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RESEARCH ARTICLE

Is climate change causing the range contraction of Cape Rock-jumpers (*Chaetops frenatus*)?

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Abstract

Species distribution models often suggest strong links between climate and species' distribution boundaries and project large distribution shifts in response to climate change. However, attributing distribution shifts to climate change requires more than correlative models. One idea is to examine correlates of the processes that cause distribution shifts, namely colonization and local extinction, by using dynamic occupancy models. The Cape Rock-jumper (*Chaetops frenatus*) has disappeared over most of its distribution where temperatures are the highest. We used dynamic occupancy models to analyse Cape Rock-jumper distribution with respect to climate (mean temperature and precipitation over the warmest annual quarter), vegetation (proportion of natural vegetation, fynbos) and land-use type (protected areas). Detection/non-detection data were collected over two phases of the Southern African Bird Atlas Project (SABAP): 1987–1991 (SABAP1) and 2008–2014 (SABAP2). The model described the contraction of the Cape Rock-jumper's distribution between SABAP1 and SABAP2 well. Occupancy probability during SABAP1 increased with the proportion of fynbos and protected area per grid cell, and decreased with increases in mean temperature and precipitation over the warmest annual quarter. Mean extinction probability increased with mean temperature and precipitation over the warmest annual quarter, although the associated confidence intervals were wide. Nonetheless, our results showed a clear correlation between climate and the distribution boundaries of the Cape Rock-jumper, and in particular, the species' aversion for higher temperatures. The data were less conclusive on whether the observed range contraction was linked to climate change or not. Examining the processes underlying distribution shifts requires large datasets and should lead to a better understanding of the drivers of these shifts.

KEYWORDS

avian demography, climate change, population demography, species range limits, statistical modeling

INTRODUCTION

Climate change has contributed substantially to the extinction (Pounds et al., 1999; Román-Palacios & Wiens, 2020) and population declines (Huntley et al., 2006; Jetz et al., 2007; Parmesan & Yohe, 2003) of species worldwide. Given a rapidly changing climate and climate change's

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long-term negative effects on biodiversity, it is of critical importance to quantify how climate change affects species' distributions and population dynamics. This information can be used for biodiversity protection and forms an important component to conservation strategies and planning (Araújo & Guisan, 2006; Hannah et al., 2002).

One way to measure how species are affected by climate and land-use change is to measure the suitability of a particular habitat for a species, with respect to climate and land uses. Typically, species distribution models (SDMs) have been used to model species' habitat suitability and have been applied over a wide range of disciplines (e.g. Elith & Graham, 2009; Morin et al., 2009). SDMs relate species' known presences to associated environmental conditions and use these relationships to project their distributions into the future (Araújo & Guisan, 2006; Dormann et al., 2007; Elith & Leathwick, 2009). However, mainstream, SDMs do not account for: (i) detection probability and (ii) the dynamic nature of species' distributions. In reality, no species is detected perfectly within all the habitats it occupies (MacKenzie et al., 2002). Failure to account for detection probability can result in underestimates of occupancy as well as biased relationships between occupancy probability and environmental conditions (Altwegg et al., 2008; Guillera-Aroita et al., 2015; Kéry, 2011; Lahoz-Monfort et al., 2014). Furthermore, using SDMs to project distributions under future climate scenarios assumes that a species currently is in equilibrium with its environment and that the environment is suitable where the species occurs and unsuitable where it does not occur (Araújo & Townsend Peterson, 2012; Hirzel et al., 2001; Yackulic et al., 2012). The equilibrium assumption is violated where species lag behind the changing climate and can lead to biased inference about environmental suitability (Clement et al., 2016; Yackulic et al., 2015). Huntley et al. (2010) therefore called for a more mechanistic approach to modelling species distributions. They suggested modelling environmental suitability, population dynamics and dispersal as separate modules (Huntley et al., 2010). Such an approach, however, requires detailed data that are not readily available for most species.

A slightly less mechanistic approach is to examine species' distribution dynamics by taking a metapopulation view and studying colonization and extinction at local sites using dynamic occupancy models (Altwegg et al., 2008; Bled et al., 2013; Yackulic et al., 2015). Colonization probability is defined as the probability that a previously unoccupied site becomes occupied, and extinction probability is the probability that an occupied site becomes unoccupied (MacKenzie et al., 2003; Royle & Kéry, 2007). Dynamic occupancy models estimate extinction and colonization directly (Kéry, 2011; Royle & Kéry, 2007). Modelling colonization and extinction directly allows researchers to examine the dynamics that lead to observed species' distributions. The power of this approach is that it allows researchers to examine the mechanisms underlying distribution dynamics and look for evidence that it may be caused by climate or land-use change.

The Cape Rock-jumper (*Chaetops frenatus*) is a medium-sized insectivorous bird, indigenous to the Western Cape of South Africa, for which land-use change and climate change pose significant extinction threats (Lee & Barnard, 2016). The Cape Rock-jumper actively avoids human-dominated land-use types such as urban and agricultural areas, and strictly inhabits the natural vegetation of the region (fynbos). Furthermore, its conservation status was recently up-listed to 'Near Threatened' in South Africa (Taylor et al., 2014), and as a result, it will probably be more dependent on protected areas for survival. Therefore, this species is likely to be negatively impacted by the loss of pristine natural habitat. The Cape Rock-jumper is vulnerable to increases in temperature caused by climate change (Milne et al., 2015); its threshold for increasing evaporative water loss at high

temperatures is relatively low compared with other birds in the region. The Cape Rock-jumper has decreased markedly in abundance and distribution extent over recent decades, indicating that a hotter and drier climate in future could pose a significant extinction risk. In this study, we examine the possible effect of climate on the Cape Rock-jumper's distribution and recent contraction. We have the following expectations:

1. If climate is limiting the distribution of the Rock-jumpers, as the physiological data suggest (Milne et al., 2015), we predict that the Rock-jumpers should be more likely to occur in the cooler and wetter parts of our study area.
2. If climate change has caused the apparent range contractions over the last two decades, we predict that the species disappeared from the hottest and driest parts of its distribution; the extinction probability increases with increasing temperature and decreasing rainfall.

