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The impact of weather variation on the body condition of cape cobras (*Naja nivea*) in the Kalahari — implications for climate change

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ABSTRACT

Hot and dry weather conditions are known to impact the body condition and the fitness of many organisms. However, this relationship has not been extensively studied in snakes. We examined the impact of variation in rainfall and temperature on body condition for a population of cape cobras (*Naja nivea*) at Tswalu Kalahari Reserve (Northern Cape Province, South Africa) over a period of five years during which time environmental conditions fluctuated substantially. We measured the mass and body length of 105 cobras, 58 from which we collected repeat measures, and calculated a body condition index (BCI) for each observation. We tested whether BCI was impacted by season, sex, and/or differences from expected mean monthly rainfall (during the preceding four-, 12-, and 24-week periods) and mean daily maximum temperature (during the preceding four-, 12-, and 24-week periods). Secondly, we tested whether BCI measures of cobras during the mating-season (September–November) were different between sexes and impacted by an index of environmental conditions (PC1 of rainfall and temperature) in the preceding summer. For our initial analysis, we found that the best-fitting model included season, sex, the relative amount of rain in the preceding twelve weeks (positive relationship), and the temperature in the preceding twelve weeks (negative relationship). Moreover, the BCI of cobras during the mating season was correlated with environmental conditions during the previous summer, with mating cobras exhibiting lower BCI measures following hot and dry summers. Our study reveals detrimental impacts of hot and dry conditions on cape cobra body condition, including measurable effects on body condition of mate-searching animals, following hot and dry summers. Taken together, we predict that prolonged hot dry periods, or increased frequency of hot dry periods in the future, might have detrimental effects on cape cobra populations in the Kalahari.

1. Introduction

Environmental conditions can have substantial impacts on individual performance, population dynamics, and life-history evolution of organisms. Changes in environmental conditions can destabilise populations (Lindström and Kokko, 2002) and increase their vulnerability to extinction. Moreover, extreme environmental conditions, such as hot and intense droughts, can impact the survival and reproductive success of many vertebrate animals including reptiles (Brown and Shine, 2007), mammals (Recher et al., 2009), and birds (George et al., 1992). Thus, ongoing climate change, including more frequent extremes of environmental conditions as forecast in many climate change scenarios (Garcia et al., 2014), might have major implications for extant biodiversity.

Direct measures of changes in survival and recruitment in response to varying environmental conditions are challenging to make for most types of organisms. This is especially true for organisms that are difficult to census, such as snakes (Durso et al., 2011). As a result, few studies have shown the impact of varying environmental conditions on snake survival and recruitment (Madsen and Shine, 2000a; Čubrić et al., 2023). Rather, most of what is known about this relationship has been inferred from changes in the body condition of individuals within a population, through time, in relation to changing environmental conditions (MacCracken, 2005), under the assumption that body condition is correlated with fitness. In such cases, body condition is viewed as a proxy of an animal's fitness that assesses the animal's energy reserves relative to its body size (Green, 2001; Falk et al., 2017).

Snakes are known to exhibit variation in body condition in response to different environmental conditions (Madsen and Shine, 2000b; Čubrić

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et al., 2023) with important implications for their biology. For instance, Madsen and Shine (2000a) observed that the body condition of individual *Acrochordus arafurae* varies annually depending on the amount of rainfall and food availability. Additionally, Dezetter et al. (2021) found that *Vipera berus* experienced dehydration and muscle mass loss due to drought. Moreover, in *Vipera aspis*, individuals with below-average body condition exhibit reduced sexual receptivity (Aubret et al., 2002). In some cases, female snakes below a specific body condition threshold may be unable to reproduce, and females that do reproduce can face a higher risk of mortality (Luiselli et al., 1996). During the mating season, male snakes generally forgo feeding (Madsen and Shine, 2000c) which can result in a decrease in body condition. Males in relatively poor body conditions may not have sufficient reserves for extensive mate-searching activities (Glaudas et al., 2020). These studies indicate the importance of environmental conditions on the body condition of snakes and how these variations can impact various aspects of their biology, especially reproduction.

The Kalahari Desert is a large, semi-arid, sandy savanna (Lovegrove, 2021). The area experiences interannual and seasonal variation in rainfall and temperature. Climate change in this region has led to reductions in moisture availability and higher evaporative water loss from certain animals as a result of temperature increases (Shongwe et al., 2009). The region is predicted to become drier and hotter in the future (Engelbrecht et al., 2015). These changing conditions are expected to impact several species, but the likely impact on reptiles remains unknown. It is unclear how increases in the frequency and duration of atypically hot and dry conditions are likely to impact snakes such as cape cobras (*Naja nivea*), which occur in hot and dry regions (Shongwe et al., 2009). These large-bodied snakes are widespread and abundant in the Kalahari and are important predators to several species, including at least one ecosystem engineer, the sociable weaver (*Philetairus socius*; Covas et al., 2004; Lowney and Thomson, 2023). During hot and dry periods, snakes may not be able to forage effectively because of high temperatures, shortages of prey animals, or dehydration from excessive water loss.

