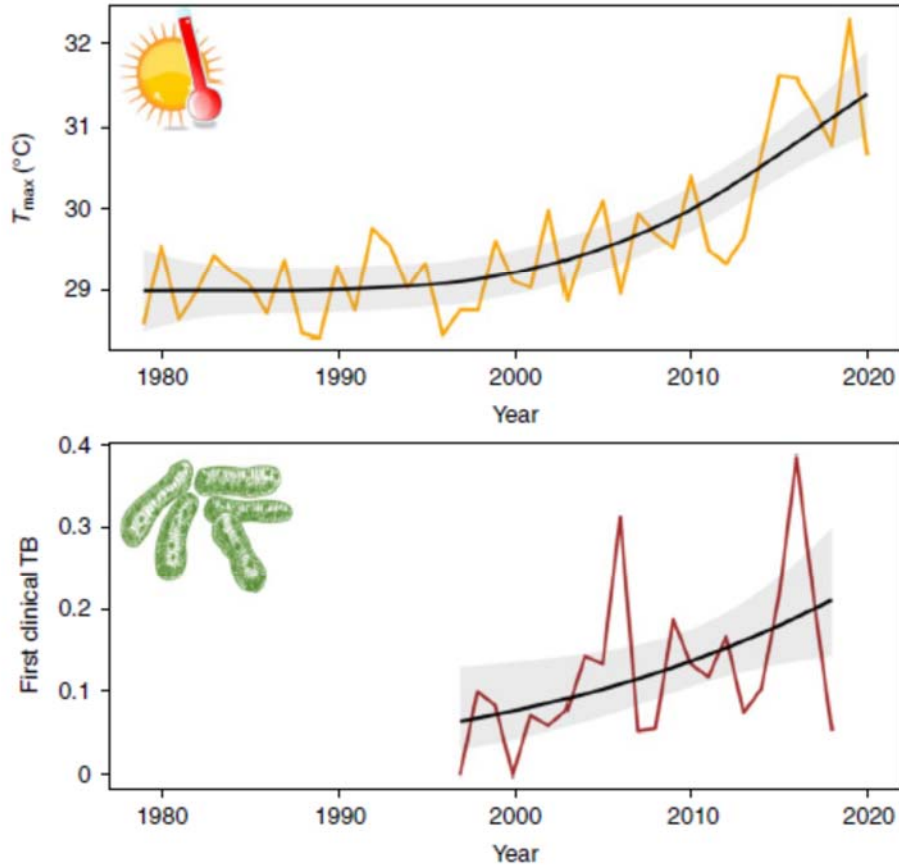


Fig. 1. Changes in maximum temperatures and disease outbreaks in meerkat groups in the Kalahari. Top: mean annual maximum temperatures (T_{max} , 1979–2020). Bottom: the proportion of meerkat groups monitored each year (1997–2018) that show clinical TB for the first time. Seasonal temperature trends are depicted in Supplementary Fig. 3.3. Lines show model predictions ($\pm 95\%$ prediction intervals as shaded areas) of a simple linear model (for T_{max} , accounting for squared effect of year) and a binomial model (for clinical TB) fitted to the data. Slope coefficients of the models were significant (95% CI did not cross 0).

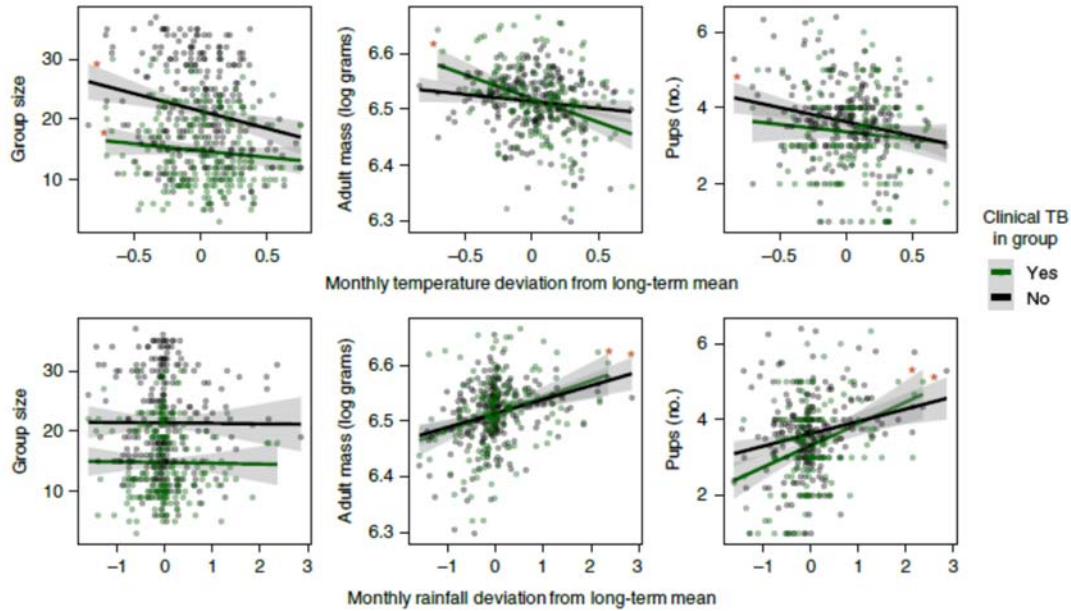


Fig. 2. Observed relationships between temperature and rainfall deviations, clinical TB and group dynamics in meerkats.

Points show monthly averages of group size, body mass and pup numbers observed at the study site, plotted against standardized deviations from long-term (1997–2018) monthly means in maximum temperatures (top row) and total rainfall (bottom row). Different colours distinguish values measured when groups had no or had at least one case of clinical TB. Lines depict mean predictions ($\pm 95\%$ prediction intervals as shaded areas) from simple linear models fitted separately to data in groups with and without clinical TB. Stars indicate significant slope coefficients of the models (95% CI did not cross 0).