METHODS

Study area and species

Our study area is situated in south-west South Africa, primarily in the Western Cape province (Figure 1), encompassing the entire distribution of the Cape Rock-jumper. This area experiences a Mediterranean climate: austral winters (June–August) are wet and cool and summers (December–February) are dry and hot (van Wilgen et al., 2016). Mean annual rainfall ranges from 150mm in the driest of regions (Karoo desert, situated inland) to about 2000mm in the mountain range that is situated along the

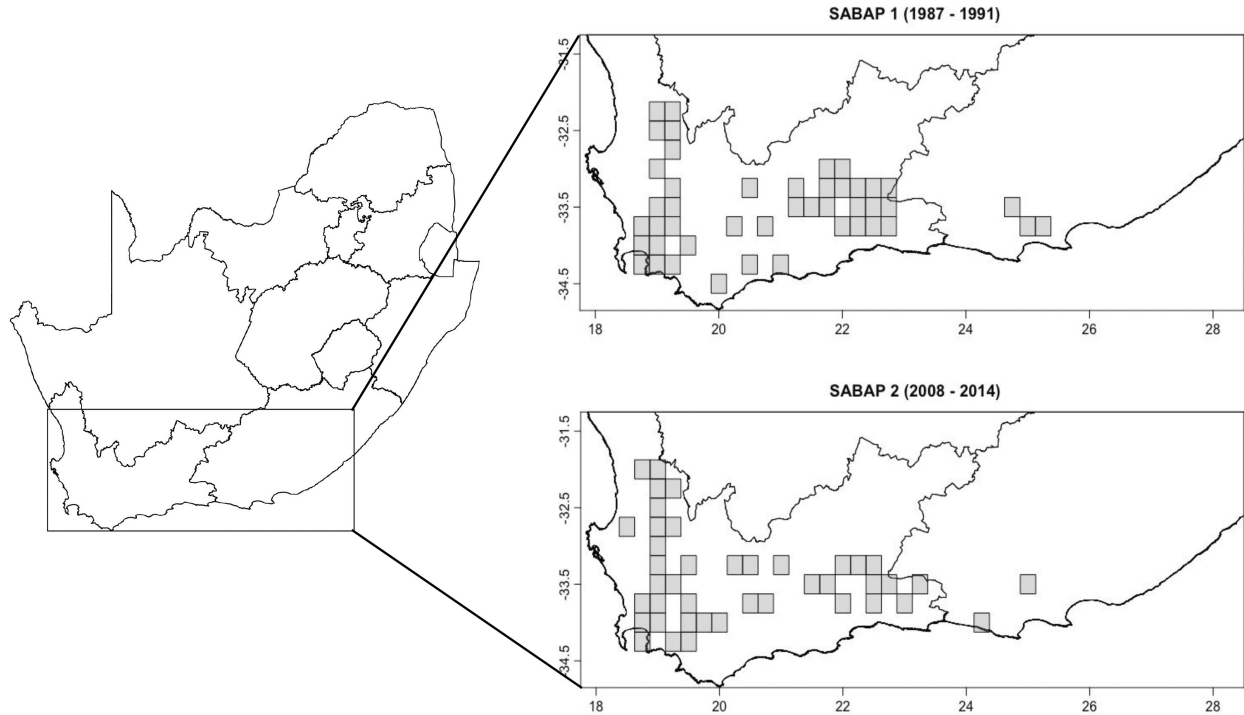


FIGURE 1 Raw detection data of the Cape Rock-jumper (*Chaetops frenatus*) from 1987 to 1991 (SABAP1) and 2007 to 2014 (SABAP2) across its entire distribution in the greater Western Cape region of South Africa. The location of the Western Cape is shown by the box outline in relation to South Africa. Data are taken from the two phases of the Southern African Bird Atlas Project (SABAP). Grey squares indicate quarter-degree grid cells (QDGCs, 15' × 15' arcminutes) in which the species has been recorded at least once during a particular time window. These are raw data and thus provide a biased indication of the real distribution. The study area is made up of 354 QDGCs, which cover approximately 200 000 km².

south-western coast of the study area. Temperatures are generally mild along the coast and rarely exceed 40°C or drop below freezing. However, temperatures become more extreme inland and in the Karoo desert, where average daily minimum temperatures in winter are –6°C, whilst average maximum temperatures are in the mid-30s during summer, but can often exceed 40°C. The landscape is characterized by extensive, rugged mountain ranges, composed of mostly granite and sandstone with large rocky outcrops. The vegetation in the region is characterized as fynbos, which is made up of sclerophyllous shrubs, and very few tall-growing endemic trees.

The Cape Rock-jumper is a medium-sized bird (20–25 cm in length) and primarily feeds on insects (Frazer, 1997). It is a conspicuous bird with a far-carrying and unique call, making it readily detectable when present.