We aimed to examine the impact of rainfall and environmental temperature on the body condition of cape cobras (*Naja nivea*) in the Kalahari Desert. Our objectives were: (1) to measure the mass and body length of snakes and calculate a body condition index (BCI) for each observation, and (2) test whether BCI is correlated with environmental conditions (temperature and rainfall) and/or season or sex. We additionally tested whether (3) BCI during the mating-season (September–November) is influenced by sex and an environmental index (PC1 = cumulative rainfall and average daily maximum temperature) from the previous summer. We chose to test the hypothesis that previous summer conditions influence snake body condition during the mating season because reproduction is energetically costly and individuals in better condition may have higher reproductive success (Naulleau and Bonnet, 1996; Aubret et al., 2002; Glaudas et al., 2020). While body condition may be influenced by multiple seasons, the previous summer may be particularly crucial for resource accumulation necessary during the mating season (Lourdais et al., 2002).

2. Materials and methods

2.1. Study species

The cape cobra (*Naja nivea*) is a medically important elapid that occurs throughout the western parts of southern Africa in a variety of habitats. Average body size is 1100 mm SVL, but some individuals can reach large body sizes of nearly 2 m (Marais, 2022). Cape cobras are dietary generalists and consume prey from a variety of tetrapod classes (Maritz et al., 2019). In the Kalahari, cape cobras also forage intensively on sociable weaver chicks and eggs when these birds breed (Maclean, 1973). Sociable weavers breed during the austral summer and breeding activity is linked to rainfall (Covas et al., 2006) meaning that drought conditions also have the potential to disrupt food availability for foraging snakes.

2.2. Study site

We studied cape cobras at Tswalu Kalahari Reserve (TKR; Fig. 1), situated in the Northern Cape Province of South Africa (27° 14′57″ S, 22° 22′52″ E; 1020–1586 masl). TKR is situated along the Korannaberg Mountains and is characterised by low-lying Kathu Bushveld, Olifantshoek Plains Thornveld and Gordonia Plains Shrubland surrounding Koranna-Langeberg Mountain Bushveld on the rocky hillslopes (Mucina and Rutherford, 2006). The region experiences variable rainfall and intermittent droughts. Rainfall occurs mainly between December and April (Davis et al., 2010). The mean annual rainfall at Tswalu Kalahari Reserve over the past 5 years averaged 377 mm ± 142.96 mm (Fig. 2). The dry season is from June to August with little or no rainfall occurring. During our study, we recorded mean maximum temperature of 31.2 °C (±5 °C), and mean minimum temperature of 11.5 °C (±7 °C) at the Van Zylsrus station (ID: 68330; 26.8787° S, 22.0554° E; located ~68 km from TKR; South African Weather Service, 2022, Fig. 2).

2.3. Data collection

We actively searched for cape cobras opportunistically between March 2017 and March 2022. Snakes were located in a variety of contexts: foraging in the open; visible in the entrance of animal burrows; coiled up in sociable weaver nest chambers; or foraging in sociable weaver nests. Females with overt signs of eggs and any animal with overt feeding bulges were not included in the analysis. Mass, snout-vent length (SVL), tail length (TL), sex, and date of capture were recorded for each snake. Captured snakes were weighed to the nearest gram using a digital scale. SVL and TL were measured by placing the anterior part of the snake's body into a transparent tube and measuring (to the nearest mm) the distance between the tip of the snout and the cloaca (SVL) and the distance between the tip of the tail and the cloaca (TL) using a tape measure. Snakes were sexed by probing (Krause et al., 2003). Each individual was implanted with a PIT tag (Passive Integrated Transponders)

