The Influence of Rainfall on the Verreaux's Eagle and its Prey Species in the Matobo Hills, Zimbabwe

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Contents

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Plagiarism Declaration

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.
2. I have used the Conservation Biology Journal convention for citation and referencing. Each contribution to, and quotation in, this project from the work(s) of other people has been attributed, and has been cited and referenced.
3. This project is my own work.
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"My only conclusion is that 25 years are insufficient to unravel the population dynamics of a bird of prey."

~ Valerie Gargett ~

Abstract

Understanding how species respond to variations in weather patterns will be crucial to improve our predictions about how species will cope with climate change. The Verreaux's Eagle (*Aquila verreauxii*) and its primary prey species the Rock Hyrax (*Procavia capensis*) and Yellow-spotted Hyrax (*Heterohyrax brucei*) have been monitored by a long-term citizen science project in the Matobo Hills, Zimbabwe. A previous study associated rainfall patterns with the establishment, breeding density and productivity of Verreaux's Eagles. Fluctuations in hyrax populations have been attributed to fluctuations in rainfall and drought. However, these studies have been limited by the use of total annual rainfall instead of targeted rainfall periods of when biological outcomes are most sensitive to weather phenomena. This study explored critical climate sensitivity windows influencing the Verreaux's Eagle's reading performance and the abundance of its main prey species. We used observations of 109 nests over 37 years (1984-2019) and counts from 20 hyrax den sites for 13 years (1993-2005), together with remotely sensed rainfall data. The probability of attempting to breeding and the probability of producing a fledgling was negatively associated with rainfall. For breeding attempt, the rainfall during June and July, 11-10 months before laying was the most relevant, whereas, for productivity, the rainfall during December to March, nine-five months before fledging was the most relevant. However, the relationship between the rainfall signal and breeding productivity was not significant. Hyrax abundance had a negative quadratic relationship with mean rainfall against their respective climate windows, whereby the abundance of adult and sub-adult hyrax increased with rainfall during July–September but declined thereafter at greater rainfall levels. The abundance of hyrax did not have a significant relationship with the breeding outcomes of the Verreaux's Eagles. This study shows the complexity of the causal relationships between climate and biological outcomes and also the value of long-term data to understanding the impacts of variations in weather patterns to better understand predator-prey dynamics.

Introduction

Climate is a critical determinant of biodiversity and ecosystem processes globally (Scheffers *et al*. 2016; Bonebrake *et al*. 2018). Projected global warming estimates are expected to have impacts that cause global scale species range loss and extinction (IPCC 2018). While extreme weather events are important in natural ecosystem processes, climate change has led to increased frequencies of these events over the last 50 years (Trenberth & Hurrell 2019), this can be detrimental to populations (Conradie *et al*. 2019). Animals that have larger bodies can physiologically endure the shocks of these climate change impacts compared to smaller animals, however, their longer generation times make them evolutionarily less adaptable and more vulnerable to extinction (Simmons *et al*. 2004).

Birds are good ecosystem indicators due to their sensitivity to environmental change and a long history of scientific observation and study (Dunn & Moller 2019). The effects of weather on birds can either be direct, indirect or interactive with other factors. Birds often shelter their young from unpleasant weather (Katzenberger *et al*. 2019), nevertheless, high mortality during brood-rearing is associated with extremes in weather such as flooding of nests (Elkins 1983; Anctil *et al*. 2014). High rainfall in spring also directly affects productivity in Hen Harriers (*Circus cyaneus*) as a result of poor prey provisioning to females by males in the pre-laying period (Amar *et al*. 2011). Another example is of Yellow-billed Hornbills (*Tockus leucomelas*) and Common Fiscals (*Lanius collaris*) breeding in the Kalahari Desert, increase in the frequency and intensity of hot days, has negatively impacted provisioning rates and the body condition, growth and survival of nestlings (Cunningham *et al*. 2013; van de Ven *et al*. 2019). While the impacts of changing temperatures are widely studied, rainfall changes have been more variable and patterns are far less obvious to interpretation (van Wilgen *et al*. 2016)

The impacts of weather on raptors are generally less well studied (Wichmann *et al*. 2003a, 2006). This is linked to the fact that raptors are long-lived, therefore particularly long-term studies are usually needed to unravel the relationships between breeding performance and the variables which drive it (Gargett 1990; Wichmann *et al*. 2006). Nevertheless, there are some established links that levels of rainfall can have both direct and indirect (via prey) effects on the breeding productivity of some raptor species. Suspected direct effects include rainfall reducing hunting success in some raptors (Olsen & Olsen 1992; Amar *et al*. 2011).

Changes in climate patterns and extreme weather events can also indirectly affect the population dynamics of species by influencing primary productivity and prey (Elkins 1983; Hustler & Howells 1990). Other Indirect effects include rainfall reducing prey abundance. The impact of this can vary between species and ecosystems. Breeding productivity in raptors with a generalist diet like Booted Eagles (*Hieraaetus pennatus*) (Bosch *et al*. 2015) may be less affected by rainfall despite high variation in inter-annual rainfall (Bosch *et al.* 2015). This is likely the case because generalist predators can swap prey resources if one is scarce in any given year. However, more specialist raptor species, particularly those whose prey is regulated by climatic factors, are likely to have their breeding performance more closely linked to climatic variables (Terraube *et al*. 2015; Garcia-Heras *et al*. 2016). An example is of Golden Eagles (*Aquila chryseatos*) in the western USA that prey mostly on Jack Rabbits (*Lepus californicus*). Interactions between extreme weather events and Jack Rabbits were found to be most useful in predicting Golden Eagle breeding success (Steenhof *et al*. 1997). A reduction in prey abundance which is also correlated with winter severity can cause raptors to change territories, skip a breeding year or reduce their clutch size (Steenhof *et al*. 1997). Pairs may decide not to attempt breeding due to females failing to build fat reserved before egg-laying due to reduced forage (Steenhof *et al*. 1997).

Failure to hunt is not the main cause of reproductive failures linked to climate change and caution should be taken with this assumption as raptors are likely to be affected differently (Olsen & Olsen 1992). Direct impacts, such as incubation failure or chick death due to exposure to rain or extreme temperatures can occur equally to both generalists and specialists (Steenhof *et al*. 1997, McDonald *et al*. 2004; Bosch *et al*. 2015). Studies on Peregrine (*Falco peregrinus*) and Brown Falcons (*Falco berigora*) in the Arctic circle and Australia show that the increased frequency of rainstorms causing flooding in nests significantly affects breeding productivity (McDonald *et al*. 2004; Anctil *et al*. 2014; Terraube *et al*. 2015). No prey deliveries were observed on rainy days in Brown Falcon nests, prolonged and chilling exposure to rain can exacerbate the stress on raptors and their nestlings if they already have poor food provision (McDonald *et al*. 2004). Protection in the form of nest boxes for Peregrine Falcons in South Africa and the Arctic circle improved the breeding success and the number of chicks fledged as these shelters buffered against storm weather (Anctil *et al*. 2014; Sumasgutner *et al*. 2020).

Long-term trends in rainfall amounts have shown an increase in rainfall in parts of North and South America, Europe and Asia but there has been increasing drying in the Mediterranean, Sub-Saharan Africa including Southern Africa (Trenberth & Hurrell 2019). Africa is the most vulnerable continent to the negative impacts of climate change (Simmons *et al*. 2004). Southern Africa has already seen an increase in extreme weather events affecting birds in arid ecosystems (Conradie *et al*. 2019). Raptor populations in arid savannah ecosystems in Africa may experience the greatest impact due to changing patterns in weather and less predictable rainfall (Hustler & Howells 1988; Wichmann *et al*. 2003). For example, modelling suggests that reduced or more variable rainfall in the Kalahari will increase the extinction likelihood of Tawny Eagles (*Aquila rapax*) (Wichmann *et al*. 2003). However, few studies have directly measured how climate change will affect the population dynamics and extinction risk of African birds especially raptors in arid-savannah ecosystems (Wichmann *et al*. 2003; Simmons *et al*. 2004) and little evidence has been presented relating rainfall to the timing of breeding and productivity.

The Verreaux's Eagle is a highly specialised raptor, whose diet in some regions can consist of more than 90% hyrax species (*Procavia and Heterohyrax*) (Gargett 1990; Chiweshe 2000), although in some populations they can diversify their diet (Murgatroyd *et al*. 2016a). Their distributional range through the mountainous regions of southern and eastern Africa is closely linked to that of their main prey species. In areas where they are specialists, this high specialisation might make them vulnerable to reduced breeding performance or population declines due to changes in the environment (Elkins 1983; Simmons *et al*. 2004; Terraube *et al*. 2015). For example, in South Africa, Verreaux's Eagle breeding success is reduced with increasing rainfall around hatching (Murgatroyd *et al*. 2016c).

The population of Verreaux's Eagle in the Matobo Hills, Zimbabwe, has been the focus of a long-term citizen scientist project commencing in1964 (Gargett 1969). In the early years of the survey, annual averages of rainfall and temperature seemed to not have an association with breeding rates, however, high rainfall years preceded poor breeding seasons (Gargett 1969). Month by month comparisons of rainfall showed no correlation and rainfall patterns in the pre-egg laying period of February and March seemed to have little relation to when and if the eagles laid eggs (Gargett 1969). A study examining the influence of rainfall on breeding rates and density using 31 years of data suggested that in years with higher rainfall, the density of resident pairs increased whilst the opposite effect was observed in lower than average rainfall years (Gargett *et al*. 1995). Consecutive high rainfall years saw an increase in new territories being established and vacant territories were re-occupied. In the period of above-average rainfall, the density of pairs increased to 10.5km^2 (59 pairs in 620km^2) (Gargett 1975).

Zimbabwe has a highly seasonal climate reflective of the variation in its topographical features (Childes & Mundy 1997). Some previous studies have explored the impacts of variation in rainfall on raptors in Zimbabwean arid-savannah ecosystems. For example, Tawny Eagles (*Aquila rapax*) and African Hawk Eagles (*Hieraaetus spilogaster*) in Hwange National Park had lower productivity in denser populations and environments with low primary productivity from season to season (Hustler & Howells 1990). However, annual rainfall is not likely to change significantly with climate change but the inter-annual variation will increase and may therefore pose a great threat to raptor populations (Wichmann *et al*. 2003), but less research on this topic has been conducted

It is important when analysing the relationships of climate and biological outcomes to consider the period of influence in which the species is most sensitive to climate, this may vary depending on species and biological variables being considered (Schwartz & Liang 2019; van de Pol & Bailey 2019). Climate impacts occur differently at different times of the year, therefore, the best weather predictors for biological traits are not always obvious, even in well studied understood systems (Bailey & De Pol 2016). To fully understand the impact of weather variation on demographic responses it is necessary to have long-term data from breeding populations. This has therefore limited the number of studies that have explored this in the global south since there are more longer-term studies on populations from the more developed global north (Møller & Hochachka 2019). Such long-term studies are important for identifying patterns over time as they can be more apparent in some years and not others (Steenhof *et al*. 1997).