Data

Detection/non-detection data (Bird atlas data)

Detection/non-detection data for the Cape Rock-jumper were obtained from a citizen science project conducted in southern Africa to monitor the distributions of bird species, namely the South African Bird Atlas Project (SABAP, Brooks et al., 2022). SABAP were collected in two phases: between 1987 and 1992 (SABAP1), and since June 2007 (SABAP2, still ongoing in 2023). For this study, we used detections recorded from January 1987 to December 1991 for SABAP1, and from January 2008 until December 2014 for SABAP2. In both phases of the project, volunteers surveyed pre-defined sampling areas over a fixed time period and submitted checklists of all bird species seen or heard. Only the presence of a species was recorded, not the number of birds seen or heard. During SABAP1, data were collected on a quarter-degree grid cell level (QDGC; 15' × 15' arcminutes in spatial resolution, which is an area of approximately 550 km², Harrison et al., 1997). Data collection during SABAP2 is on a pentad scale (5' × 5' arcminutes, covering approximately 63 km², one-ninth of a QDGC).

Most of the data were collected by volunteers birding intensely for a few hours on a single day, although volunteers were allowed to add species to their checklists for up to and including 30 days in SABAP1, and 5 days in SABAP2. The protocol for SABAP2 further required volunteers to have birded intensely for at least 2 h. In both projects, the data were vetted by a committee (Frazer, 1997; Harebottle et al., 2007). For the data analysis, SABAP2 data were pooled over the nine pentads that make up a QDGC in order to compare data at the same scale for the two atlas projects (as data for SABAP1 were on a QDGC scale). Our study area consisted of 354 QDGCs, which corresponded to an area of approximately 195 000 km². See [Figure S1](#) for the sampling effort during each SABAP.

Climate data

Variable selection

Lee and Barnard (2016) modelled the distribution of Cape Rock-jumper between 1987 and 2013 as a function of temperature and rainfall. They found the mean temperature over the warmest annual quarter (a consecutive 3-month period for which the average temperature is the highest in a 12-month calendar year) was the most significant variable limiting the Cape Rock-jumper's distribution. Following Lee and Barnard (2016), and given the inability of the species to cope with prolonged periods of high

temperatures (Milne et al., 2015), we selected the mean temperature during the warmest annual quarter as a climate covariate in our analysis.

Higher mean temperatures brought about through climate change lead to more water being lost to the environment via evaporative water loss, affecting the Cape Rock-jumper. For this reason, we selected precipitation over the warmest annual quarter to represent water availability over the warmest period (when evaporation demands of Cape Rock-jumper are the highest) as an additional climate covariate in our analysis.

Data sources and computation

We sourced daily data for rainfall and minimum and maximum temperature from the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP) dataset (Thrasher et al., 2012). The data are derived from the General Circulation Model (GCM) runs performed under the Coupled Model Intercomparison Project Phase 5 (CMIP5) for the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5). The dataset contains data downscaled to a spatial resolution of 0.25 degrees (~25 km × 25 km) using the Bias-Correction Spatial Disaggregation (BCSD) method for statistical downscaling. We selected one GCM that is deemed to perform well over South Africa (C. Leonard, personal communication), the GFDL-CM3 (Donner et al., 2011) and extracted the data for this model's historical experiment for the period between 1986 and 2005.

Computation of climatic data

We first identified the warmest annual quarter of the year: For each day of each calendar year, we calculated the mean temperature as the mean of the daily maximum and minimum. We then calculated the monthly mean as the mean of the daily means. Thereafter, we scanned all monthly means within a calendar year and identified a consecutive 3-month period for which the 3-monthly mean was highest; this period was identified as the warmest annual quarter of each calendar year. Because we allowed the warmest quarter of the year to constitute any consecutive 3-month period of the calendar year, the warmest quarter of the year may not constitute the same 3-month period each calendar year.

For precipitation, we summed the daily precipitation for each warmest annual quarter to obtain total precipitation over the warmest quarter. For temperature, over each of the quarters, we averaged the monthly temperature means to obtain the mean temperature over the warmest quarter for each calendar year.

Land-use type data

The Cape Rock-jumper is endemic to the fynbos region and generally avoids human-dominated landscapes (Frazer, 1997). Loss of natural fynbos habitat could potentially limit its persistence. Thus, we included the percentage of each QDGC that is occupied by fynbos vegetation as a continuous covariate in our modelling framework (data from Mucina & Rutherford, 2006).

The conservation status of Cape Rock-jumper is 'Near threatened' (Taylor et al., 2014), and the species' persistence may critically depend on protected areas. Thus, we also included the proportion of a QDGC that is officially protected (private and public) as a covariate within our modelling framework. These data were obtained from the South African national land-cover dataset (South African National Biodiversity Institute, 2009), which computed the total land-cover uses over the whole of South Africa as of 2009, and were included as a continuous covariate in the model.

Model structure and details

A dynamic occupancy model was used to analyse the distribution of the Cape Rock-jumper. Dynamic occupancy models are a suite of models that account for the detection process in detection/non-detection data (MacKenzie et al., 2002). During atlas surveys, a species is not always detected in areas where it really does occur (these cases are referred to as false negatives), and ignoring the issue of detection in species' distribution models can potentially produce biased results (Altwegg & Nichols, 2019). Dynamic occupancy models incorporate the detection process into the modelling framework by allocating a separate component to model the detection probability explicitly. Dynamic occupancy models differ from simpler single-season occupancy models in that they can estimate the changes in species' occupancy probability over time (i.e. between seasons). A season can be a specified period of any reasonable length during which the occupancy status of a site is assumed to stay constant. Changes in occupancy probability over time are calculated by estimating the dynamic components, colonization and persistence between each season. To estimate these components, it is necessary to collect repeated detection/non-detection data for each season over the duration of the study.