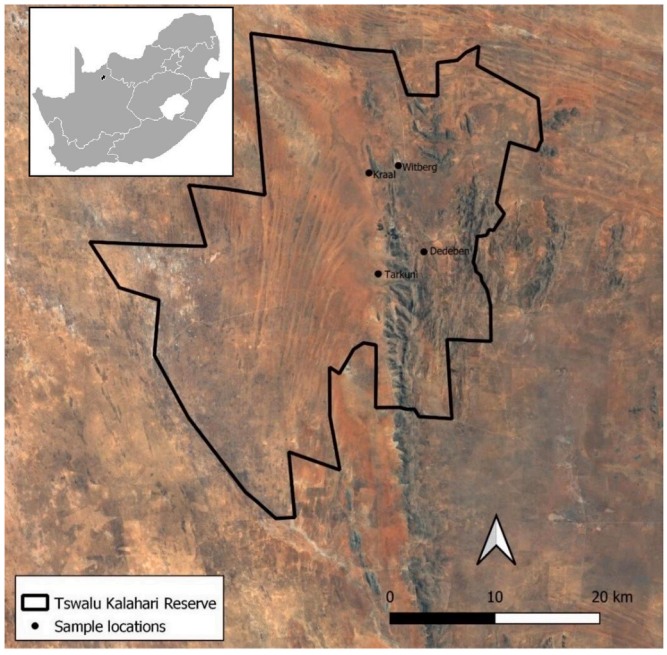


Fig. 1. Geographical location of Tswalu Kalahari Reserve, located in the Northern Cape Province, South Africa. The Korranaberg mountains can be seen running along a north-south axis. Sample locations are reflected as black dots.

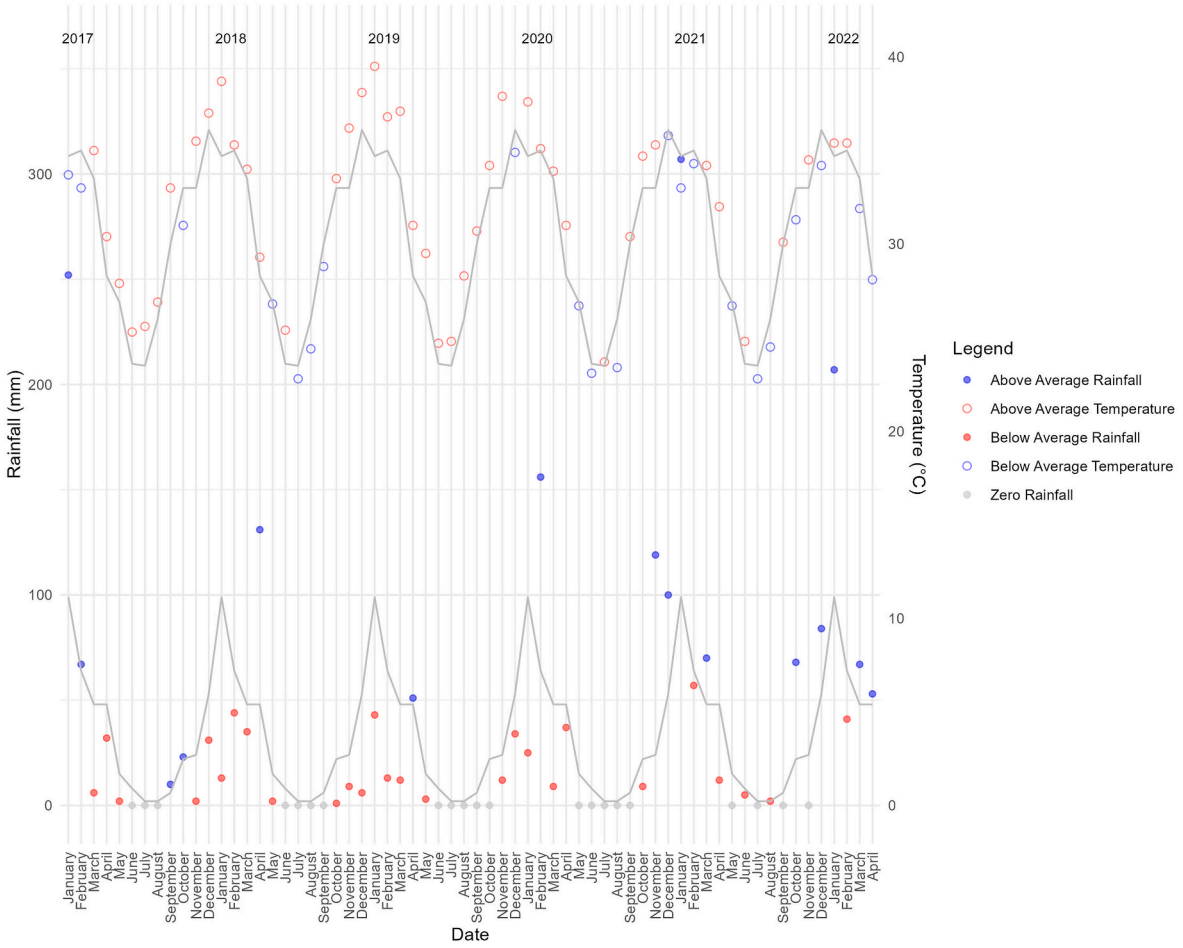


Fig. 2. Long-term monthly average rainfall (a) and temperature (b) in grey lines, with observed monthly rainfall and temperature at Tswalu Kalahari Reserve between January 2017 and April 2022 shown as mean value across four rain gauges. Grey circles represent winter (no rainfall) months. Red circles represent months with below average rainfall or higher temperature. Blue circles represent months with above average rainfall and cooler temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

for unique identification. All captured snakes were released at or near their point of capture following measurements. We captured, processed, and released 105 individual cobras, with 58 individuals being sampled more than once. These included 56 males, 39 females and 10 juveniles.