Two species of hyrax; the Rock Hyrax (*Procavia capensis*) and the Yellow-spotted Hyrax (*Heterohyrax brucei*) consist >90% of the diet of Verreaux's Eagles in Matobo prey indiscriminately on the two which consist (Chiweshe 2000). In other study areas in South Africa, the availability of a diverse prey base contributed to the adaptability of the Verreaux's Eagle populations studied in the transformed habitats of the Sandveld and Magaliesberg, South Africa (Murgatroyd *et al*. 2016d; Padayachee *et al*. 2020). However, despite the reduction in Hyrax numbers in the past due to persistent droughts, they still constituted over 90% of the eagles' diet possibly due to a lack of adequate alternative prey options in Matobo (Gargett *et al*. 1995). The combination of traits Verreaux's Eagles possess that is; a large body and long generation time, specialised predator and specific hilly habitat needs in semi-arid to arid savannah ecosystems in Southern Africa, makes them potentially vulnerable to the impacts of climate change.

This study seeks to explore the possible climate sensitivity periods of the Verreaux's Eagle and Hyraxes and test their effect on the breeding rates, the abundance of Hyrax prey and the effect of prey numbers on eagle breeding productivity. An understanding of this system will allow for better predictions on how this species may respond to future climate change and better conservation management actions.

Methods

Study Area

The Matobo Hills (20^{o}30’S, 28^{o}30E) in South Western Zimbabwe covers an area of C. 3500km^2 (Cotterill *et al*. 2018). It is on the central plateau of Zimbabwe at an elevation of 1200–1530m above sea level (Barry *et al*. 2015). There are three main land-use systems within the main study area boundary, the Matobo National Park (MNP) covers an area of 42.4km^2 and the remainder is communal land and commercial cattle farms (Gargett, Gargett & Damania, 1995; Chiweshe, 2007). In total, the survey area covers 620km^2 (Gargett 1990).

Three distinct climatic seasons occur (Figure 1), the cool dry winter season (May–mid-August), hot dry summer (October–November) and the hot wet summer season (November–April) (Cotterill *et al*. 2018). Late August and September have intermediate and variable weather from cold, to hot and drizzly to windy weather. The daily temperature in the summer months ranges from 15–36^{o}C, while daily winter temperatures range between 3–21^{o}C with frosts (0–2^{o}C) occurring in low lying valleys (Cotterill *et al*. 2018).

Wet seasons typically extend from November until April with the most rain received between November and March (Figure 1). Winter rainfall occurs between June and September and is usually negligible (Gargett *et al*. 1995). Annual rainfall is unpredictable and fluctuates variably from a total of 1043mm in 1977–78 to 273mm in 1991–92 (Gargett *et al*. 1995). The long-term mean annual rainfall ranges between 575–630mm (Gargett *et al*. 1995; Cotterill *et al*.

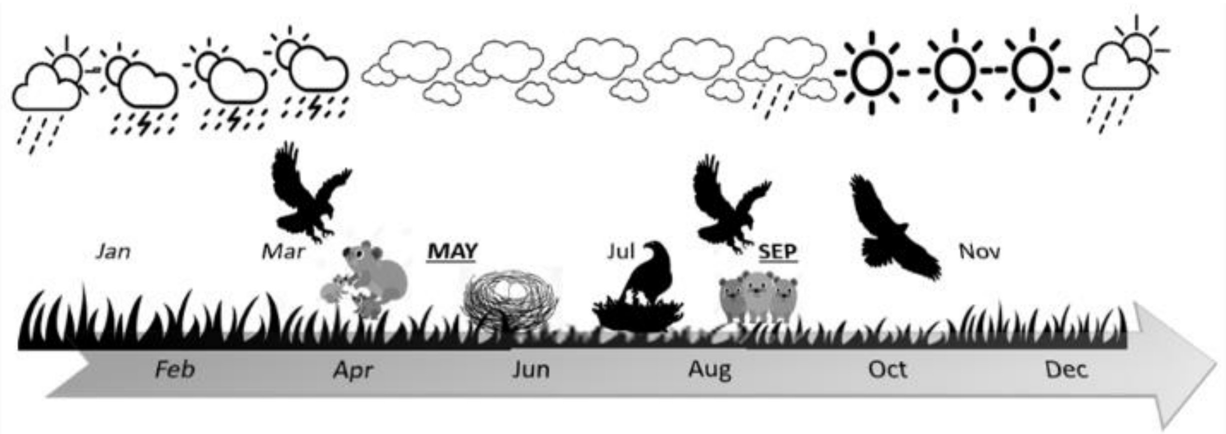

Figure 1:The climate and breeding season of the Verreaux's Eagles and hyrax in the Matobo Hills. Breeding starts in April, hyrax give birth to their young between April and May, eagles peak laying period is May and chicks fledge in September.

2018) and good rainfall years are often followed by a series of drought years for two more years (Gargett 1990).

The general landscape of Matobo is broken bare granite boulders (Figure 2). Although it is in the semi-arid Southern Matabeleland savannah, Matobo is an isolated moist island due to locally higher rainfall especially in the eastern parts (Cotterill *et al*. 2018). Rainfall-runoff on granitic surfaces creates a dense network of tributaries, as a result, a mosaic of habitats and vegetation types occur that include pockets of Miombo (*Brachystegia* and *Julbernardia* species), Mopane (*Coleophospermum mopane*) woodland in sodic soils, mixed woodlands with thickets, forest patches, grasslands and dambos (Cotterill *et al*. 2018). Other common vegetation types also include; Commiphora, Kirkia, Ficus, Combretum, Strychnos and Euphorbia (Barry 1996; Barry *et al*. 2015). Matobo has a diverse vegetation assemblage that includes moisture dependent and drought-tolerant species, with at least nine endemics (Chiweshe 2007).

Figure 2: The general granite boulder strewn landscape of Matobo Hills. To the left, a Verreaux's Eagle perches on a boulder (image by Merlyn Nkomo). To the right Matobo in the wet summer season (image by Qhelani Moyo).

Study Species

The Verreaux’s Eagle is a large eagle, with little sexual size dimorphism; females are slightly larger and heavier than males (Gargett 1990). The species breeds in established territories and pairs are resident in the Matobo Hills throughout the year. Pairs are mostly always seen together and can be identified by their proximity to known territory. The behaviour of pairs varies greatly depending on the breeding stage. In the Matobo Hills, the eagles breed during the winter months, egg-laying usually starts in late April, peaking in late May and going into early June (Chiweshe 2007) and chicks usually fledge in September. The species produces a clutch of either one or two eggs, however, only one chick is raised due to obligate siblicide (Gargett 1990).

Eagle Data

Although Verreaux's Eagle has been monitored in the survey area since 1964 (Gargett 1969). The Survey team consists of experienced birders from the BirdLife Zimbabwe's Matabeleland branch. Annually, at the start of the breeding season, the team members volunteer as small teams of two to three individuals and are assigned up to five nest sites each to monitor for the course of the season. Teams are expected to do at least three nest visits and reports, however, more visits are encouraged. Nest and alternative nest GPS coordinates are given to the team leader and the team visits the study area to check all sites for activity. The first report is expected before the end of May confirming territory occupation, the second at the end of July confirming breeding attempt and the last, at the end of September confirming breeding outcomes. Teams use binoculars and spotting scopes from a vantage point to monitor each nest for at least two hours for activity which they record.

In our analysis, we used data only from 1984-2019 due to the lack of historic records and corresponding precipitation data as the remote sensed weather data spanned the period 1981-mid 2020. We used observations made between May and September each year since 1984 to determine if territories were occupied, whether pairs attempted to breed (breeding rate), and whether they successfully produced a fledgling each year (breeding productivity). Nests were recorded as either occupied or unoccupied based on the presence of a breeding pair in the territory. When pair sightings were not recorded, field signs like nest refurbishment and muting were used to conclude territory occupation. Territories that recorded three or more consecutive years of inoccupation were excluded from the analysis and considered inactive (Gargett *et al*. 1995). They were included in the analysis again once re-establishment was confirmed.

Most territories had only one nest, however, where nests were closer than 1km and behavioural observations confirmed them to be alternative nests belonging to the same pair, the nests were grouped by territory and all analyses were done at the territory level.

Eagle Breeding Performance Parameters

For all active territories (i.e. those that had been active at least twice in the last three years), we determined whether a breeding attempt was made, based on the following criteria: A bird was observed incubating or sitting on the nest in the months between May and August, or eggs were seen in the nest by observers. If no observations occurred during these months, then the occurrence of an attempt was unconfirmed and these records were not used for the analysis of the breeding rate.

We considered breeding as successful if a large chick (> ca. 65 days /nine weeks) was observed on the nest, or a fledgling was seen close to the nest (Gargett 1990). If no observations occurred at a time when the chick was old enough to be considered successful, the nesting outcome was recorded as unconfirmed and those records were not used in the analysis of productivity.

Hyrax Data

Data on numbers of both Rock Hyrax and the Yellow-spotted Hyrax were collected through an annual census between April and May from 1993–2005. This survey period corresponds to the period after the pups are born (Skinner & Chimimba 2006; Chiweshe 2007). Two observers counted the number of hyrax at 20 established sites ranging from 0.02–0.41 km^2 in size, which were located within a 1km radius of eight well-defined eagle territories (Barry, 1996; Barry, Chiweshe & Mundy, 2015). The hyrax sampling stations represent the different vegetation types and landscapes in Matobo National Park with eight sites occurring outside of the park, four in commercial farmland and four in communal lands. Observers used binoculars to conduct the counts starting at dawn while hyraxes are basking in the sun on the exposed rock outside their dens. Hyraxes were identified by species and aged according to size into three categories; pups, sub-adults and adults (Chiweshe 2007).