Initial occupancy, which is the probability that site i is occupied in season 1 is $\psi_{i,1}$, and the occupancy state $Z_{i,1}$ (0 if unoccupied and 1 if occupied) follows a Bernoulli distribution:

$$Z_{i,1} = \text{Bernoulli}(\psi_{i,1}) \quad (1)$$

For all later seasons, ($t=2, 3, 4, \dots, T$) occupancy probabilities at site i are a function of the previous season's occupancy probability, and the dynamic components extinction (ϵ) and colonization (γ). Extinction probability refers to the probability site i is unoccupied at season t , given it was occupied at season $t-1$. Colonization probability is defined as the probability a species occupies site i at time t , given the site was unoccupied at season $t-1$. These are linked by the following equation:

$$Z_{i,t} = \text{Bernoulli}(Z_{i,t-1} \times (\gamma_{i,t-1}) + (1 - Z_{i,t-1}) \times \epsilon_{i,t-1}), \text{ for } t > 1 \quad (2)$$

ϵ and γ can depend on season- and site-specific covariates (MacKenzie et al., 2003). The model allows for extinctions and colonization events between seasons, but sites are assumed to remain either occupied or unoccupied during each season.

Here, we model the distribution of the Cape Rock-jumper in two seasons; we consider SABAP1 the first season and SABAP2 the second season. We assume demographic closure within each phase of SABAP; the Cape Rock-jumper is a resident endemic to the region, generally occurs in groups and can be territorial, suggesting relative stability from year to year (and potential lags behind climate change).

Occupancy during SABAP1 was modelled in the following form:

$$\text{logit}(\psi_{i,1}) = \beta_0 + \beta_1 \times \text{PA}_i + \beta_2 \times \text{Fynbos}_i + \beta_3 \times \text{Temp}_i + \beta_4 \times \text{Precip}_i \quad (3)$$

where for site i , Temp_i is the mean temperature over the warmest annual quarter, and Precip_i is the precipitation over the warmest annual quarter, both averaged over the period 1986–1990 (Figure 2). PA_i and Fynbos_i represent the proportion of site i occupied by protected area and fynbos vegetation respectively.

Colonization was modelled in the following form:

$$\text{logit}(\gamma_{i,1}) = \beta_5 \quad (4)$$

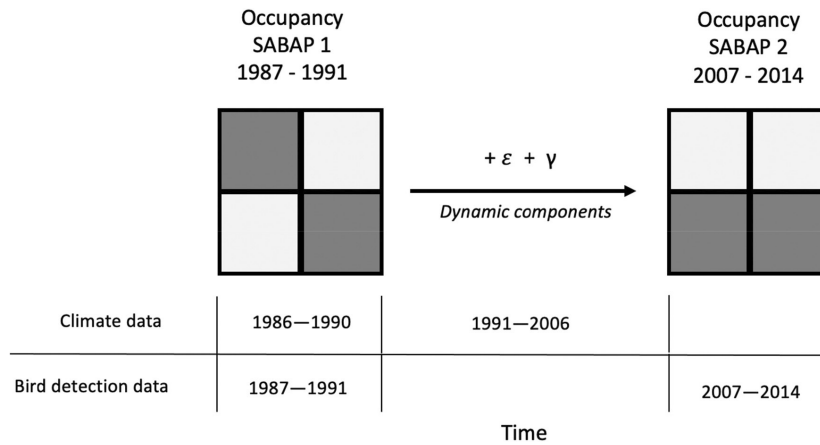


FIGURE 2 Diagram of the dynamic occupancy model used to examine the distribution dynamics of Cape Rock-jumper (*Chaetops frenatus*) in South Africa during the period 1987–2014. The four grid cells represent a simple spatial arrangement where Cape Rock-jumper may be present (dark grid cells) or absent (light grid cells). The spatial grids represent, from left to right, occupancy probability during SABAP1 and SABAP2. Occupancy status of SABAP1 is directly estimated by the model. Occupancy status during SABAP2 is derived from the occupancy status during SABAP1 and the dynamic components extinction (ε) and colonization (γ) (see Equation 4 for the model parameterization). The time period below each model component indicates the duration of that component for the bird detection data, and the climate data which were averaged over the specified period.

where β_5 is the colonization intercept.

Extinction was modelled in the following form:

$$\text{logit}(\varepsilon_{i,1}) = \beta_6 + \beta_7 \times \text{Temp}_i + \beta_8 \times \text{Precip}_i \quad (5)$$

where for site i , Temp_i and Precip_i represent the same climatic covariates as described in Equation 3, except they were averaged over the period 1991–2006 (Figure 2), and β_6 is the intercept.

The observations (detections/non-detections) are related to detection probability in the following form:

$$Y_{i,j,t} = \text{Bernoulli}(Z_{i,t} \times X_{i,j,t}) \quad (6)$$

where $Y_{i,j,t}$ is the detection/non-detection observation at site i , survey j , and season t . $Z_{i,t}$ is the observed detection/non-detection at site i and season t (i.e. 1 if the species is ever recorded at site i over all T seasons). $X_{i,j,t}$ is the detection probability at site i , survey j , and season t .