To assess the demographic effects of climate variation and clinical TB on group dynamics, we first modelled the probability that a group showed clinical TB cases as a function of climate variation (that is, rainfall and temperature deviations from seasonal means) and social factors (group size, immigrant numbers and female/male ratio). We then used monthly life-history data from >2,600 male and female meerkats collected in 1997–2018 to model demographic rates (survival, growth, reproduction, emigration and immigration) of different life-cycle stages (pups, juveniles, subadults, helpers or dominants; Extended Data Fig. 2) as functions of climate variation and TB status of a group, that is, before or after first clinical TB cases were observed in a group. We also accounted for the effects of individual traits (age and body mass) and social factors (same as for the clinical TB model) on demography. We used generalized additive models (GAMs; following ref. ³²) to parameterize all models, which allowed us to flexibly fit pairwise nonlinear interactions among all predictors.

Temperature extremes affect clinical TB occurrence

We show both direct and indirect effects of climate on the probability of initial clinical, end-stage TB cases being present in groups. First, this probability directly increases with above-average temperatures (that is, positive deviations from monthly means in the clinical TB probability submodel) (Fig. 3a and Supplementary Fig. 1.8). Higher temperatures have been associated with physiological stress in meerkats³⁰, and stress has been shown to increase TB outbreaks in other wildlife populations (for example, ref. ³³). Second, when temperatures are above average, the probability of clinical TB is particularly high if groups have had a high

number of male immigrants in the 5 months preceding the first clinical TB cases³⁴ (Fig. 3a and Supplementary Fig. 1.8). Both in meerkats and other mammals, dispersing males are important carriers of TB^{15,33}. Temperature extremes increase male emigration in the demographic models, which then favours immigration, thereby increasing the likelihood of TB outbreaks.

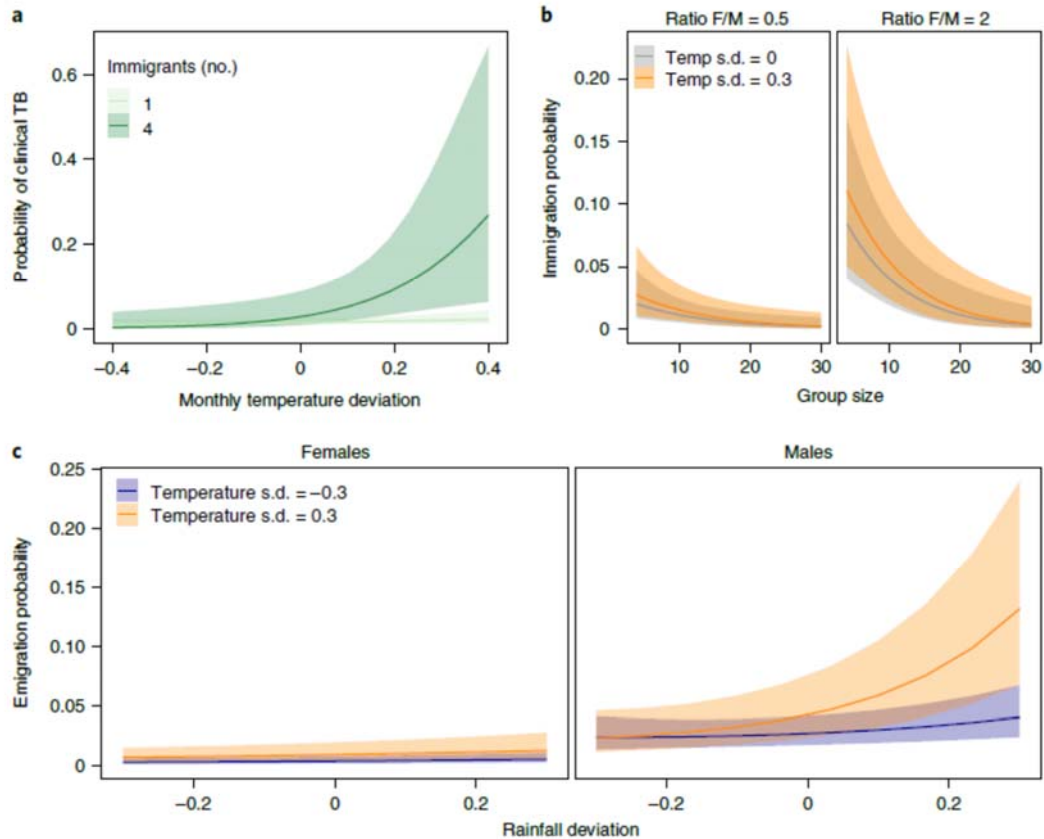


Fig. 3. Weather extremes impact the occurrence of clinical TB directly and indirectly via dispersal. **a–c**, Plots show predictions ($\pm 95\%$ prediction interval as shaded area) of GAM models for group-level processes (**a,b**) and sex-specific emigration (**c**) (see Supplementary Materials 1 and 3 for goodness-of-fit of predictions). Predictions were obtained by setting other predictors to their averages and month to 7 (corresponding to the highest numbers of immigrants). **b** and **c** show probabilities before the occurrence of the first clinical TB cases. Group size, number of individuals >6 months old. Ratio F/M, ratio of adult females to males. Weather effects show standardized deviations (s.d.) of maximum temperatures and rainfall from seasonal means.

Male immigration into groups is strongly positively affected by the ratio of females to males (Fig. 3b). This ratio is determined in part by differences in female and male emigration in response to climate. Most emigration in both sexes occurs at the start of the breeding season between July and September²¹, when pregnant dominant females evict subordinate females³⁵. A majority of these females return to their group under most climatic conditions³⁶. In contrast, males, emigrating voluntarily, more readily disperse permanently and over large distances. The readiness of males to emigrate is particularly high in above-average warm and wet springs (Fig. 3c), which are associated with higher body mass (Supplementary Material 1.3) and therefore higher survival during emigration^{36,37}. Climate change resulting in more frequent above-average temperatures may therefore affect the frequency of male emigration

relative to female emigration, which may decrease group sizes, increase the female/male ratio in groups, and thereby increase the chances of immigration of potential TB carriers (Fig. 3c and Supplementary Table 1.1).