Climate Data

We acquired rainfall data for the study area from January 1984 to August 2019 from the Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) through Google Earth Engine (Gorelick *et al*. 2017; Levick 2020). The database surpasses other quantitative precipitation estimates in terms of high spatial resolution and length (Gorelick *et al*. 2017; Bai *et al*. 2018). The CHIRPS dataset is a database for precipitation (Bai *et al*. 2018) that provides estimates of Cold Cloud Duration (CCD) precipitation with a latency of approximately two days. It combines Infrared satellite observations with station data using a technique that assigns CCD interpolation weights at a resolution of 0.05^{o} (5.4km) (Funk *et al*. 2015; Bai *et al*. 2018). Thus, we had a single measure of rainfall data across our study area (i.e. no spatial variation). We used this dataset to calculate total monthly rainfall for each month from a sum of the pentadal (five-day interval) totals from 1984–2019. The CHIRPS data reflected data from field stations very well (Supp. S1).

Statistical Analysis

ClimWin Analysis – Identifying Climate Windows

All models and analysis were done in R (R Core Team 2020). The package ClimWin (van de Pol *et al*. 2016) was used to determine the period of climate sensitivity for each response variable using a sliding window (SlidingWin) function. ClimWin tests the effects of different climate windows on the biological response variables (Bailey & De Pol 2016). The response variables for the analysis were:

- Eagle breeding rate (binary: attempt (1) or not (0))
- Eagle breeding productivity (large chick produced (1) or not (0))
- Hyrax total counts
- Hyrax adult counts
- Hyrax sub-adult counts
- Hyrax pup counts

All models with the eagle breeding parameters as the response variable were binomial (i.e. the response variable was 0 or 1), while all models with hyrax abundance as the response variable were run with a Gaussian distribution. For each biological response variable, we followed a stepwise approach to modelling. Firstly, a baseline null model was created, not including any weather effects. Secondly, a competing model was built including rainfall variables as a fixed effect with a flexible sliding window. This window allowed the full range of possible rainfall periods to be tested for, from the months before the response variable (i.e. any contiguous range of months before breeding, fledging or counting of hyraxes). The models had a monthly interval defined and had a range of up to 12 months before the response variable.

In the first explorative stage, the models tested both the mean and the maximum rainfall and the linear, logistic and quadratic functions for possible relationships between the rainfall data and each response variable (Bailey & De Pol 2016). After running the various models (the full range of possible weather periods), their Akaike Information Criterion (AIC) values were compared to that of the null model (Bailey & van de Pol 2020). We then selected the model with the lowest Delta AIC (ΔAIC) value (relative to the null model) and performed randomization that identifies the likelihood that such a signal could occur by chance. The function RandWin was used, which is similar to SlidingWin but has the 'repeats' argument that allows specifying the number of repetitions the model should do. Randomization accounts for model overfitting, the greater the number of repeats the better (Bailey & van de Pol 2020). For this study, we chose a standard of 1000 repeats. The randomization re-runs the ClimWin analysis on a dataset in which date information has been rearranged and associations of climate and response variables have been removed, to determine the likelihood of finding the same window again by chance.

After this step, the Plotall function is used to visualize and assess confidence in the results. The Plotall function plots a histogram of ΔAIC values from the randomization. The histogram also gives a *P*-value estimate of the likelihood of a false positive. Model confidence weights were also plotted along with, the median opening and closing time of the best models. The Plotall function also produces the best model plot which plots the predictions of the best model over the biological variable data to visualize their relationship. Alternative relationships can be explored by changing the function (*func*) in the model if the relationship proves inappropriate or outliers are present. Where the best-selected model included a quadratic relationship, we first explored the relationships in detail to see if they made biological sense or they were driven by outliers in the data. For all the breeding parameters these relationships were not robust and thus we chose the next best fitting linear models (see supplementary materials).

The final models were then run, using the rainfall data extracted from the best climate window, within a Generalized Linear Mixed Model (GLMM). We specified the random effects of ‘Nest’ and ‘Year’ to control for the lack of independence of measurements from the same nest sites between years, and also from different nest sites during the same year for 109 nests and 1308 eagle breeding years. These were not originally included in the ClimWin analysis since the model took too long to run. All fixed effects were standardised at model fitting (by subtracting the sample mean and dividing by the sample standard deviation) to aid model convergence (Schielzeth 2010).

Lastly, once rainfall sensitivity windows had been identified for the eagle breeding parameters, we fitted another GLMMs including both the relevant rainfall signal and the hyrax counts to explore whether terms influenced together influenced breeding performance, including nest-ID and year as random terms. For this step, we used eagle and hyrax data from the same 13 years’ period (1993-2005).

Results

We used 1308 observations of breeding attempts and productivity from 109 eagle territories monitored between 1984-2005. The average breeding rate was 0.49 and the average productivity was 0.35. For the hyrax, we used data of 13 years between 1993-2005 and 87 eagle breeding territories monitored during this period. A total of 11330 hyraxes were counted at 20 sites. Eagle breeding had a negative linear relationship with rainfall and hyrax numbers had a quadratic relationship with rainfall, increasing with an increase in rainfall to a certain point.

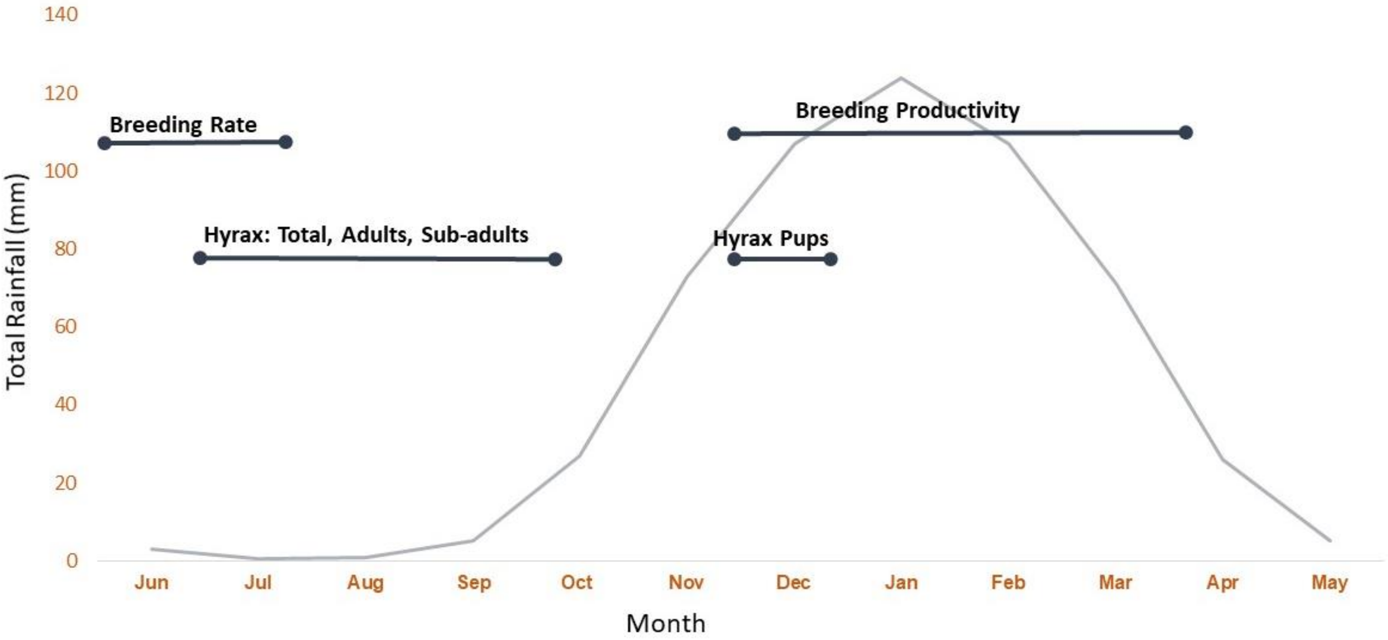

Figure 3: The Climate Windows associated with the response variables, the time of year they occur and the amount of rainfall expected during that time.

Our analysis identified mean rainfall between June and July of the preceding year as a time window having the strongest association with the breeding rate (Suppl. Table S1). Higher levels of rain, during this dry period, decreased the probability of breeding 10 months later. However, despite being the best model and showing a significant trend, randomization trials suggested that this window was weak with a confidence weight of 50% of the 95% confidence set (Suppl. S2). This indicates that about 50% of the randomizations arrived at a similar window by chance. Consequently, the selected window could be unreliable as it could be a result of a chance arrangement. Nevertheless, the final model, including the random terms of nest-ID and year, suggested that the relationship between breeding rate and mean rainfall between June and July of the previous year was significant (Figure 4A, Table 1). This rainfall window explained around 24% of the variation in the productivity data (R^2=0.234)

Breeding productivity was associated with the mean rainfall in the combined months of December, January, February and March before the start of the breeding season (Suppl. Table S2). This is the main rainy season when most rain occurs during the year, and higher rainfall reduced the probability of successful breeding in the following season (Fig 4B). Randomization showed, however, that this relationship was weak with a confidence weight of 83% of the 95% confidence set falling within the chosen window (Suppl. S3). As a result, this window is considered to be unreliable and was also statistically insignificant (Table 1). The relationship between breeding productivity and rainfall in the selected window (December-March) was marginally non-significant (*p*=0.077) (Figure 4B, Table. 1). Rainfall during this window explained only around 17% of the variation in the productivity data (R^2=0.174.

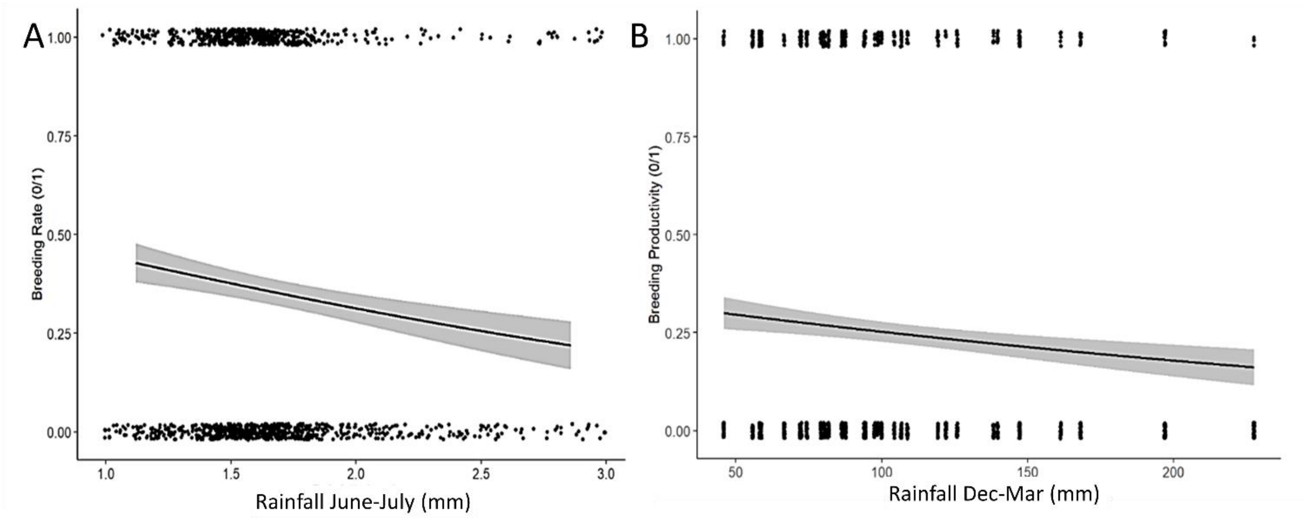

*Figure 4: **A**- The effect of an increase in rainfall (mm) during the June-July Climate window of the previous year. **B**- The relationship between rainfall in December to March and the breeding productivity of the subsequent season. An increase in rainfall during the climate window reduces the likelihood of breeding attempts and success in Verreaux's Eagles.*

Table 1: Results of the GLMM between the selected rainfall windows and Verreaux's Eagle breeding parameters.