2.4. BCI analysis

To estimate body condition, we performed a linear regression analysis between log-transformed mass and log-transformed SVL on the entire dataset. A residual analysis was conducted to check for assumptions of linearity, normality and homoscedasticity. We tested for linearity in the relationship between mass and SVL by creating scatter plots of the raw and log-transformed data, visually assessing the fit of the linear model. Normality ($W = 0.98$, $P = 0.12$) and homoscedasticity ($BP = 1.11$, df $= 1$, $P = 0.29$) assumptions were not violated. Body condition index (BCI), defined as the residuals of the regression of mass on SVL, was calculated as the residual scores from the linear regression of log-transformed mass versus log-transformed SVL (Fig. 3). Positive BCI measures correspond to individuals with above average body condition (i.e., higher mass than expected for a typical snake of that length) and negative BCI measures correspond to individuals with poor body condition (i.e., lower mass than expected for a snake of that length). We also calculated the BCI measure for each observation ($N = 163$).

All statistical analyses were carried out using R software (R Core Team, 2017). The following R packages were used for data cleaning and modelling: tidyverse (Wickham et al., 2019), lmtest (Hothorn et al., 2015), dplyr (Wickham and Bryan, 2023), lubridate (Grolemund and Wickham, 2011).

2.5. Environmental covariates

2.5.1. Rainfall and temperature

Rainfall data from TKR were used to calculate average monthly rainfall across four rain gauge stations (Dedeben, Kraal, Witberg, and Tarkuni) within the reserve from 2001 to 2022 (Fig. 2). Lagged rainfall was calculated as the sum of rainfall over the previous 4-weeks, 12-weeks, and 24-weeks for each snake observation date. These measure account for the lagged effects of rainfall on snake traits, primarily body mass (g). We calculated average maximum temperature using daily maximum temperature data (2017–2022) from the Van Zylrus weather station (ID: 68330; 26.8787° S, 22.0554° E; located ~68 km from TKR), which was provided by the South African Weather Services (Fig. 2). Lagged temperature was calculated as the average maximum temperature over the past 4-weeks, 12-weeks, and 24-weeks for each day.

Cumulative rainfall and temperature in the preceding summer (December–April) were used to assess the effects of weather conditions on body condition of snakes in the mating season (September–November). The data included observations from the mating season (Spring) and individuals with SVL greater than 1000 mm. Because measures of cumulative rainfall and temperature were strongly correlated ($r = -0.86$), we performed a principal component analysis (PCA) to reduce the two correlated variables to a single variable (PC1) which