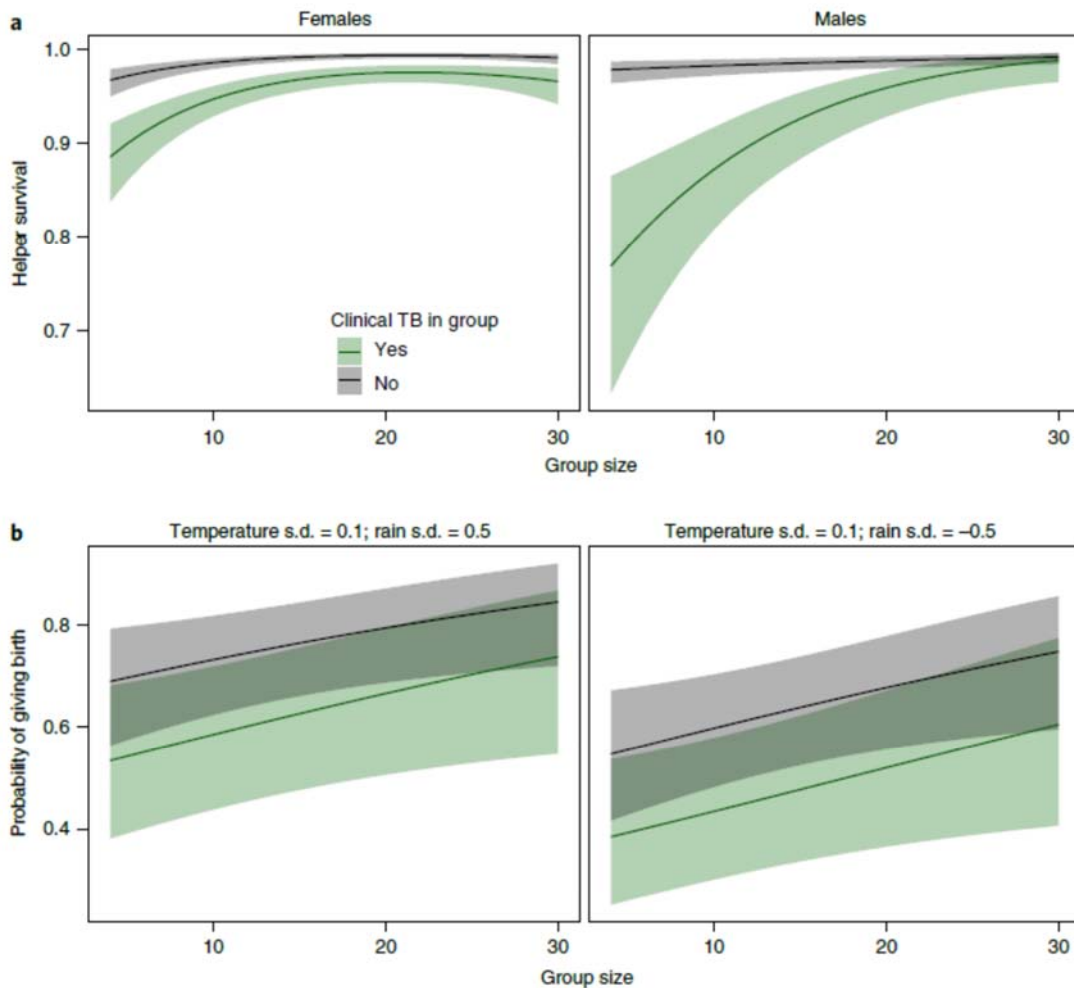


Fig. 4. Climate–TB interactions affect predictions of key demographic rates in meerkats.

a,b, Plots show predictions ($\pm 95\%$ prediction interval as shaded area) of GAM models for demographic rates identified to contribute most to group dynamics (see Supplementary Materials 1 and 3 for goodness-of-fit of predictions). Predictions were obtained by setting other predictors to their averages and month to 12 for seasonal effects. Group size, number of individuals >6 months old. Plot **b** shows reproductive output for dominant females. Weather effects show s.d. of maximum temperatures and rainfall from seasonal means.

Temperature extremes exacerbate demographic effects of TB

Effects of rainfall and temperature on meerkat demographic rates have been discussed in previous work and are summarized in Supplementary Material 1.2. Here we focus on novel aspects of how key demographic rates are simultaneously affected by the interactions of climate variation and disease. Once a group has at least one individual with clinical, end-stage TB, there is a rapid decrease in adult survival and reproductive success (Fig. 4a,b), which are principal drivers of group dynamics³⁸. Decreases in survival may be due to clinical TB worsening body condition (for example, lower body mass) (Fig. 2), which can be exacerbated

in small groups and adverse climatic conditions (Supplementary Material 1.3). This can make males, in particular, more susceptible to other causes of death during frequent roving expeditions, which are energetically costly²¹. More generally, TB infection rates are typically higher in males in many species, and has been linked to sex-specific immunological responses (reviewed in ref. 33). It has been shown in badgers (*Meles meles*) that males die at higher rates from TB³⁹, but in meerkats, sex-specific disease progression requires further investigation³⁴.

Similar to survival, an overall lower reproductive output of dominant females in TB-affected groups (Fig. 4b) may be due to decreases in energy available for reproduction under clinical TB²⁵; yet dominant females are the least likely members of the group to get TB²², hence this effect could be more due to the impact of TB on the other group members that help to raise offspring. Importantly, the decreases in reproductive output under clinical TB are exacerbated by weather patterns that may be more likely in a warmer future. The probability of successfully giving birth in the peak of the reproductive season (December) decreases when conditions are warmer and drier than when they are warmer and wetter (Fig. 4b). Such extremes lower the body mass of individuals (Supplementary Material 1.3) and negatively impact reproductive success³². Reproduction is also negatively affected by a reduced group size associated with clinical TB in groups (Fig. 2 and Supplementary Fig. 3.16), group size being a key determinant of reproductive success (Fig. 4b)³⁸.