We were primarily interested in how detection probability changed through time, because the species is decreasing in abundance and distribution extent (Huntley et al., 2012; Lee & Barnard, 2016) and is likely to be more scarce over time and more difficult to detect year on year. Thus, we added to our model the year in which each survey was conducted as a factor covariate and allowed the model to estimate year-specific detection probability. This was modelled in the form:

$$\text{logit}(X_{i,j,t}) = \beta_9 + \beta_y \times P_y \quad (7)$$

where $X_{i,j,t}$ is the detection probability at site i , during survey j and season t . P_y is the year y in which survey j was conducted in season t , at site i . β_9 is the intercept, and β_y is the β coefficient representing detection for each year. Each continuous covariate was scaled to a mean of 0 and a standard deviation of 1 before being entered into the model. To allow for lagged (Roy

et al., 2001; Pearce-Higgins et al., 2015) or indirect (Rotenberry & Wiens, 2009) species' responses to climate, we chose slightly earlier climate periods compared with the bird atlas data. We used environmental data (i.e. data for mean temperature and precipitation) for the period 1986–1990 for SABAP1 and 1992–2007 for the SABAP1–SABAP2 transitional period (Figure 2). See Figures S2 and S3 that showing the values for mean precipitation and mean temperature per each QDGC over the study area, and for each SABAP, used in the model.

No covariate was specified for the colonization probability of Cape Rock-jumper between SABAP1 and SABAP2. The colonization model was estimated with an intercept only (a single average over the whole study region). As the Cape Rock-jumper's distribution has shrunk significantly over the last few decades (Huntley et al., 2012; Lee & Barnard, 2016; Milne et al., 2015), few colonization events have occurred between SABAP1 and SABAP2. Thus, the relationship between mean colonization and the model covariates would not be well estimated, irrespective of the covariates chosen. All data preparation and analyses were carried out in the program R version 3.4.1 (R Development Core Team, 2019). The R package 'dismo' (Hijmans et al., 2021) was used to compute the temperature and precipitation-based climatic variables. The R package 'unmarked' (Fiske & Chandler, 2011) was used to run the dynamic occupancy models.

Assessment of multicollinearity in explanatory climate data

We checked for multicollinearity in our explanatory variables for each model component using the variance inflation factor (VIF). All of the calculated VIFs were lower than 5 for our predictors, indicating no strong multicollinearity (Table S1).

RESULTS

Estimates for occupancy probability during SABAP1

During SABAP1, the Cape Rock-jumper's distribution was estimated to have occupied the south-western parts of the study area, along the western (up to approximately -31.5 degrees latitude) and south-eastern coastlines (up to approximately 26 degrees longitude), and was largely absent inland (Figure 3a). The core (as defined by an occupancy probability >0.6 , identified by green-coloured QDGCs) of Cape Rock-jumper's distribution appeared to be split into two spatially separated sections; the western section extended north to south in the south-western part of its distribution at approximately 19 degrees longitude (indicated by black-lined oval, Figure 3a). The second, south-eastern section was a cluster of QDGCs running west to east, along the south-eastern portion of its distribution at approximately 22–25 degrees longitude (indicated by black-lined oval, Figure 3a). The mean occupancy probability over all grid cells of the study region during SABAP1 was 0.22.

Mean relationships between the model covariates and mean occupancy during SABAP1 (1987–1991)

Occupancy probability during SABAP1 increased significantly as proportions of both fynbos and protected area increased within a QDGC (Figure 4a,b; mean occupancy estimate (and 95% confidence interval) on

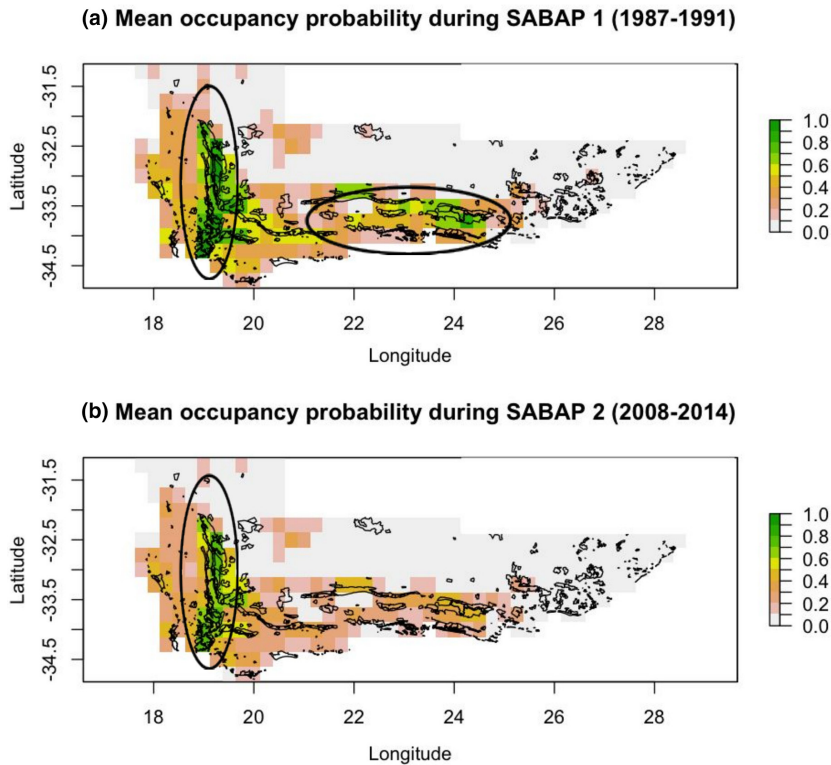


FIGURE 3 Predictions of mean occupancy probability for the endemic Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. (a) indicates mean estimates of occupancy based on checklists collected during bird atlas projects running between 1987 and 1991 (SABAP1), and (b) during 2008–2014 (SABAP2). Polygons represent protected areas, both private and public. Each grid cell represents a $15' \times 15'$ arcminute square and the total area of the study region is approximately $200\,000\text{ km}^2$. Ovals in the (a) and (b) indicates the Cape Rock-jumper's core range (as defined by estimated occupancy probability greater than 0.6).

the logit scale: 1.023 (0.541, 1.506) and 0.578 (0.200, 0.956) for fynbos and protected areas, respectively: [Table S1](#); See). As the mean temperature of the warmest annual quarter increased, occupancy probability decreased ([Figure 4c](#), -0.381 (-0.853 , 0.091)). As the rainfall over the warmest annual quarter increased, occupancy probability during SABAP1 decreased but the confidence interval overlapped 0 widely ([Figure 4d](#), -0.176 (-0.699 , 0.348)).