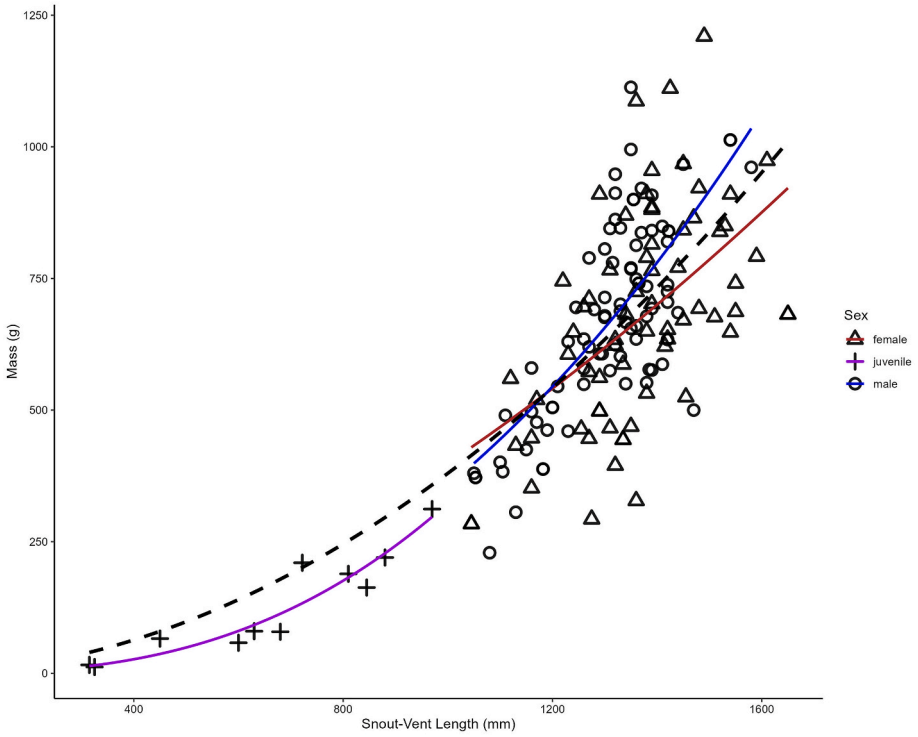


Fig. 3. The relationship between mass and snout-vent length (SVL) in a population of Cape cobras (*Naja nivea*). Curves were fit using a power function to the untransformed data, with statistical analyses performed on log-transformed values. Fitted lines are represented for each group: males (blue), females (brown), and juveniles (purple). An overall fit for all data is shown as a dashed black line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

explained 93 % of the variance of rainfall and temperature. PC1 can be interpreted as describing environmental conditions along a cool/wet to hot/dry gradient.

2.5.2. Season and sex

Because body condition can vary seasonally, and between sexes, we incorporated these variables into the analysis. BCI measures were classified into one of four seasons based on their date of measurement ('Spring' = September, October, November; 'Summer' = December, January, February; 'Autumn' = March, April, May; 'Winter' = June, July, August). Because snakes generally brumate through winter, we excluded winter months from our analyses, excluding four observations of snakes. Sex was assessed by including both juvenile and adult males and females in the overall analysis.

2.5.3. Size and maturity

Individuals larger than 1000 mm SVL were classified as adults and under 1000 mm SVL were classified as juveniles. Males and females do not differ substantially in their morphology (Shine et al., 2007) suggesting that they mature at similar rates and reach adulthood at comparable sizes. In the absence of any data for size at maturity, we selected 1000 mm based on our field observations that dark throat band present in juvenile animals is lost at approximately this size. Animals below 1000 mm SVL were excluded from the mating season analysis. Most individuals in the study were recorded in the dataset only once. However, six individuals had multiple observations, primarily in different years. Only one individual had multiple observations in the same year, but these were from different months.

2.6. Model building and model selection

2.6.1. The impact of environmental conditions on BCI – general model

Linear regression models with normal error distributions were used to test the effect of rainfall, temperature, sex and season on body condition. Using the full dataset (all 163 BCI measures), we evaluated 29 different models which correspond to specific plausible biological hypotheses (Burnham and Anderson, 1998). The corrected Akaike's Information Criterion (AICc) was used to choose between different models, treating different models with ΔAICc >2 as performing differently. The model with the lowest AICc value was considered the best compromise between model deviance and model complexity. Additionally, AICc weight (w) is reported, which reflects the relative likelihood of a specific model being the best-fitting model among all the possible models (Anderson and Burnham, 2002).

2.6.2. The impact of environmental conditions during the preceding summer on BCI – mating-season model

We modelled PC1 (cumulative rainfall and average daily maximum temperature) in the preceding summer (December–April) and sex as predictor variables for the 51 BCI measures collected from adult snakes (males and females) during the mating period. The corrected Akaike's Information Criterion (AICc) was employed to differentiate between competing models. Additionally, we predicted the BCI of mating-season cobras across the range of PC1 values.

3. Results

3.1. Body condition

There was a significant linear relationship between log transformed mass and log transformed SVL (ln Mass = 2.56 × ln SVL – 11.79; R^2 = 0.86; $P < 0.001$; Fig. 3).

3.2. The impact of environmental conditions on BCI – overall model

The top performing model (BCI ~ Season + Sex + Rain 12 + Temp

12) outperformed all other models (including the null model; Table 1) and was selected as our preferred model based on its low corrected Akaike Information Criterion (ΔAICc = 0.00) and relatively high Akaike weight (AICcwt = 0.82). In the preferred model, BCI was significantly impacted by season (ANOVA; $F_{2,156} = 4.64$; $P = 0.011$), rainfall in the preceding 12-weeks (ANOVA; $F_{1,156} = 52.41$; $P < 0.001$), temperature in the preceding 12-weeks (ANOVA; $F_{1,156} = 21.97$; $P < 0.001$), and sex (ANOVA; $F_{2,156} = 6.86$; $P = 0.003$). Specifically, males had a higher BCI compared to females (β = 0.11, SE = 0.03, $P < 0.001$; Table 2). BCI was positively correlated with rainfall and negatively correlated with temperature within 12-weeks preceding capture in all plausible models (Table 1).

Because we detected a sex effect in the analysis, we additionally reran the models separately for males and females. The findings of these sex-specific models were broadly congruent with our analysis of the pooled data. For females, the comparative model (BCI ~ Season + Rain 12 + Temp 12) was among the top performing models (ΔAICc = 1.56; Supplementary Table S1). Among males, however, the comparative model (BCI ~ Season + Rain 12 + Temp 12) ranked second (ΔAICc = 4.12; Supplementary Table S2) behind a model without season (BCI ~ Rain 12 + Temp 12; AICc wt = 0.79). Thus, it appears as though the season effect seen in our pooled model is likely driven by females.