Group extinction under climate change

To assess how the interaction between projected increases in maximum temperatures and clinical TB affects group persistence via their demographic effects, we parameterized an individual-based model (IBM) using GAMs³⁸. This allowed us to simulate emergent group dynamics from individual fates in discrete 1-month steps. We simulated the persistence of 10 groups, and initiated all simulations using different group characteristics, including group sizes (Extended Data Fig. 3 and Supplementary Table 3.1). In the IBM, groups have no clinical TB cases at the beginning of simulations. In each month, individuals go through life-cycle events (for example, survival, growth, reproduction, emigration or transitions through reproductive stages), with probabilities determined by predictions from the demographic-rate models (Extended Data Fig. 3). Males can then immigrate into a group. Finally, the group has a probability, determined by temperature deviations and number of immigrants, to become affected by clinical TB if previously not TB affected. The robust design of the GAM demographic-rate models translates into an accurate fit of IBM simulations to observed group and trait dynamics (Extended Data Figs. 4 and 5, and Supplementary Fig. 3.1), and projections showed a relatively low uncertainty due to parameter estimates (Supplementary Material 5).

We used the IBM to project the consequences of temperature–TB interactions on group dynamics under different scenarios of expected increases in maximum temperatures. We found that extinction probabilities increased under all scenarios and particularly when increasing the frequency of years with maximum temperatures above their seasonal average >10 months (Extended Data Fig. 6). Increases in such temperature extremes escalate the cumulative risk of group extinction (only one adult individual or no female adults) by up to 15 percentage points in 12 years compared with baseline projections assuming the absence of such extreme temperatures (Fig. 5 and Extended Data Fig. 6). However, under baseline projections, up to 50% of groups that were initially small (<7 individuals) go extinct within 2 years, and climate change has a negligible effect on extinction in this period (Fig. 5). This shows that stochastic mortality is a strong determinant of group persistence in small

groups⁴⁰, including newly formed ones where many extinction events occur before the manifestation of cumulative climate change and clinical TB effects³⁴.

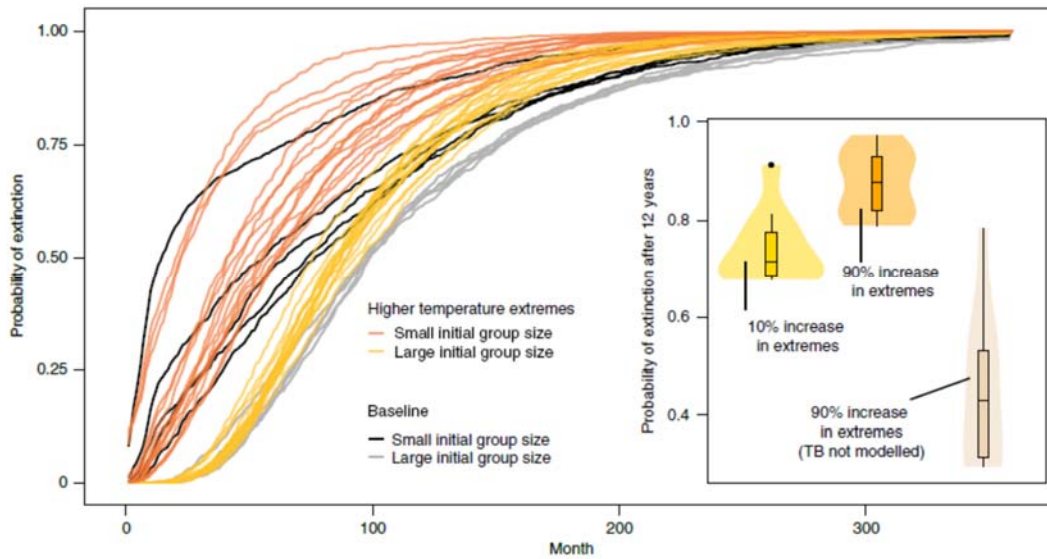


Fig. 5. Temperature–disease interactions under climate change destabilize meerkat groups. Lines show cumulative monthly extinction probabilities, calculated as the proportion of 1,000 IBM simulations where groups go extinct. Different line colours show simulations with different initial conditions (<7 and >10 individuals in initially small and large groups, respectively) under baseline simulations (years with the most extreme temperature deviations observed excluded) and under climate change simulations (increasing the frequency of years with temperature extremes to 0.45, 0.75, 0.90). Inset: comparison of climate change simulations to alternative simulations, that is, projecting climate change but omitting TB occurrence and its demographic effects in simulations. Box and whisker plots show the minimum, first quartile, median, third quartile and maximum extinction probability (point shows outlier) for ten different initial group conditions

Once chances of stochastic mortality decrease in larger, established groups, climate change progressively increases extinction risk (Fig. 5). This can have detrimental consequences for local population dynamics^{19,41} because established groups are the main breeding units providing new individuals to replace failed groups and keeping local population dynamics stable⁴². Along with higher extinction risk, the probability of TB occurrence in groups also increases under climate change, with >95% of baseline or climate-change simulations that end in extinction of established groups occurring after groups have shown clinical TB cases (Extended Data Fig. 7). This agrees with previous observations that TB is the main cause of failure of established groups²⁴.

All scenarios of increases in temperature extremes agreed with climate-change projections from global circulation models used by the IPCC (Extended Data Figs. 8 and 9). According to a majority of these models, the frequency of temperature extremes that are currently rare (<10% of years) is expected to increase >7-fold by 2100 in the Kalahari, assuming the intermediate and high greenhouse gas concentration pathways (Extended Data Fig. 10). At the same time, such pathways depicting the greatest levels of radiative forcing by 2100 are increasingly found to best reflect current trends of climate change⁴³. This indicates a high risk of climate–TB interactions leading to group failure in meerkat groups under future climate change.

The climate-change projections of group dynamics assume that weather patterns, as well as the probability of clinical TB, change through time. To test how much accounting for clinical TB in the projections impacted results, we refit demographic-rate models excluding TB status of the group as a predictor and projected group dynamics on the basis of a reparameterized IBM. Results from these projections indicate that the group extinction risk is underestimated by 20–50 percentage points when disease dynamics and their effects on demography are not accounted for explicitly (Fig. 5 inset and Supplementary Fig. 3.5). This provides direct evidence that species interactions, such as those between pathogens and host, can be critical in mediating climate effects on natural populations. Nonlinear dynamics in such interactions require an explicit consideration of these effects for robust inference^{44,45}.