Response Variable	**Predictor**	**Estimate**	***SE***	***Z***	***df***	***R^2***	***P***	***Random effects***	
								Nest	**Year**
Breeding Rate	Intercept	-0.59	0.14	-4.18	1304	0.234	<0.001	0.79	0.17
	Rain	**-0.197**	**0.09**	**-2.09**			**0.036**		
Breeding Productivity	Intercept	-1.105	0.136	-8.103	1301	0.174	<0.001	0.48	0.18
	Rain	-0.176	0.99	-1.77			0.077		

Relationship Between Rainfall and Hyrax Counts

ClimWin analysis for the total numbers of hyrax, adult hyraxes, sub-adult hyraxes and pups suggested a shared sensitivity window during the dry winter season between July and September of the preceding year. This window occurs eight–ten months before the annual count in May (Suppl. Table S3, S4 & S5) The relationship between rainfall in this window and hyrax numbers was quadratic, suggesting that for total Hyrax, adult hyrax and sub-adult hyrax increasing amounts of rainfall increased their abundance up to a point, above which higher levels of rainfall decreased their abundance.

The randomization tests showed that the selected windows for the three of the hyrax parameters were robust (total, sub-adult and adult hyrax, but not pups). The SlidingWin model for total hyrax numbers had 0% of the models run in the randomization falling within the best window estimate. This provides strong support for the window as it is not likely to have been selected by chance. Hyrax adult and sub-adult number's randomizations also give strong support for the selected window with 2% of the models run falling within the 95% confidence set (Suppl. S5, S7 & S8).

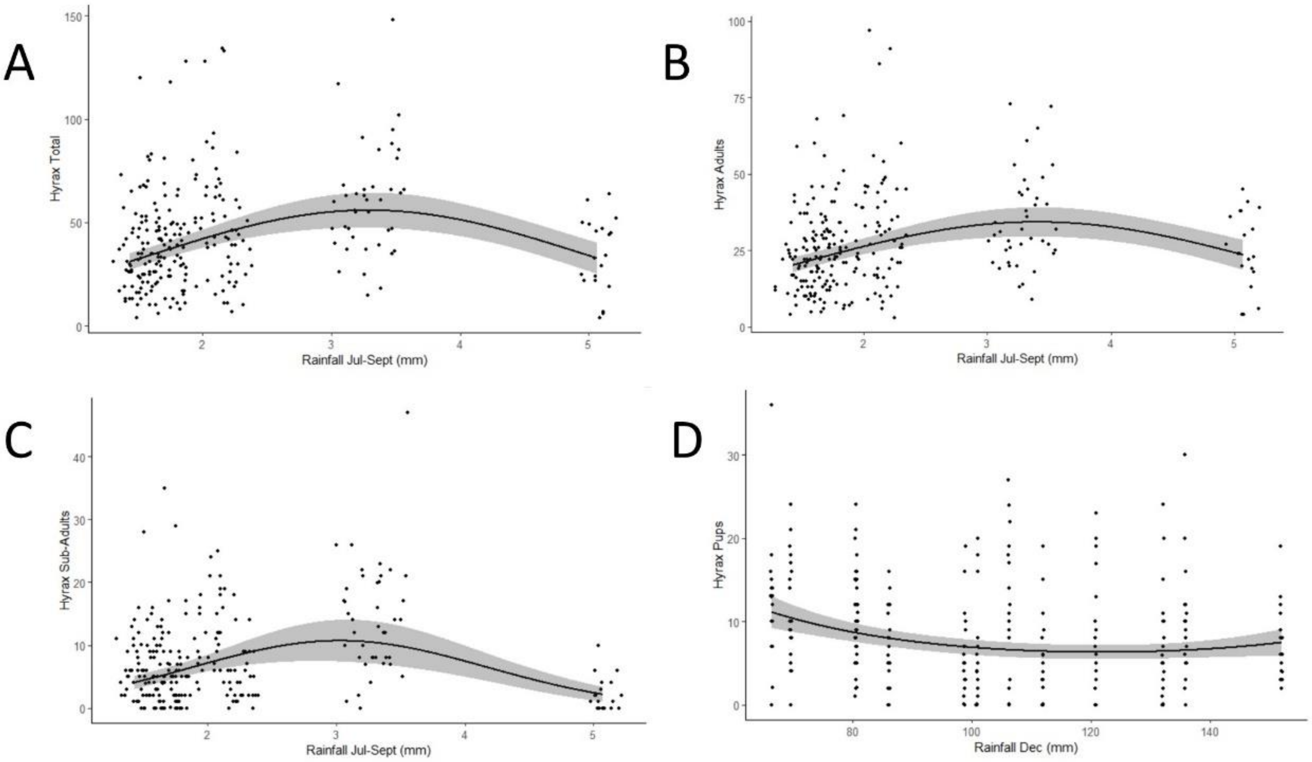

*Figure 5: **A B** & **C**- The relationship between rainfall in July-September of the previous year has a with hyrax totals (A), hyrax adult (B) and hyrax sub-adults (C). Increase in rainfall increases the numbers of hyrax to a point after which further increase reduces the numbers of Hyraxes. **D**- The relationship between pups and rainfall in December of the previous year.*

Hyrax pup numbers and rainfall in December in the preceding year had a reversed quadratic relationship, whereby an increase in rainfall in December up to around 100mm results in a slight decrease in the pups counted in the following year in May (Fig 5D, Table 2). However, this trend was not significant.

Table 2: The results of the Generalized Linear Mixed Models between the selected rainfall windows and hyrax parameters.

Response Variable	**Predictor**	**Estimate**	***SE***	***Z***	***df***	R^2	***P***	***Random effects***	
								Sites	**Year**
Hyrax Totals	Intercept	4.72	0.36	12.99	255	0.892	<0.001	0.12	0.05
	Rain	**1.12**	**0.36**	**3.11**			**0.002**		
	Rain^2	**--0.17**	**0.057**	**-2.99**			**0.003**		
Hyrax Adults	Intercept	4.06	0.33	12.43	255	0.821	<0.001	0.11	0.04
	Rain	**0.92**	**0.32**	**2.86**			**0.04**		
	Rain^2	**-0.14**	**0.05**	**-2.66**			**0.008**		
Hyrax Sub-adults	Intercept	4.12	0.87	4.74	255	0.785	<0.001	0.12	0.27
	Rain	**2.31**	**0.88**	**2.64**			**0.008**		
	Rain^2	**-0.38**	**0.14**	**-2.74**			**0.006**		
Hyrax Pups	Intercept	-6.49	1.083	-0.060	255	0.683	0.95	0.19	0.05
	Rain	**-1.15**	**5.24**	**-2.20**			**0.028**		
	Rain^2	**1.85**	**9.52**	**1.94**			**0.05**		

Relationship Between Eagle Breeding Performance, Hyrax Abundance and Rainfall

When combined with rainfall, we found no significant association between any of the measures of hyrax abundance on either of our measures of Verreaux's Eagles' breeding performance (Table 3 & 4). In this reduced data set (over a more limited number of years) rainfall had a significant negative relationship with the breeding rate (Table 3), but not productivity (Table 4).

Table 3: The results of the Generalized Linear Mixed Models between eagle breeding rate, rainfall windows and hyraxes numbers from 1993-2005. For Hyrax Totals, Adults and Sub adults, the rainfall between July-September was used, for Pups, the rainfall in December was used. Significant variables are shown in bold.

Response Variable	**Predictor**	**Estimate**	***SE***	***Z***	***df***	R^2	***P***	**Random effects**	
								Nest	**Year**
Breeding Rate	Intercept	-0.59	0.19	-2.99	576	0.335	0.003	1.14	0.12
	Rain	**-0.63**	**0.15**	**-4.14**			**<0.001**		
	Hyrax Total	-0.06	0.14	-0.46			0.68		
Breeding Rate	Intercept	-0.59	0.19	-2.99	576	0.335	0.003	1.14	0.12
	Rain	**-0.62**	**0.15**	**-4.042**			**<0.001**		
	Hyrax Adults	0.026	0.14	0.19			0.85		
Breeding Rate	Intercept	-0.59	0.19	-3.033	576	0.335	0.002	1.12	0.11
	Rain	**-0.64**	**0.15**	**-4.26**			**<0.001**		
	Hyrax Sub-Adults	-0.13	0.14	-0.96			0.33		
Breeding Rate	Intercept	-0.59	0.19	-3.041	576	0.334	0.002	1.14	0.11
	Rain	**0.63**	**0.15**	**-4.22**			**<0.001**		
	Hyrax Pups	-0.13	0.14	-0.98			0.33		

Table 4: The results of the Generalized Linear Mixed Models between eagle breeding productivity, rainfall windows and hyraxes numbers from 1993-2005. For hyrax totals, adults and sub-adults, the rainfall between July-September was used, for pups, the rainfall in December was used. Significant variables are shown in bold.