3.3. The impact of environmental conditions during the preceding summer on BCI – mating-season model

The first (BCI ~ PC1) and second (saturated) models performed similarly (ΔAICc = 0.96) and both outperformed the remaining models, including the null model (Table 3). The variance of the first model (BCI ~ PC1; $R^2 = 0.12$) and the second model (BCI ~ PC1 + Sex; $R^2 = 0.14$) were similar with AICc weights of 0.54 and 0.34 respectively. ANOVA revealed that BCI was significantly impacted by PC1 (ANOVA; $F_{1,49} = 7.007$; $P = 0.010$). Based on AICc, the model with the lowest AICc (BCI ~ PC1) was selected as the best model (β = −0.06, SE = 0.02, $P < 0.05$; Table 4). However, sex may have an impact on BCI during the breeding season (Supplementary Table S3).

Body condition increased as conditions became cooler and wetter. This suggests that hot and dry periods during the previous summer results in poorer BCI measures for mating-season snakes (Fig. 4).

Table 2
Summary of model parameters for the best-fitting model explaining BCI variation. Estimates, standard errors, and significance tests are shown for the effects of season (reference: Winter), rainfall in the preceding 12-weeks, temperature in the preceding 12-weeks, and sex (reference: Female).

Variable	Estimate	Std. Error	T	P
Season (Spring)	−0.19	0.09	−1.98	0.040
Season (Summer)	−0.06	0.03	−1.77	0.077
Sex (Juvenile)	−0.01	0.06	−0.27	0.782
Sex (Male)	0.11	0.03	3.71	<0.001
Rainfall (12 weeks)	0.00	0.00	4.65	<0.001
Temperature (12 weeks)	−0.04	0.01	−3.90	<0.001

Table 3
Model selection based on linear regression models of mating-season snakes. Model parameters include sex (male and female) and PC1 (an index of environmental conditions). K is the number of parameters in the model. AICc is the corrected Akaike Information Criterion. ΔAICc is the difference between the best model (lowest AICc) and the AICc of the model considered. AICcw is the AIC weight representing the relative likelihood of the model considered. The best-fitting model is shown in bold.

Model	K	AICc	ΔAICc	AICc wt
PC1	**3**	**−16.28**	**0.00**	**0.54**
PC1+Sex	4	−15.31	0.96	0.34
Sex	3	−12.08	4.20	0.07
Null	2	−11.72	4.56	0.06

Table 1
Model selection based on linear regression. Model parameters included season (summer, autumn, spring), sex (male, female, juvenile), rainfall (in the preceding 4-, 12-, 24- weeks), and temperature (in the preceding 4-, 12-, 24- weeks). K is the number of parameters in the model. AICc is the corrected Akaike Information Criterion. ΔAICc is the difference between the best model (lowest AICc) and the AICc of the model considered. AICcw is the AIC weight representing the relative likelihood of the model considered. The best-fitting model is shown in bold.

Model	K	AICc	ΔAICc	AICc wt
Season + Sex + Rain12+Temp12	**8**	**−68.90**	**0.00**	**0.72**
Sex + Rain12+Temp12	6	−66.97	1.93	0.28
Season + Sex + Rain12	7	−55.91	12.99	0.00
Season + Sex + Temp12	7	−54.12	14.78	0.00
Season + Sex + Rain4+Temp4	8	−47.46	21.44	0.00
Sex + Rain24	5	−46.16	22.74	0.00
Sex + Rain4+Temp4	6	−45.24	23.66	0.00
Season + Sex + Rain24	6	−44.89	24.01	0.00
Season + Sex + Temp4	7	−44.65	24.25	0.00
Sex + Rain24+Temp24	6	−44.34	24.56	0.00
Season + Rain12	5	−43.94	24.96	0.00
Season + Sex + Rain24+Temp24	7	−42.61	26.29	0.00
Sex + Rain12	5	−37.56	31.34	0.00
Season + Sex + Rain4+Temp4+Rain12+Temp12+Rain24+Temp24	11	−37.26	31.64	0.00
Rain24	3	−35.69	33.21	0.00
Season + Rain24	4	−34.82	34.08	0.00
Temp4	3	−34.54	34.36	0.00
Rain12	3	−28.77	40.13	0.00
Season + Sex + Temp24	7	−28.40	40.50	0.00
Season + Sex + Rain4	7	−25.31	43.59	0.00
Temp12	3	−16.34	52.56	0.00
Season + Rain4	5	−14.67	54.23	0.00
Season + Sex	6	−12.85	56.05	0.00
Sex + Rain4	5	−11.48	57.42	0.00
Sex	4	−11.04	57.86	0.00
Season	4	−7.70	61.20	0.00
Temp24	3	−6.15	62.75	0.00
Null	2	−5.80	63.10	0.00
Rain4	3	−4.87	64.03	0.00

Table 4
Summary of best-fitting model to explain BCI variation. Estimates, standard errors, and significance tests are shown for the effects of environmental conditions (PC1 of rainfall and temperature).