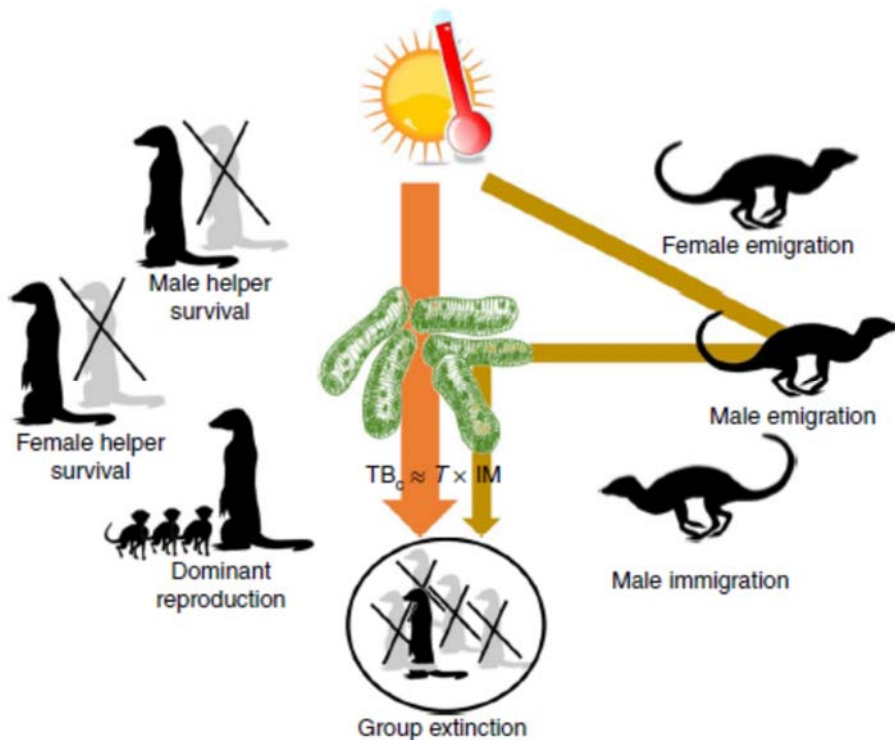


Fig. 6. Climate change increases group extinction via clinical TB outbreaks.

Arrows show increases in the probability of group extinction under different IBM perturbations, compared with a baseline IBM where climate change did not affect demographic rates, but clinical TB occurred in groups. Arrow size is proportional to effect size (Supplementary Table 3.3); no arrows, no effect of perturbing relevant demographic rate. Highest effects are seen in perturbations introducing higher temperature extremes (T) when predicting the probability of clinical TB occurrence (TB_c) or when predicting male emigration, which then affects TB occurrence by changing group size and composition and therefore immigration (IM).

Pathways of climate-change effects on group extinction

To gain a mechanistic understanding of climate impacts on meerkats, we explored the main demographic pathways through which climate change affects the persistence of established groups. We performed short-term perturbations, over the average lifespan of large established groups, of a baseline IBM that included clinical TB occurrence but no increases in temperature extremes. We then perturbed this IBM by introducing higher temperature

extremes when predicting the probability of clinical TB, or when predicting key demographic rates. These perturbations show that higher temperature extremes increase group extinction mainly by increasing the probability of clinical TB (Fig. 6). Similarly, temperature effects on demographic rates, which lead to changes in group sizes, increase group extinction only when such changes increase immigration and therefore the spread of TB carriers into groups. In comparison, perturbations of demographic rates that do not include alterations of clinical TB occurrence do not influence group extinction risk (Fig. 6).

Compared to baseline simulations, increases in group extinction were highest (>15%) when higher temperature extremes were included as a covariate in the predictions of clinical TB (Fig. 6; see Supplementary Table 3.3 for all effect sizes), highlighting the key role direct climate–disease interactions play on group persistence of this and probably other social species⁸. Nevertheless, the effects of climate change on dispersal patterns may be as important in determining group fates under disease dynamics^{46,47}. In the perturbation analysis, temperature effects on male emigration changed the probability of clinical TB via immigration and had the second strongest effect on group extinction. More frequent temperature extremes that increase male emigration (Fig. 3c) decrease the group size and increase the ratio of females to males in a group. Both processes are important (Supplementary Fig. 3.16a) in increasing immigration and subsequently the probability of clinical TB, leading to higher rates of group extinction (Fig. 6). These results show a potentially important role of male dispersal in disease dynamics and their effects on breeding groups, and suggest that males and their dispersal patterns should be considered more rigorously in demographic analyses⁴⁸.

Unlike effects via changes in the probability of clinical TB, temperature effects on key demographic rates did not impact extinction risk when the TB status of groups from the baseline simulations was maintained, that is, the probability of clinical TB did not increase (Fig. 6 and Supplementary Fig. 3.14). This may in part be because meerkats, as most mammals, have evolved complex demographic mechanisms to buffer climatic variation³². For instance, a lower dominant reproduction in drought conditions decreases group size, but adverse effects on groups can be offset by fewer helper females emigrating, as dominants may make reproductive concessions to quickly augment group size³⁸. However, as our results demonstrate, disease dynamics driven by climate change can destabilize demographic buffering in systems where compensatory recruitment does not follow increased adult mortality under disease⁴⁹, that is, when there is no strong negative density dependence in recruitment. For the meerkats, the resulting decreases in group size (Supplementary Figs. 3.16, 3.6–3.12) substantially increase the risk of extinction in groups that have clinical TB (Extended Data Fig. 7). Such climate–disease interactions also decrease the body mass of adults and make it more variable (Fig. 2 and Supplementary Fig. 3.13), which confirms that climate change may adversely affect group dynamics by decreasing body condition^{13,32}.