Response Variable	**Predictor**	**Estimate**	***SE***	***Z***	***df***	R^2	***P***	**Random effects**	
								Nest	**Year**
Breeding Productivity	Intercept	-1.23	0.20	-6.12	564	0.195	<0.001	0.55	0.23
	Rain	0.09	0.17	0.58			0.564		
	Hyrax Total	0.03	0.17	0.18			0.861		
Breeding Productivity	Intercept	-1.23	0.19	-6.16	564	0.196	<0.001	0.56	0.23
	Rain	0.08	0.17	0.49			0.62		
	Hyrax Adult	0.11	0.17	0.62			0.53		
Breeding Productivity	Intercept	-1.23	0.19	-6.16	564	0.194	<0.001	0.55	0.23
	Rain	0.08	0.18	0.45			0.66		
	Hyrax Sub-Adults	-0.07	0.17473	-0.385			0.700		
Breeding Productivity	Intercept	-1.23	0.2	-6.14	564	0.195	<0.002	0.55	0.23
	Rain	0.09	0.17	0.55			0.58		
	Hyrax Pups	-0.03	0.17	-0.17			0.87		

Breeding rate and breeding productivity were tested in separate models of hyrax abundance indices i.e. adults, sub-adults, pups and their total against each of the hyrax indices' climate sensitivity window. For each of the models, hyrax numbers and their individual climate sensitivity windows did not have an effect on either breeding rate or breeding productivity.

Discussion

Our study sought to understand the dynamics of the relationship between Verreaux's Eagles, hyraxes and rainfall. We used ClimWin models to find climate sensitivity periods for eagle breeding performance and hyrax abundance over 37 years and 13 years respectively. The amount of rainfall received in the climate windows selected affected the breeding of Verreaux's Eagles and the number of hyraxes, but somewhat surprisingly breeding performance was not related to the abundance of hyrax.

Rainfall had a negative effect on the breeding rate and productivity of the eagles. As both breeding parameters had a lag response to rainfall of up to 11 months for breeding rate and nine months for productivity, this impact could not be driven by a direct effect. Overall Hyrax abundance (across all ages) and two of the three specific age categories were affected by rainfall (July–September) during the dry winter. However, in contrast, hyrax pups were the only ones affected by rainfall during the rainy season in December. However, we did not detect any relationship between hyrax numbers and eagle breeding performance. Our analysis did not, therefore, suggest a simple relationship whereby the same weather period influenced Hyrax and also indirectly eagle productivity, suggesting that the relationships within this system may be more complex than originally suspected.

In this study, the Verreaux's Eagle the climate sensitivity window lies between June and July of the previous year. However, this result was also somewhat surprising, since this covers the dry season, and rainfall at this time is negligible (Gargett 1990; Gargett et al. 1995). Persistent rainfall during the breeding period is often more important for breeding outcomes than the overall total rainfall received in the season (Anctil et al. 2014; Bosch et al. 2015), however during this window, pairs would have been incubating or brooding young chicks of the previous season. Breeding failures are recorded at a higher rate during incubation time (Gargett et al. 1995), it is possible therefore that this window is driven by the influence of the previous year's breeding outcomes on the next season's time of laying. Whereby, higher rainfall in the previous year's breeding could cause more failures, and pairs that failed to successfully raise a chick had a higher likelihood of attempting to breed again in the following year compared to successful pairs (Gargett 1990). In addition, these previously failed pair may be able to get into breeding condition and lay eggs sooner than they would have if they had reared chicks through to fledging. Earlier laying has previously been associated with better breeding success in this species (Gargett 1990, Murgatroyd *et al*. 2016). However, rainfall only varied between 1 – 5mm during this period it is therefore impossible that this level of variation in rainfall could have such a profound influence on breeding success.

The negative relationship between rainfall from December to March and reproductive productivity was not statistically significant when included in a full mixed model with random effects. This result was similar to the findings of a previous study on this population where no correlation was found between rainfall and productivity (Gargett 1990). In the same way, the productivity of Booted Eagles, studied in a similar system with inter-annually variable rainfall patterns also did not show a significant response to rainfall (Bosch *et al*. 2015). This is despite projections in the same climate the north-west of Zimbabwe finding that increase in inter-annual variation of rainfall will be the most detrimental to raptor populations (Wichmann *et al*. 2003). The Matobo Hills habitat may offer a buffer to the effects of this variation due to its water retention qualities and the micro-climates in the valleys and bases of kopjes (Cotterill *et al*. 2018). Consecutive years of high rainfall have previously been associated with an increase in density and re-establishment of vacant territories (Gargett 1975; Gargett *et al*. 1995), it is possible that the effect of rainfall on productivity is being obscured by density-dependent factors.

Hyrax abundance (i.e. totals, adults and sub-adults) had a quadratic relationship with rainfall. The climate sensitivity window affecting hyrax abundance was July to September of the previous year before they were counted. This climate window occurs at the height of the dry season when food availability is low and the hyraxes are most susceptible to predation due to increased foraging distances and low vegetation cover. Although rain during the winter is negligible the water retention property of kopjes makes it possible for a vegetation flush to occur (Gargett 1990; Cotterill *et al*. 2018), sustaining hyrax and offering vegetation cover until the wet season begins. It is also a possibility that further increase in rainfall does not necessarily translate to the decrease in hyrax numbers shown but a decrease in numbers seen during censuses due to the increased refugia and reduced need to venture out in wet years. Hyraxes are said to be encountered more frequently as prey items than during censuses (Chiweshe 2000). However, it also appears that this quadratic relationship may have driven by an outlier and further analysis needs to be undertaken to establish how robust this quadratic relationship is.

Hyrax pups in the Matobo Hills are born between April and May each year (Skinner & Chimimba 2006). Pup numbers were associated with the climate window of mean rainfall in December of the previous year, five months before parturition. A previous study associated the success of hyrax breeding to a similar period (November), stating that a prolonged dry spell during this time delays the growth and reduces the amount of vegetation, prompting failures in the gestation of hyraxes (Chiweshe 2007). Both species of hyrax synchronise their births and this is governed by a single peak in rainfall (Barry 1993). Although Verreaux's Eagles prey on all age groups and species of hyrax indiscriminately (Gargett 1990), later studies on the prey of the eagles stated that they prey heavily and more consistently on immature hyrax (Chiweshe 2000). Prey remains at the base of nests both in Matobo and South Africa found that hyrax pups were extremely uncommon (Gargett 1990, Murgatroyd pers comms). This suggests that this age group is not as important as prey for the Verreaux's Eagles and explains the insignificance of their relationship with eagle breeding parameters for this age group. There is however, a high mortality rate of pups as noted in the months before the census, pups consisted 6% of the hyrax population before new births in April–May when they were 25% of the population (Barry 1993). This could have implications on the number of immatures available in the following seasons.

Our mixed effects models found no relationship between hyrax numbers and the eagle breeding rate and productivity. There is a possibility that hyrax are abundant in the system and the Verreaux's Eagle predation pressure is very low such that only a severe population decline (e.g. after consecutive years of drought or disease outbreak) can be to the detriment of the eagles (Gargett 1990). Unlike lemmings (*Dicrostonyx groenlandicus*) in the Arctic ecosystems which have a cyclic and highly fluctuating population dynamic that affects Snowy Owls (*Bubo scandiacus*) (Schmidt *et al*. 2012), hyrax populations are not cyclic and respond to scarcity over a series of drought years. This could be the reason for the lack of a significant relationship between the eagles and the hyrax. Alternatively, any increased hyrax abundance, might not be of functional use to eagles. A theory could be that although increasing rainfall may increase the numbers of hyraxes, it also increases primary productivity and vegetation cover, concealing hyraxes and reducing the foraging distances they traverse for food, making it harder for the eagles to catch them (Gargett 1990). Therefore, the density of prey may be of no effect if it is concealed by vegetation, reducing the foraging efficiency of eagles. Similar results were found on the foraging of Swainson's Hawks (*Buteo swainsonii*) as it had a negative correlation with plant cover as they hunted in cultivated fields only after they had been cleared despite their high prey density (Bechard 1982). Verreaux's Eagles inhabiting an agricultural mosaic landscape in South Africa have also been shown to have a preference for slightly altered habitats, over natural vegetation patches, and this was hypothesised to be related to better prey availability through more accessible hunting opportunities (Murgatroyd *et al*. 2016b).

Comprehensive studies on the breeding ecology and the population dynamics of both hyrax species have not been done in Matobo (Gargett 1990; Barry 1993). The limited studies that have been done have cited the hunting pressure of hyraxes in the communal lands outside the protected area of the Matobo National Park as a cause for reduced eagle productivity and loss of territories (Chiweshe 2000, 2007). The data used for this study was from counts of hyraxes over a 13 year period (Barry *et al*. 2015) which may not be a sufficient period to see causal patterns in long-lived species (Gargett 1990).

Weather, unlike other factors affecting breeding, is expected to affect breeding pairs equally in a uniform environment like the Matobo Hills (Gargett 1990). Climate windows may be inappropriate due to the complexity of rainfall and breeding rate relationships (Bailey & De Pol 2016), on the other hand, some climate windows affect prey abundance and thus affect eagle breeding rates. Furthermore, CHIRPS is reported to have poor accuracy in estimating precipitation intensity especially over periods of low precipitation (Bai *et al*. 2018) which would cover the windows associated with breeding rate, hyrax total, hyrax adults and hyrax sub-adult numbers. Generally, CHIRPS is more accurate during the summer than in the winter (Bai *et al*. 2018). The mixed models did reveal, however, that the random effects tested contributed to more variation than rainfall highlighting the importance of the different conditions and history of breeding pairs and territories in this system.

There are numerous other factors affecting Verreaux's Eagles' breeding in the Matobo Hills that affect pairs differently, for example; temperature, time of laying, age of parents, population density, natural enemies and previous year's breeding record have been identified (Gargett 1990). It is therefore important to not study these factors in isolation as considering different environmental variables offers better insights (Bionda & Brambilla 2012). More research is needed comparing raptor populations across temporal and spatial scales to gain a better understanding of the mechanisms and importance of climate effects (Wichmann *et al*. 2006).

Future recommendations

This study would not have been possible without the exceptional efforts of the Matobo Black Eagle Survey, which is the world's longest-running citizen science raptor monitoring project. Long-term monitoring of long-lived raptors is essential to understand the potentially diverse variables contributing to their survival, and understanding this is of particular importance in the face of climate change. To make the most of citizen science data, we recommend that data collection standards for the minimum visits to nests per season and their critical times be adhered to by survey teams to improve confirmed breeding attempt records. Hyrax census and studies should be done with the same effort and approach as the eagle breeding survey as they are valuable to understanding the causal relationships of this system.

Future studies should aim to collect prey remains to assess whether or not hyrax still make up 90% of the prey of Verreaux's Eagles in Matobo, and whether this varies between years. Additionally, human use and its impact on hyrax populations need to be studied across the three different land-use types. Climate variables like temperature and primary productivity (e.g. NDVI), although said to be of no effect on the eagles, should be built into the model to add understanding to the dynamics of weather and breeding. Other important climate change indicators to consider in future studies in this system would be quantifying inter-annual variation in rainfall extremes, the number of hot and cold days and also fire and fire management, as it is an important driver in this ecosystem. In the future, marking pairs, employing GPS tracking approaches to understand their use of the environment and considering their breeding density can also improve our understanding of the system for better conservation management.