Variable	Estimate	Std. Error	T	P
PC1	−0.07	0.02	−2.64	0.010

4. Discussion

Our results revealed that body condition of cape cobras was strongly influenced by rainfall and temperature, with hot and dry conditions resulting in poorer body condition. Moreover, this effect was detectable throughout the dataset, and within a subset of measures made during the mating period, with implications for organismal fitness. Although our work was based on indirect measures of fitness, our findings strongly suggest that bouts of hot and dry weather have fitness effects on Kalahari cape cobras and are likely to have negative impacts on populations, with prolonged or more frequent bouts of hot and dry weather resulting in reductions of population sizes.

Cape cobra body condition showed a positive relationship with rainfall and a negative relationship with temperature. There are two mechanisms which might result low BCI measures during hot and dry weather—reduced energy reserves and/or dehydration. However, energy reserves and water balance are not independent physiological factors. Water intake for most arid zone snakes is dominated by water from prey (Lillywhite, 2017). Thus, dehydration may result from reduced prey intake, which in turn could also result in reduced energy reserves. Moreover, water retention is facilitated by fat within the body such that reductions in energy reserves (stored as fat) are likely to limit water storage capacity (Jones et al., 2020). Regardless of cause, dehydration can have substantial impacts on fitness, primarily through its impact on reproduction (Dezetter et al., 2021).

Reduced energy reserves due to hot/dry periods are likely to arise through a combination of factors including (1) reduced food availability, (2) reduced foraging time, and (3) higher foraging costs. Prey availability can be strongly influenced by rainfall (e.g., Madsen and Shine, 2000a). In arid environments in particular, high rainfall typically increases food availability while low rainfall disrupts primary productivity and can limit prey abundance (Hsu et al., 2012). In the Kalahari, sociable weavers drastically reduce or even cease breeding during periods of low rainfall. Because it is primarily the eggs and chicks of sociable weavers that are consumed by cobras (Covas et al., 2004), a reduction in sociable weaver breeding resulting from hot and dry conditions is likely to drastically reduce food availability for the cape cobras in the Kalahari. Low rainfall is also likely to reduce populations of small mammals (Linzey and Kesner, 1997)—another important component of cobra diets (Maritz et al., 2019). Even without prey declines, hot conditions may limit the amount of time that cobras are able to allocate to foraging, thereby limiting energy intake. Surface temperatures at TKR regularly exceed temperatures that would be lethal to a cobra foraging on the surface for a sustained period. Importantly, although cape cobras are predominantly diurnal, we have observed surface activity at nighttime during bouts of hot weather. This behavioural shift may somewhat mitigate against the effect of extreme temperatures on foraging time. Finally, hot and dry conditions might increase foraging costs through higher metabolic expenditure such that less energy is stored. These pathways are not-mutually exclusive, and the variation in body condition observed during our study may be the result of these mechanisms working synergistically.

We found that males are generally heavier than females of the same length. Sex effects such as these are common in measures of body condition in snakes (Čubrić et al., 2023). One explanation for such sex effects is sexual dimorphism in gross morphology (Shine, 1989), however, previous studies on *N. nivea* have indicated limited evidence of sexual dimorphism in body size (Shine et al., 2007). In the absence of overt sexual dimorphism in gross morphology, sex effects may arise because of sex differences in life history (Madsen and Shine, 2000c). Females may experience variation in body condition due to the process of resource accumulation for breeding, carrying eggs, and the associated costs (Lourdais et al., 2002), while extensive mate searching by males could potentially decrease their body condition (Glaudas et al., 2020). The relative energetic costs of these behaviours have not previously been studied in cobras, but the large number of sex-specific energetic costs