Estimates for occupancy probability during SABAP2 (2008–2014)

Across the whole study area, the estimated occupancy probability of Cape Rock-jumper during SABAP2 decreased markedly compared with the estimated occupancy probability during SABAP1 ([Figure 3](#)). The mean occupancy probability in the study region during SABAP2 was 0.16 (comparatively lower than the 0.22 estimate for SABAP1.)

The two sections making up Cape Rock-jumper's SABAP1 core distribution experienced considerable declines in estimated occupancy probability during SABAP2, relative to SABAP1. Over the western section of the species' SABAP1 core distribution, a general decrease in occupancy probability was apparent in all QDGCs that make up the area. For example, in this region, occupancy probability was estimated to be 0.6 or higher for 22 QDGCs during SABAP1, but for only 14 QDGCs during SABAP2. This change indicates a shrinking of Cape Rock-jumper's core distribution from SABAP1 to SABAP2.

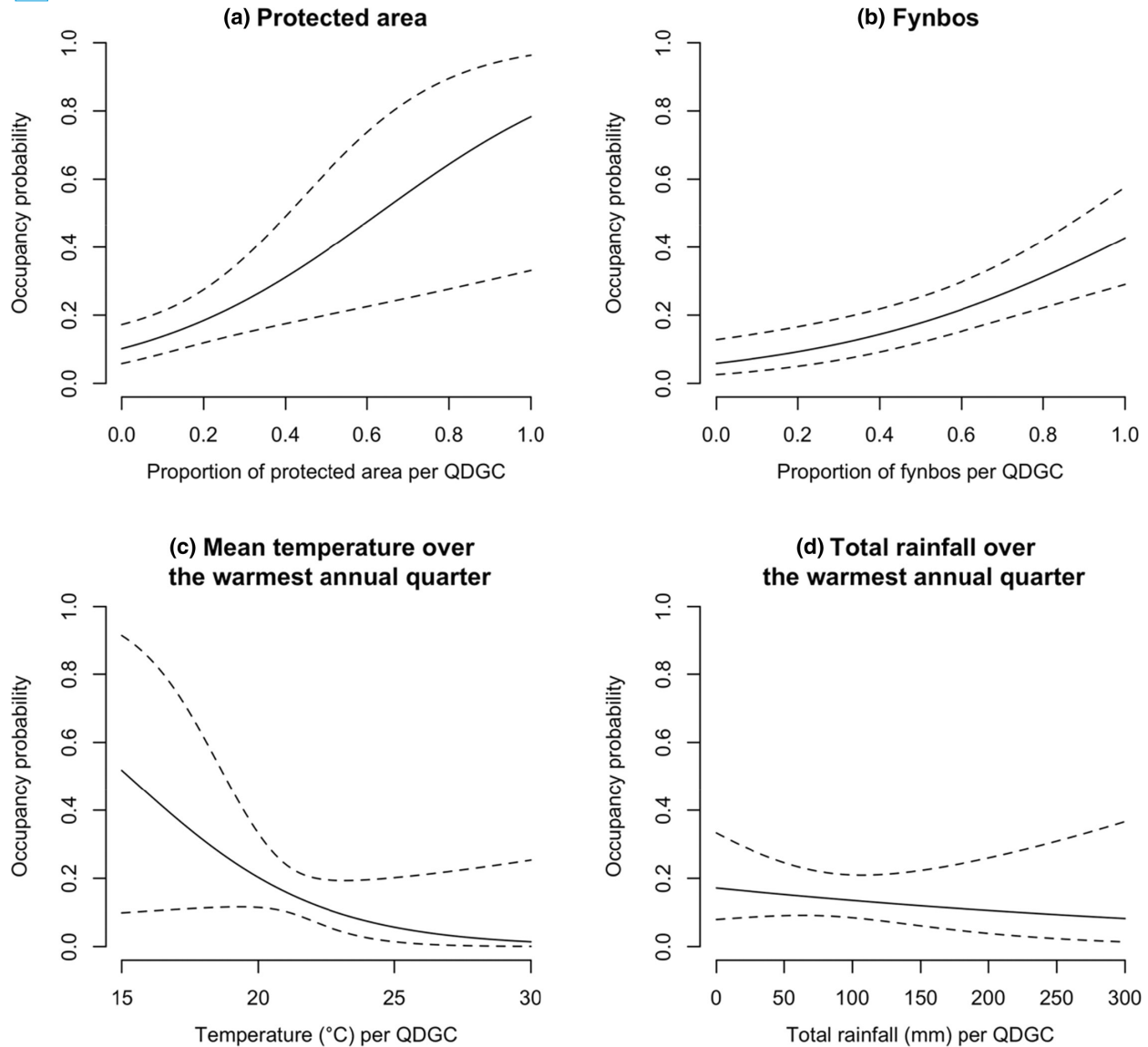


FIGURE 4 Estimated mean relationship between occupancy probability (y-axis) and the model covariates (x-axis) proportion of protected area (a), proportion of fynbos vegetation (b), mean temperature over the warmest annual quarter (c) and precipitation over the warmest annual quarter (d) during SABAP1 (1987–1991) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. See Equation 3 for the specification of the relationship between SABAP1 occupancy and model covariates. See Table S1 for mean estimates, standard errors and *p*-values for all model components).