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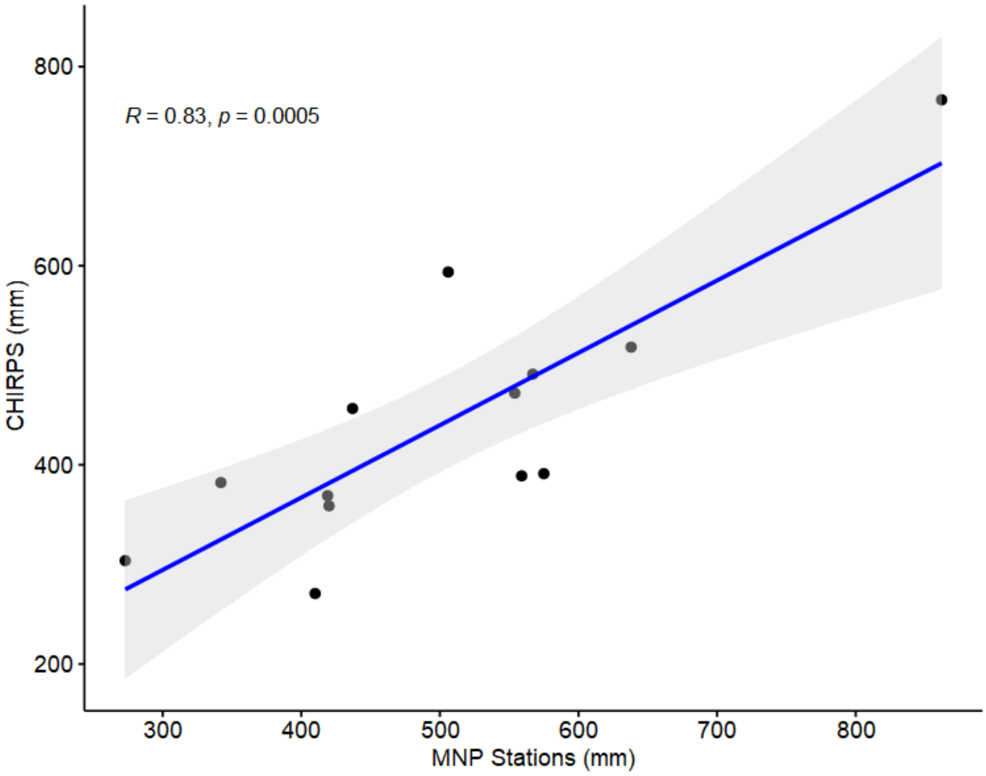
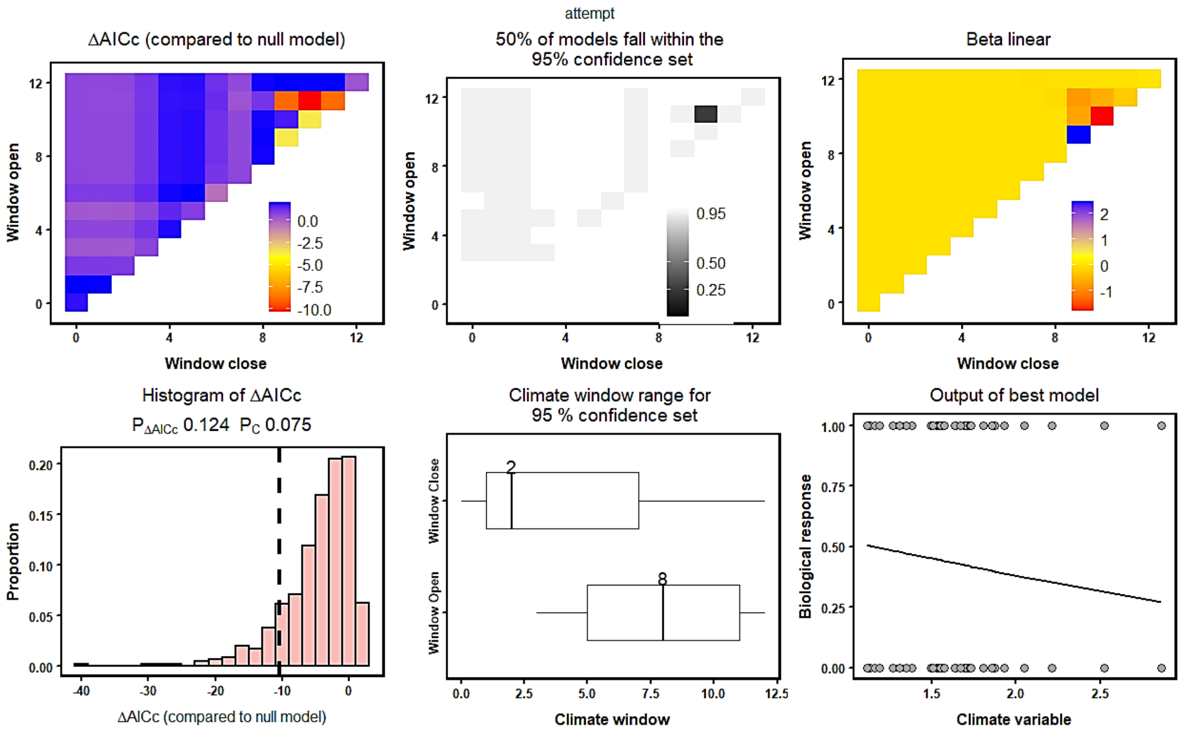
Supplementary Materials



S 1: Rainfall correlation plot between CHIRPS data and Matobo National Park station between 1981-1994.

Table S 1: Top Models for each aggregate statistic and function tested for Breeding Rate

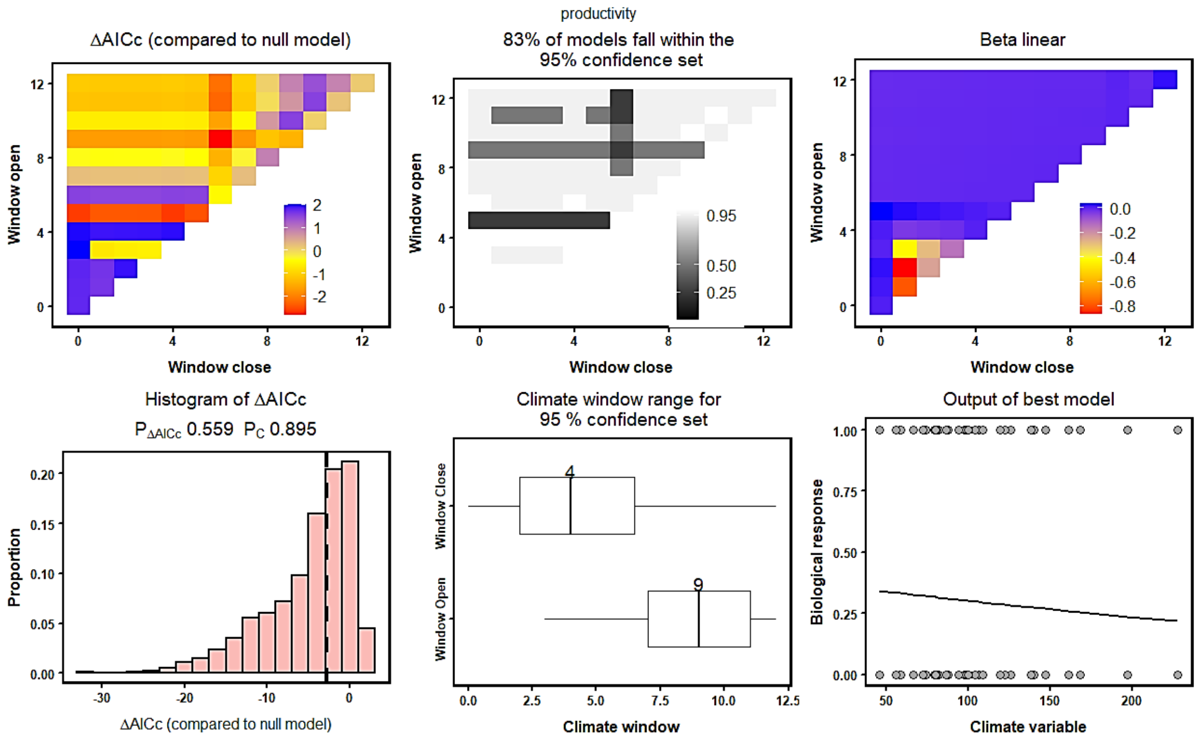
Response	*Climate*	*Type*	*Stat*	*Func*	*Delta AICc*	*Window Open*	*Window Close*
Attempt	Rain	Absolute	Mean	Log	-10.10	11	10
Attempt	Rain	Absolute	Max	Log	-8.55	11	11
Attempt	Rain	Absolute	Mean	Lin	-10.37	11	10
Attempt	Rain	Absolute	Max	Lin	-8.82	11	11
Attempt	Rain	Absolute	Mean	Quad	-28.95	9	9
Attempt	Rain	Absolute	Max	Quad	-28.95	9	9



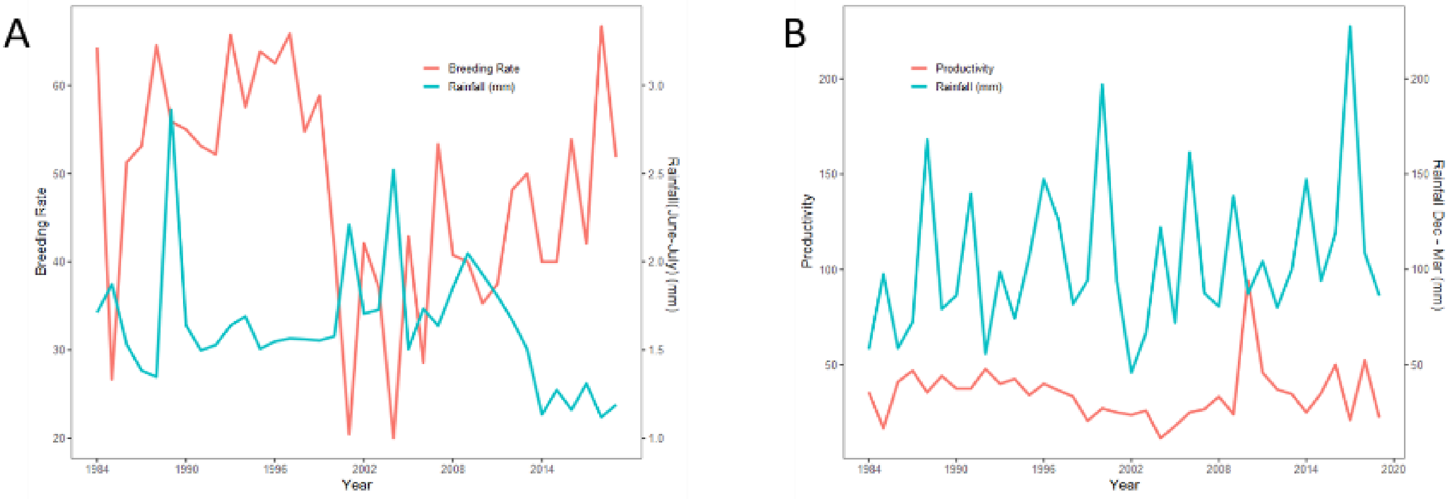
S 2:*Breeding Rate model performance estimates. The best models appear in months against the AICs of the baseline model as the lowest ΔAIC values (red regions).*