This work shows that nonlinear interactions between climate, disease outbreaks and demographic processes can substantially exacerbate negative impacts of increases in weather extremes on social mammals. It emphasizes that understanding the magnitude of climate-change effects on disease patterns is critical to assessing the vulnerability of natural populations to global change^{8,50,51}. Dispersal, in particular, may be a key factor driving increased individual and group risks of being adversely affected by disease¹⁵. More socially dynamic species may respond to changes in group dynamics under climate change, including increased impacts of pathogen infections, by more frequent movement of individuals between groups⁵². This can increase interactions between groups and facilitate the spread of

infectious diseases⁵³. In turn, an increased disease incidence often has particularly negative effects on the demography of adults, threatening those individuals that are typically buffered from climate effects on physiology or food availability^{54,55}.

When increased recruitment can compensate for disease-related adult mortality, infectious disease can persist in social mammals⁴⁹. Even the cooperatively breeding meerkats, where adult mortality may jeopardize future recruitment, have co-evolved with *M. suricattae*, leading to chronic infections that can remain undetected for years²³. However, for a wide range of animals, climate change is likely to worsen the health conditions and reproductive output of individuals through adverse effects on physiology and resources¹. This may lead to increases in fatal diseases from chronic infections that cannot be sufficiently compensated by recruitment⁷. Such climate–disease interactions may be particularly relevant for TB, which is a global health threat to humans, wildlife and domestic animals. While research has focused on shifting ranges of biological vectors of infectious disease⁵, this work suggests that insights into the demographic pathways that may more generally determine the prevalence of infectious diseases under climate change are also needed for a wider range of species.

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Methods

Study system. The IBM was parameterized using data from a population of habituated, wild meerkat groups around the Kuruman River Reserve, South Africa (KRR, 26°58' S, 21°49' E). The habitat is characterized by seasonal variation and high interannual unpredictability in rainfall and temperature. Reproduction is mostly confined to the rainy season between August and April and is least frequent in June–July, in the middle of the dry season⁵⁶. Subordinate female helpers can emigrate to form new groups³⁶, while female immigration into an existing social group is extremely rare⁵⁷. Subordinate males emigrate voluntarily from their birth groups after reaching sexual maturity and either immigrate into established breeding groups or found new breeding groups with dispersing females. For details on the study system, see Supplementary Material 1.

Annual rainfall in the southern Kalahari is low (typically <250 mm yr⁻¹) and is extremely variable. In the 22 years of demographic data collection, the Kalahari meerkats have experienced a variety of rainfall conditions, including extreme drought events¹³. Annual daytime temperatures vary throughout the year, with maximum temperature reaching <25 °C in July to >40 °C in January, and have increased over the last 22 years. Rates of predation are high (20–25%) across all group members⁵⁶, and an endemic form of TB, *M. suricattae*, has been continuously present in the population and directly causes an additional 6% deaths of the total adult population per year^{24,25}. These factors create ideal conditions to explore how interactions between climate change and disease can predict group dynamics.

Life-history data. During weekly visits, data on birth, death, emigration, reproductive condition, body mass and social status were collected from individually tagged meerkats²¹. We used the individual-level data of 1,194 females and 1,497 males from 85 groups to generate monthly, discrete-step censuses of individuals between 15 January 1997 and 15 December 2018, following the approach in refs. ^{32,38}. At the beginning of each monthly census, we recorded which individuals survived from the previous month and remained in a group. We determined emigration from a group on the basis of the observed behaviour of individuals, such as increases in roving expeditions or extended absences from groups of female coalitions^{32,38} (for sensitivity analyses of how emigration vs death assignment affected results, see Supplementary Material 4). We also recorded which individuals entered a group as adult male immigrants or offspring born into a group. From this information, we calculated 'effective' group size, that is, number of individuals >6 months old, which engage in cooperative behaviour⁵⁸. We also estimated body mass for each individual at the beginning of a monthly census, as body mass is an important trait mediating demography (see Supplementary Material 1).

Climate data. Interannual deviations from the seasonal means in rainfall and temperature were calculated from long-term gauge and satellite data obtained from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (CPC) available at <https://psl.noaa.gov/data/gridded>. These data were also used to produce Fig. 1 and Extended Data Fig. 1. To calculate monthly deviations of weather used in demographic-rate models, we first obtained total daily rainfall (using the GPCP Version 2.3 Combined Precipitation Data Set)⁵⁹ and the mean of the maximum daily temperature (using the CPC Global Temperature data) of the 1.5 months before each census. For both variables, we then created standardized deviations from monthly means (for details, see ref. 32). We chose the 1.5-month window as it accurately accounts for lagged effects of environmental factors on life-history processes in meerkats³⁸.

To assess how likely the projections using observed weather trends (that is, sampling years with increasingly more extreme temperature deviations, see 'IBM projections') are under projected climate change from global circulation models, we obtained future estimates of maximum

temperatures from the Coupled Model Intercomparison Project 5 (CMIP5) used by the IPCC60. All data are freely available online at the World Climate Research Programme (<https://esgf-node.llnl.gov/projects/cmip5/>). The CMIP5 provides projections from a suite of global circulation models (GCMs). These GCMs produce climate projections for four atmospheric greenhouse gas Representative Concentration Pathways (RCPs): one high pathway with radiative forcing up to 8.5 W m⁻² by 2100 (RCP 8.5), two intermediate pathways (RCP 4.5 and RCP 6.0) and one low pathway (RCP 2.6). We downloaded projections (2006–2100) of monthly mean maximum temperatures ('tasm_{max}') from 21 GCMs using simulations for ensemble 'r1i1p1', as this ensemble generally provided the best representation of the present climate⁶¹. We used maximum temperature values that were interpolated at the grid point closest to the centre of the study site (using average values interpolated at the two closest grid points did not change results; Supplementary Material 3.2). To cover the entire range of past observed meerkat population dynamics (1997–2018), we also obtained reconstructed historical simulations (1997–2005). We visually ensured that the GCMs produced past maximum temperatures in the range of estimates by the CPC data used to model demographic rates.