The south-eastern section of the SABAP1 core distribution has also undergone severe decreases in occupancy probability between SABAP1 and SABAP2. Estimated occupancy probability for 11 QDGCs in this region was greater than 0.6 during SABAP1. At SABAP2, no QDGC in this region had an estimated occupancy probability of 0.5 or higher. See Figure S5 for estimates of the standard error of mean occupancy probability per QDGC in the study area, for each SABAP,

Estimates for mean extinction and colonization probability as a function of climate between SABAP1 and SABAP2

Extinction

As the mean temperature and total precipitation during the warmest annual quarter increased, extinction probability increased (mean extinction

estimate on the logit scale and 95% confidence interval for mean temperature: 0.403 (−0.920, 1.726), [Figure 5a](#); and for total precipitation: 0.744 (−0.252, 1.734), [Figure 5b](#)), even though the confidence intervals for both effects included 0.

Mean extinction probability for Cape Rock-jumper increased from west to east, with the highest probabilities estimated at the easternmost region of the study area ([Figure 6](#), see [Figure S6](#) for estimates of the standard error of mean extinction probability throughout the study area between SABAP1 and SABAP2). Relatively low extinction probabilities were evident in the top half of the region making up the western section of Cape Rock-jumper's SABAP1 core distribution (as indicated by the solid-lined circle on the left in [Figure 3a](#)).

Colonization

Mean colonization probability across the study area was poorly estimated with a point estimate close to zero, when converted from the logit scale to probabilities (mean estimate on the logit scale: −37.301 (−339.341, 331.875), reflecting the fact that the distribution of this species mostly shrank.

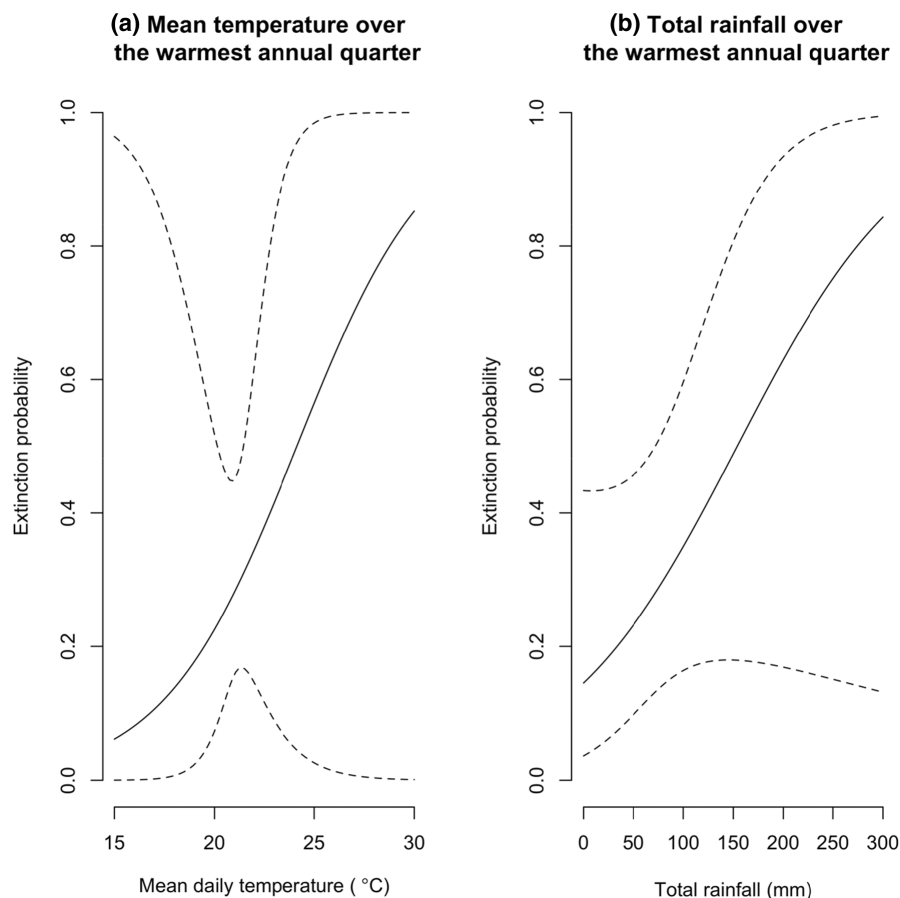


FIGURE 5 Estimated mean relationship between the extinction probability (y-axis) and the model covariates (x-axis) mean temperature of the warmest annual quarter (a) and precipitation of the warmest annual quarter (b) between the periods 1987 and 1991 (SABAP1) and 2008–2014 (SABAP2) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. See [Equation 5](#) for the specification of extinction probability. See [Table S1](#) for mean estimates, standard errors and *p*-values for all model components.