Table S 2: Top Models for each aggregate statistic and function tested for Breeding Productivity

Response	*Climate*	*Type*	*Stat*	*Func*	*Delta AICc*	*Window Open*	*Window Close*
Productivity	Rain	Absolute	Mean	Log	-1.77	9	9
Productivity	Rain	Absolute	Max	Log	-1.77	9	9
Productivity	Rain	Absolute	Mean	Lin	-2.83	9	6
Productivity	Rain	Absolute	Max	Lin	-2.46	5	5
Productivity	Rain	Absolute	Mean	Quad	-13.01	5	1
Productivity	Rain	Absolute	Max	Quad	-12.06	5	4



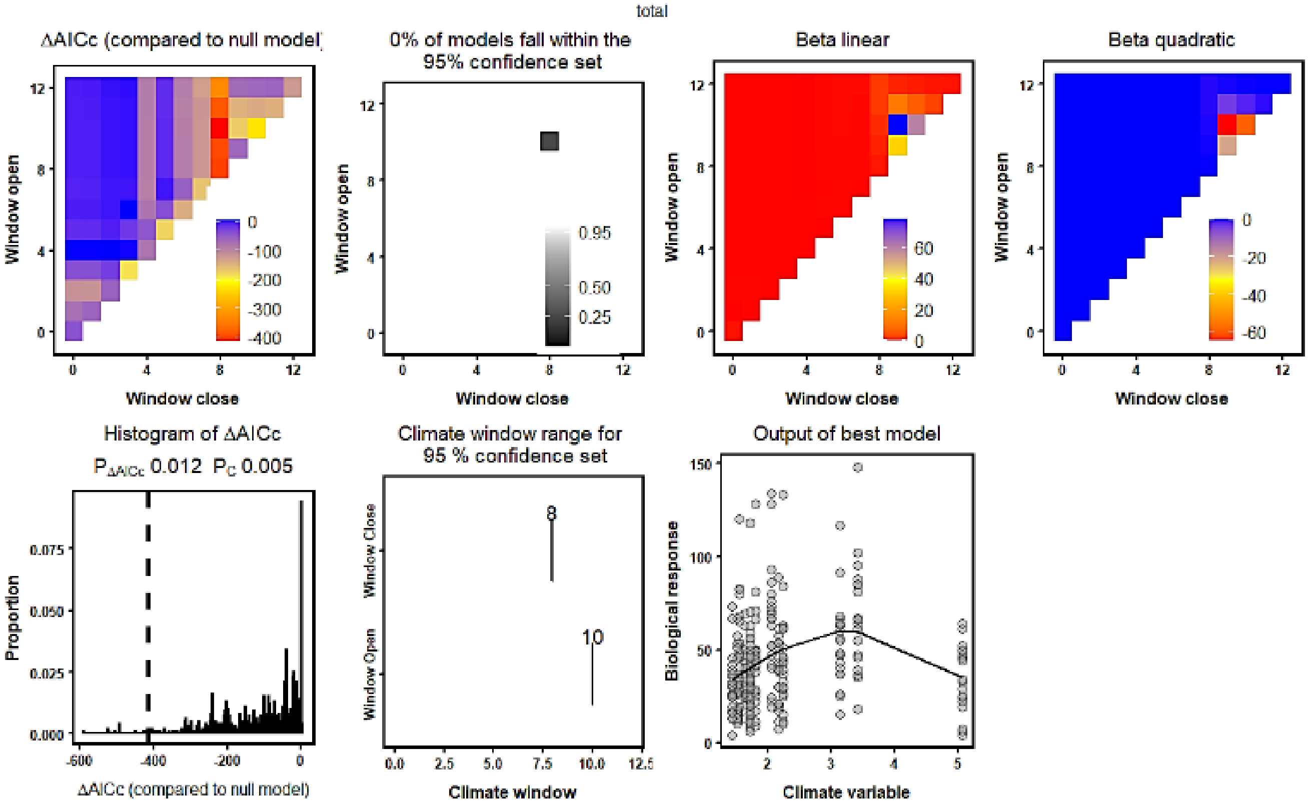
S 3: Model performance estimates for eagle breeding productivity



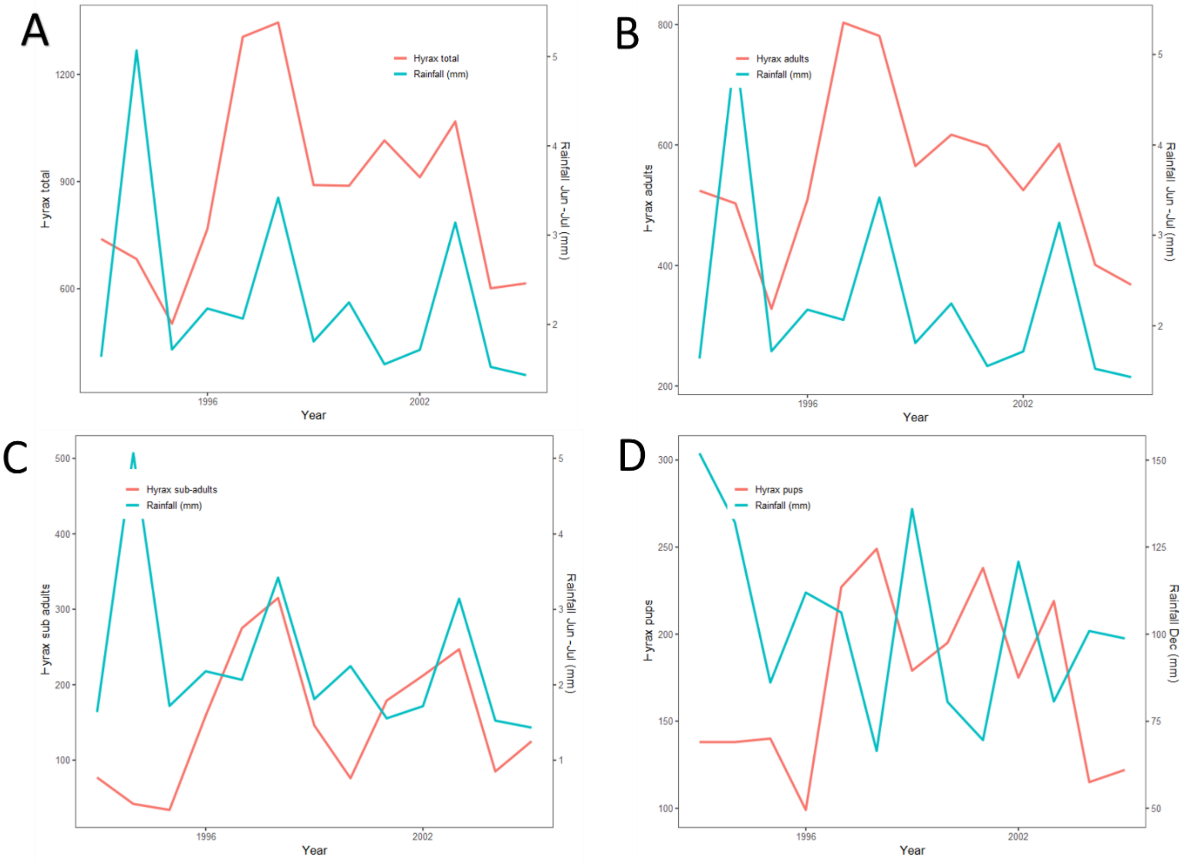
*S 4: **A -** Breeding Rate and rainfall in the climate window June-July from 1984-2019. **B** – Breeding Productivity and Rainfall between December- March*

Table S 3: Top models for each aggregate statistic and function for total numbers of Hyraxes

Response	*Climate*	*Type*	*Statistic*	*Function*	*DeltaAICc*	*Window open*	*Window close*
Totals	Rain	Absolute	Mean	Log	-145.34	3	3
Totals	Rain	Absolute	Max	Log	-145.34	3	3
Totals	Rain	Absolute	Mean	Lin	-124.03	7	7
Totals	Rain	Absolute	Max	Lin	-137.57	8	7
Totals	Rain	Absolute	Mean	Quad	-414.33	10	8
Totals	Rain	Absolute	Max	Quad	-400.37	8	8