TB in meerkat groups. In the study population, the pathology of the meerkat-specific *M. suricattae* infection has been studied since 1996. In the absence of a viable biomarker, visual clinical signs, mainly submandibular swellings, have been used to identify clinical TB^{23,25,34}. Although we did not confirm that every lump was TB at the time of first clinical TB cases, studies confirmed >80% of cases through mycobacterial culture from clinical samples collected during life or later when the animals died^{23–25}. We used available information on periods when clinical TB was first observed in meerkat groups to assign first dates of clinical disease to each group in the dataset. This approach therefore assumed TB to be a group-level variable. If members of a group showed clinical TB signs, the group was characterized as 'TB affected', and once affected by clinical TB, we assumed that TB persisted in the groups until group failure (similar assumptions have been made to model *Mycobacterium* infections in badgers^{62,63}). In the absence of exact periods of individual clinical TB occurrence for all adults across the study period, this was the most robust characterization of clinical TB, and has been shown to provide an effective measure in other systems⁶⁴. Nevertheless, as stage-specific demographic rates and the effects of all considered predictors on these rates differed depending on group TB status, we implicitly accounted for stage-specific differences in the effects of clinical TB.

The meerkat-specific TB strain was initially identified as bovine TB and was thought to be a by-product of cattle ranching. A practice of euthanizing individuals whose lymphatic swellings ruptured, a sign of late-stage TB, was therefore implemented and has been maintained to reduce the impact of the disease³⁴. The effectiveness of the euthanasia policy is unclear, but it is likely that the results of this study represent an underestimate of the impact of clinical TB on the population²⁴.

We modelled the probability of clinical TB occurring in a group in any given month as a function of group size, number of immigration events, female/male ratio, season, rainfall and temperature deviation, and two-way interactions of these predictors using the same GAM parameterization approach as for the demographic rates (see Modelling demographic responses to climate–TB interactions). Before fitting the main effects and their interactions with several predictors, we first tested for the best temporal lag (summing or averaging predictor values over 1–15 months) that explained the effect of each predictor on the monthly probability of clinical TB. Results indicated that group size at the beginning of a month and the total number of immigrants over the past 5 months best explained the probability of clinical TB³⁴.

Modelling demographic responses to climate–TB interactions. To gain a mechanistic understanding of the processes affecting meerkat group dynamics, we analysed the drivers of demographic rates including survival, growth, reproduction, recruitment, stage transitions, emigration and immigration (both the probability of a non-native male entering a group at the beginning of a monthly census and the number of males entering; Supplementary Material 1). We fitted all models using GAMs to account for nonlinear additive and interaction effects³². GAMs were fitted separately for each life-history

stage, including pups (aged 1–3 months), juveniles (4–6 months), subadults (7–12 months), adult (>12 months) dominant breeding females (that were either natal animals or founding members of the group), dominant breeding males (that were always immigrants) and helpers (that were mostly natal animals together with a small number of immigrant subordinate males (on average 10% of all adults in a group)) (Extended Data Fig. 2). Adult females were further subdivided into three pregnancy categories (Extended Data Fig. 2 and Supplementary Table 1.1). As male adult helpers and natal dominants do not differ in survival, we modelled their demographic rates jointly (as adult helpers).

We tested for additive and two-way interaction effects of individual factors (body mass, age), social factors (group size, female/male ratio, number of immigrant males), deterministic seasonal fluctuations (month-of-year) and stochastic climate (rainfall and temperature) deviations from these fluctuations on demographic rates. We also tested whether these effects differed depending on the TB status of a group. Lastly, we included year as a random effect in all models to account for interannual variation not captured by the other variables (adding a further group ID random effect did not improve the model fit for most demographic rates and led to convergence problems). Selection of the most parsimonious GAM structure was based on Akaike's information criterion (AIC)⁶⁵, where we chose the model with a higher number of parameters only if the more complex model decreased AIC by >2. All analyses were implemented in R version 4.0.0 using the 'mgcv' package⁶⁶ to fit GAMs (Supplementary Material 1).

Results from the most parsimonious GAMs reflect previous published findings^{32,38,58} and are summarized in Supplementary Material 1.1. In the main text, we describe novel aspects of how key demographic processes are simultaneously affected by the interactions of climate variation and disease.

Group extinction under climate change. We constructed an IBM on the basis of the most parsimonious model structure for each demographic rate following ref.³⁸. The IBM allowed us to simulate emergent group properties from individual fates (Extended Data Fig. 3). We provide the detailed overview, design concepts and details (ODD) protocol of the IBM⁶⁷ in Supplementary Material 2.

Each simulation run of the IBM follows individuals in discrete one-month steps. Each individual is characterized by state variables, which include an ID and all the parameters necessary to fit demographic-rate models. Individuals survive, and conditional on survival, change mass, reproduce, emigrate from the group and change stage from one time-step to the next on the basis of these state variables (Extended Data Fig. 2). If the dominant female dies, the oldest adult female helper takes its place; if there are >1 potential successors of the same age, the heaviest one replaces the dominant. Upon death or emigration of the dominant male, the oldest and, if there are >1 potential candidates, the heaviest resident immigrant male gains dominance. If no resident immigrant male is available, the oldest and heaviest natal male gains dominance²¹. If no adult males are in a group, a new male immigrant gains dominance. At the end of each time-step, males can immigrate into a group, and the group can become TB affected if previously without clinical TB cases. A group is considered extinct if it consists of a single adult or if all adults are males, corresponding to minimum observed numbers in the empirical life-history data.

The IBM implements demographic stochasticity by treating survival, emigration, immigration and pregnancy as binomial probability events, and recruitment as a Poisson count event. Stochasticity in clinical TB is implemented by treating TB occurrence as a binomial probability event. We also implemented non-parametric bootstrapping to assess the contribution of parameter uncertainty to IBM outputs (see Supplementary Material 5).

To initiate simulations, we used observed initial characteristics, for example, female/male ratio, individual age, from 10 groups. Five of these groups had <7 individuals (small initial group sizes) and the other five had >10 individuals (intermediate to large initial sizes; Supplementary Table 3.1). After each simulation run, we recorded the following metrics summarizing group dynamics: group

extinction and clinical TB probabilities; group lifespan (months to extinction); average, and coefficient of variation in group size, numbers of female and male adults, and adult body mass; reproductive success (average number of pups surviving to adulthood); and monthly average numbers of emigrants and immigrants.