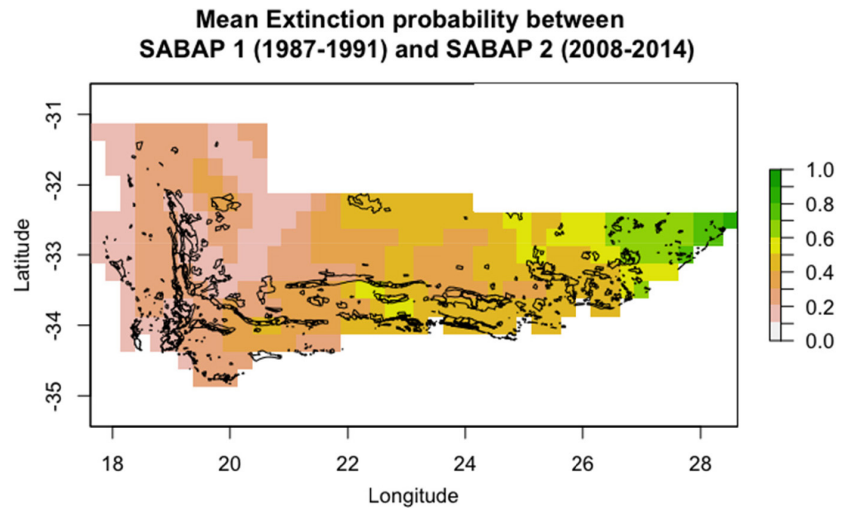


FIGURE 6 Realized mean extinction probability over the study area between SABAP1 (1987–1991) and SABAP2 (2008–2014) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. Realized mean extinction probability was modelled as a function of the mean temperature and total rainfall over the warmest annual quarter (see equation 6 for further details). Polygons represent protected areas, both private and public. Each grid cell represents a 15' × 15' regular square in arcminutes, and the total area of the study region is approximately 200 000 km².

Detection probability

Mean detection probability varied substantially across the duration of the study period, with no linear trend (Figure S4).

DISCUSSION

The Cape Rock-jumper inhabits an area where temperatures are often close to the species' thermal physiological limit (Milne et al., 2015) and so the recent distribution contraction could well have been caused by temperature increases induced by climate change (Lee & Barnard, 2016; Milne et al., 2015). We tested whether the occupancy probability of this species across its distribution was related to the climatic variables that are predicted to limit the species, temperature and rainfall during the warmest quarters of the year, and whether the extinction probability was related to these same variables. With respect to the expectations outlined in the introduction, we found that (1) whilst the Cape Rock-jumper is more likely to occur in the cooler parts of our study area, the effect of rainfall was minor (Figure 5a,b). And (2) an increase in the mean temperature and total precipitation during the warmest annual quarter was associated with a higher extinction probability of the Cape Rock-jumper, although both of these relationships were not statistically significant.

Species distribution models often show strong associations between species' distributions and climate even though such correlations do not necessarily indicate causal relationships (Beale et al., 2008). If the relationships were causal, then we would expect that the climatic variables that appear to limit species' distributions also explain variation in the extinction and colonization probabilities: the species should go extinct from those areas that have become climatically unsuitable and colonize those that have become climatically suitable. We found some evidence that this could be the case for the Cape Rock-jumper. The extinction probability was highest in the hotter and wetter parts of the distribution, which matches

the observation that occupancy probabilities were lower in these areas, suggesting that they could be marginal for this species. Despite wide confidence intervals for some of these relationships, the direction of the effects was consistent with earlier studies showing that the Cape Rock-jumper is limited by high temperatures (Huntley & Barnard, 2012; Lee & Barnard, 2016; Milne et al., 2015).

We did not find strong evidence for a relationship between precipitation and SABAP1 occupancy probability (Figure 4d), nor extinction probability (Figure 5b). This finding agrees with the conclusion of Lee and Barnard (2016), who studied climatic effects on the distribution dynamics of six species endemic to the fynbos vegetation (including the Cape Rock-jumper), and found that changes in the distributions of these species were largely due to changes in temperature, rather than in precipitation.

Compared with the climatic variables, both protection status and proportion of fynbos had clear effects on the probability that a grid cell was occupied by Rock-jumpers during SABAP1. Clearly, the protected high-altitude fynbos areas are important for the persistence of this species. Cape Rock-jumper avoids human-dominated landscapes and prefers to occupy natural fynbos (Frazer, 1997). However, much of the natural fynbos in the region has been converted to agricultural land, even before the initiation of SABAP1 (Cowling et al., 1986). The large network of protected areas in the region conserve Cape Rock-jumper's preferred habitat (Lee & Barnard, 2016), and here, we show that the species' occupancy probability is strongly dependent on protected areas.

Despite the large uncertainties about the drivers of extinction in this study, we argue that examining variation in extinction and colonization probabilities has the potential to clarify the effects of climate change and other factors on species distribution shifts. Yackulic et al. (2015) showed that examining colonization and extinction gives a better description of a species' niche than the commonly used static species distribution models, at least when species are not in equilibrium with climate (see also Clement et al., 2016). The limitations of static models is well known and various attempts have been made to model species' distribution dynamics (Huntley et al., 2010; Midgley et al., 2010). Dynamic occupancy models offer a powerful analytical tool for studying distribution dynamics (Altwegg et al., 2008), and we expect them to play an increasingly important role in species distribution modelling as large-scale citizen science data are becoming available (Altwegg & Nichols, 2019).

AUTHOR CONTRIBUTIONS

Gregory D. Duckworth: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead). **Rheinhardt Scholtz:** Formal analysis (equal); investigation (equal). **Raquel A. Garcia:** Data curation (lead); formal analysis (equal); investigation (equal); methodology (equal). **Res Altwegg:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data derived from public domain resources.

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