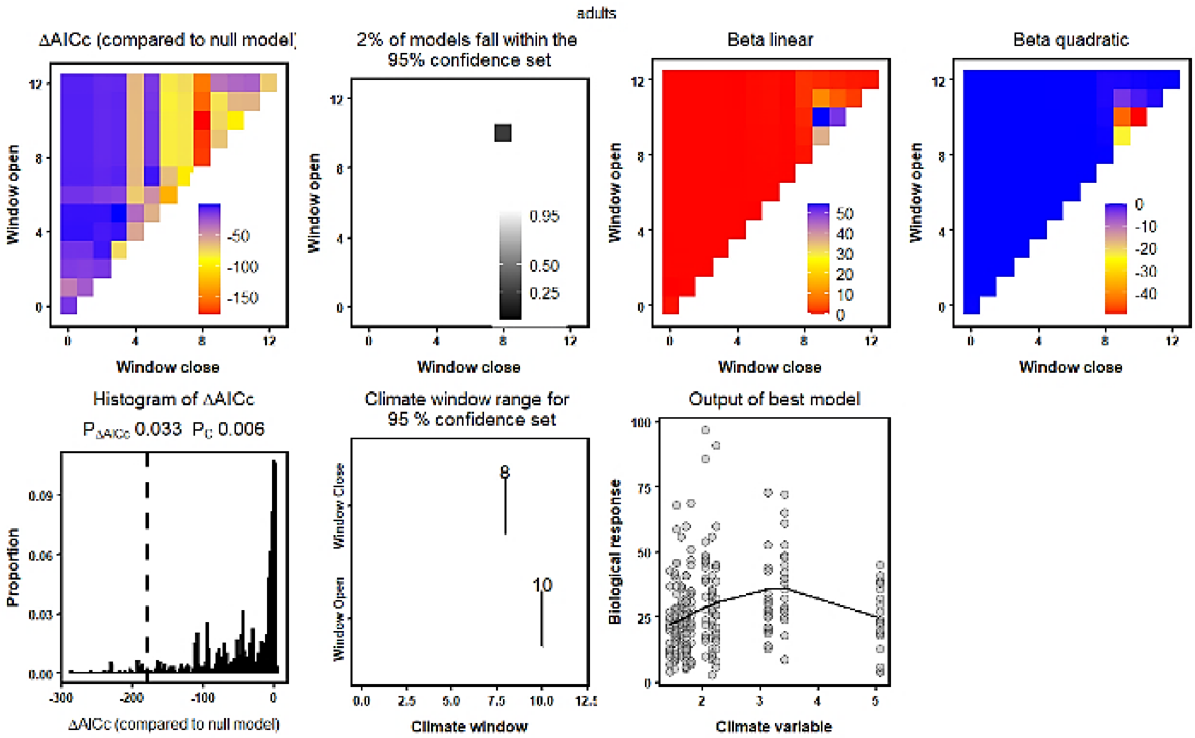
S 5: : ΔAIC performance estimates for the Total number of Hyrax counted. The lowest ΔAIC values are shaded and shown in red against the AIC values of the null model.



S 6: A, B, C – Hyrax Total, Adults and Sub-Adult numbers and rainfall within the July-Sept climate window D- Hyrax Pup numbers and rainfall within the Dec climate window

Table S 4: Top models for each aggregate statistic and function for the Adult Hyrax counted

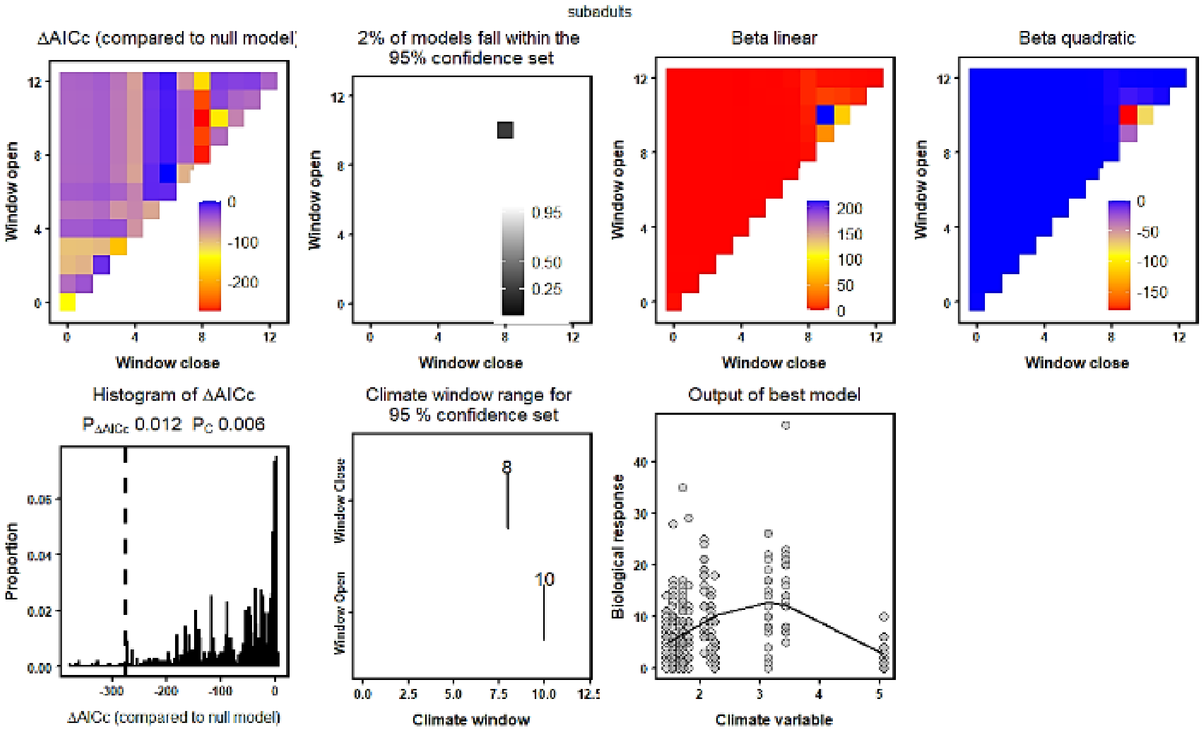
Response	*Climate*	*Type*	*Statistic*	*Function*	*DeltaAICc*	*Window open*	*Window close*
Adults	Rain	Absolute	Mean	Log	-106.48	6	6
Adults	Rain	Absolute	Max	Log	-108.52	7	6
Adults	Rain	Absolute	Mean	Lin	-97.10	7	7
Adults	Rain	Absolute	Max	Lin	-102.96	8	7
Adults	Rain	Absolute	Mean	Quad	-179.03	10	8
Adults	Rain	Absolute	Max	Quad	-171.58	8	8



S 7: Model performance estimates for the numbers of Adult Hyraxes.

Table S 5: Top models for each aggregate statistics and function for Hyrax sub-adults and rainfall

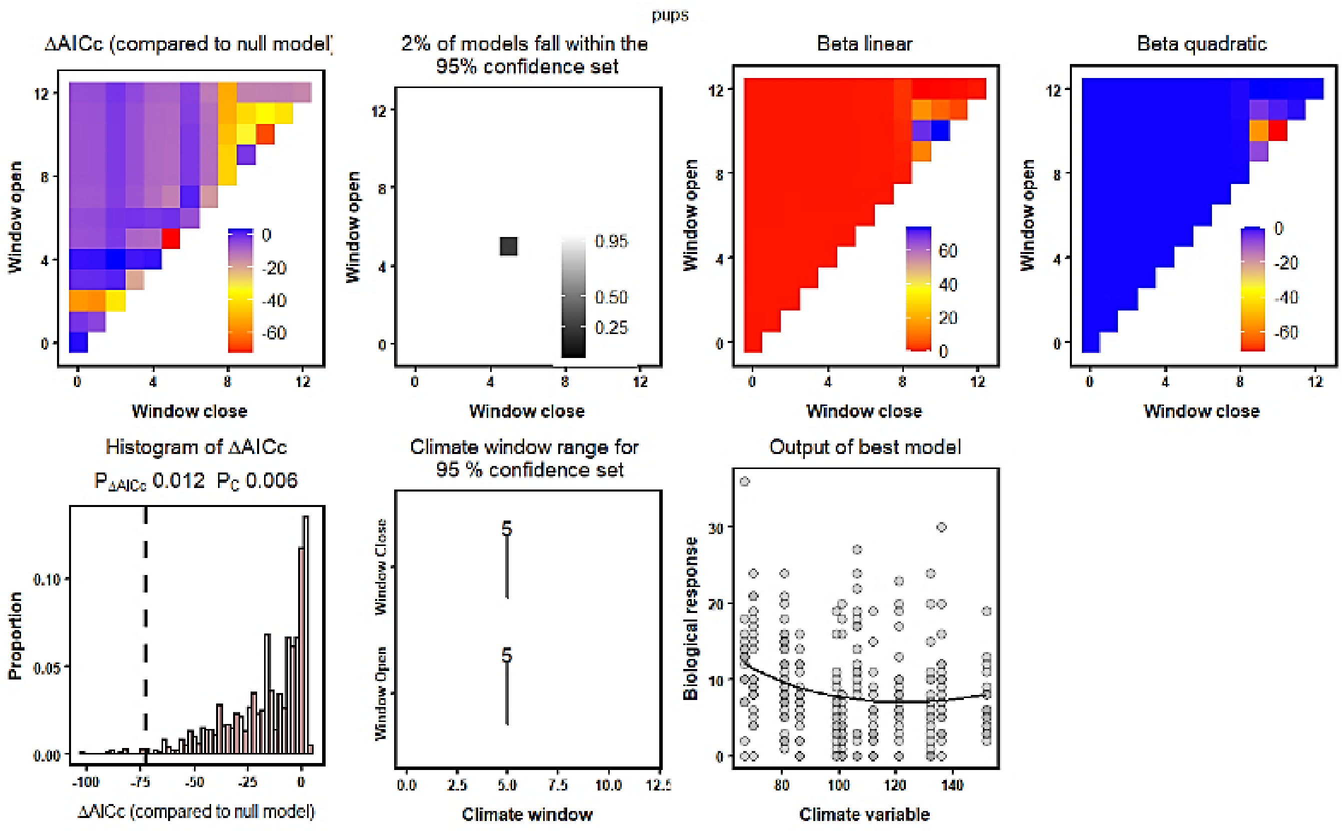
Response	*Climate*	*Type*	*Statistic*	*Function*	*DeltaAICc*	*Window open*	*Window close*
Sub-adults	Rain	Absolute	Mean	Log	-219.34	3	3
Sub-adults	Rain	Absolute	Max	Log	-219.34	3	3
Sub-adults	Rain	Absolute	Mean	Lin	-149.49	3	3
Sub-adults	Rain	Absolute	Max	Lin	-149.34	3	3
Sub-adults	Rain	Absolute	Mean	Quad	-274.43	10	8
Sub-adults	Rain	Absolute	Max	Quad	-272.39	8	8



S 8: Model performance estimates for the numbers of Hyrax sub-adults

Table S 6: Top models for each aggregate statistics and function for Hyrax pups and rainfall

Response	*Climate*	*Type*	*Statistic*	*Function*	*DeltaAICc*	*Window open*	*Window close*
Pups	Rain	Absolute	Mean	Log	-57.85	5	5
Pups	Rain	Absolute	Max	Log	-57.85	5	5
Pups	Rain	Absolute	Mean	Lin	-48.99	5	5
Pups	Rain	Absolute	Max	Lin	-48.99	5	5
Pups	Rain	Absolute	Mean	Quad	-72.33	5	5
Pups	Rain	Absolute	Max	Quad	-72.33	5	5



S 9: Model performance estimates for Hyrax pups