We visually assessed the performance of the IBM by comparing outputs of simulations to observed data following ref. ³⁸; that is, starting at a specific date on which each of the 10 groups was observed (between 15 January 1997 and 15 January 2013), we projected individual fates using past observed rainfall and temperature deviations for the lifespan of a group or until the end of 2018 using 1,000 simulation runs. We also assessed how much accounting for weather deviations and clinical TB occurrence in the GAMs improved the predictive power of the IBM. To this end, we reparameterized demographic-rate models excluding either rainfall and temperature deviations, group TB status or all three as predictors and reran all IBM simulations with the altered model structures. We then used the synthetic likelihood approach⁶⁸ to compare the output metrics from the different implementations of IBMs to observed data³⁸ (Supplementary Material 3).

IBM projections under increases in temperature extremes. To test the sensitivity of group dynamics to temperature extremes, we projected group dynamics using four scenarios of increasingly more frequent above-average temperatures. These scenarios delimited ‘hot years’, that is, temperature deviations above their long-term average for >6, 7, 8, 9 or 10 months of the year (1997–2018). When projecting, these years were randomly sampled (we did not detect autocorrelation GAM model residuals or year random effects) with a probability of 0.6 or 0.9, and we simulated group dynamics sequentially using temperature and rainfall deviations for all months of a given sampled year to predict demographic rates from GAMs, as well as clinical TB occurrence. We compared a key metric, group extinction (as defined above in ‘Group extinction under climate change’), from these projections and a baseline scenario, where we exclusively sampled the remaining years not delimited as hot years. Sampling entire years, as opposed to perturbing temperature deviations for each month, allowed us to maintain within-year correlations of the monthly sequence of rainfall and temperature deviations – and therefore produce projection results that were tractable in their interpretation. Projections ran for 360 months (30 years), which is approximately twice the length of the observed group age of the longest persisting groups in the study population.

Results from the IBM projections of sensitivity to temperature extremes showed that group extinction increased strongest when extreme years (temperature deviations >0 for more than 10 months) were sampled (Extended Data Fig. 6). We therefore repeated more detailed projections of these extremes, sampling them with probabilities of 0.1 (corresponding to their observed frequency in 1997–2018), 0.45, 0.75 and 0.9 (corresponding to the range of increases in frequency projected by the 21 GCMs; see Likelihood of temperature extremes under IPCC projections).

Likelihood of temperature extremes under IPCC projections. To assess how likely the scenarios of increasingly more frequent above-average temperatures were to occur in the future, we calculated changes in the frequency of prolonged temperature extremes for each GCM and RCP. We first quantified future standardized deviations in maximum temperatures (2019–2060) from monthly means calculated over the period 1997–2018 (past conditions). We then calculated the frequency of hot years, as defined in IBM projections under increases in temperature extremes, for the past (1997–2018), by mid century (2041–2061) and by end century (2079–2100). Finally, to assess the risk of climate-change impacts⁶⁹, we calculated the proportion of projections, across all GCM and RCP combinations, in which the frequency of hot years (as defined in our scenarios) at least doubled by the mid and end century compared to their current frequency (for details, see Supplementary Material 3.2).

Pathways of temperature effects on group extinction. To explore the pathways through which higher temperature extremes may act on group dynamics, we assessed the effects of introducing climate

change on group quasi-extinction when predicting the probability of clinical TB occurrence or when predicting key demographic rates. We first simulated group dynamics starting with medium and large initial group sizes (as stochastic mortality was large in very small groups) for 12 years (the lifespan of large established groups) using 1,000 iterations of a baseline IBM, where extremely hot years (2015 and 2016) were excluded from projections and groups could change TB status, that is, clinical TB probability was predicted. We kept a record of the years sampled and monthly TB status (no clinical TB or TB affected) during these simulations. We then repeated the iterations of this baseline IBM, but introduced climate-change effects in specific submodels of the IBM, that is, sampling weather from 2015 and 2016 with a probability of 0.75, which corresponds to the scenario of increasing temperature extremes to which group dynamics were most sensitive (Extended Data Fig. 6). We introduced these climate-change effects in the clinical TB probability model. We also introduced climate change in single demographic-rate models, first repeating the monthly TB status of the baseline IBM, that is, without changing clinical TB occurrence. We then allowed for TB occurrence to change (that is, predicting the probability of clinical TB in each iteration of a simulation) when perturbing a demographic rate. Non-perturbed demographic rates were simulated under the same sequence of years as in the baseline IBM. The perturbed demographic rates included male and female helper survival and emigration, dominant reproductive output (probability of giving birth) and male immigration probability, as these have been shown to have an important influence on group sizes, which ultimately affect extinction^{32,38} either directly or by favouring immigration and therefore clinical TB occurrence (see also Supplementary Material 3.4).

We assessed the effect of each climate-change pathway perturbation by fitting generalized linear mixed models, where we modelled the probability of group extinction (binomial response) as a function of IBM perturbation (fixed effect, with baseline IBM as intercept comparing the remaining perturbations to the baseline), with initial group size as a random effect. Additional IBM perturbations that monitor different output metrics and ones that assess climate effects via changes in group size and composition can be found in Supplementary Material 3.

Data availability

All data to construct and project the individual-based model have been deposited on Zenodo: <https://doi.org/10.5281/zenodo.5784649>.

Code availability

All R scripts to construct and project the individual-based model have been deposited on Zenodo: <https://doi.org/10.5281/zenodo.5784649>.

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Author contributions

T.C.-B. and M.M. led the long-term study and data collection; M.P., A.O. and T.C.-B. conceived the ideas for the paper and its structure; M.P., C.D. and F.G. designed the analyses; M.P. conducted the analyses with help from A.O. and wrote the manuscript; J.A.D. guided the TB epidemiology aspects of the study; all authors discussed the results and commented on the manuscript.

Competing interests

The authors declare no competing interests.