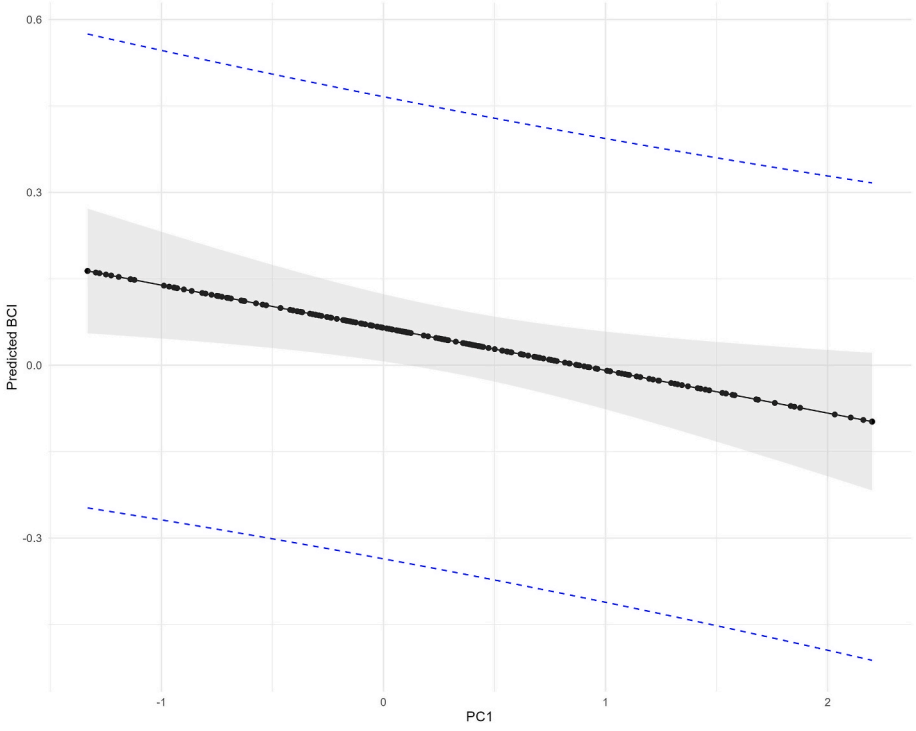


Fig. 4. Predicted body condition index (BCI) based on rainfall and temperature in the preceding summer (PC1). Predicted intervals are included.

experienced by female and male snakes make the presence of sex effects in our study unsurprising.

Our work revealed important lag periods in the clearest relationships between environmental conditions and the body condition of cobras. The overall model included rainfall in the preceding 12-weeks as a factor outperformed competing models based on four or 24-weeks. A 12-week lag period may reflect a balance in the amount of time required for mammalian and avian prey populations to become available as food sources for cobras. In many desert rodent species, reproductive activity is closely linked to rainfall and the resulting increase in primary production (Christian, 1979, 1980). Similarly, rainfall influences breeding in birds in arid regions, often resulting in increased clutch sizes and breeding success. Rainfall promotes rapid vegetation growth, and birds typically begin laying eggs within two weeks of summer rainfall in the Kalahari (Maclean, 1969). Thus, the 12-week lag period likely represents the time required for plant growth, animal reproduction and subsequent increases in potential prey availability, and the consumption of multiple meals by foraging snakes. We also found a significant effect of environmental conditions from the preceding summer on mate-searching snakes, suggesting potential longer-term effects. Taken together, these findings emphasise that environmental extremes can impact animals at different temporal scales.

So, are cape cobra populations likely to be sensitive to reductions in fecundity resulting from poor body condition? Relatively little is known about the demography or population dynamics of cape cobras (Shine et al., 2007), and much of what is known is potentially derived from populations in cooler, more mesic environments closer to major urban centres. Cape cobras appear to have seasonal reproduction (Shine et al., 2007), laying 8–20 eggs (Branch, 1998). Relatively small clutch sizes, and the scarcity of juveniles in our study may suggest relatively low fecundity. Low fecundity is presumably offset by relatively high survival rates (although survival rates remain to be estimated for any population of cape cobras) but may indicate limited capacity to recover from large population declines. Any reduction in fecundity or reduction in hatchling survival resulting from mothers in poor condition could potentially have substantial negative impacts on populations.

Despite the correlational nature of this study, the observed relationships between body condition and environmental factors clearly suggest that hotter and drier conditions can challenge the fitness of cape cobras, and other species in arid environments. These findings highlight the demographic risks posed extreme weather events, particularly in already extreme environments. They also highlight a potential pathway through which climate change might impact similar fauna. By doing so, our study contributes to a broader ecological understanding of climate impacts in desert environments and offers a framework for predicting similar challenges and risk for other desert ectotherms.

5. Conclusion

In conclusion, hot and dry periods have strong effects on body condition in cape cobras, with periods of drought causing poorer snake BCI. Prolonged hot and dry periods, or increased frequency of hot and dry periods in the future may have detrimental effects on cobra fitness, and thus populations, in the Kalahari. While cape cobras appear to cope with current conditions, an increase in the duration or frequency of hot and dry periods is likely to have substantial demographic effects, with potential effects of declines in some populations.

CRediT authorship contribution statement

Kim J. Scholtz: Writing – original draft, Methodology, Investigation, Formal analysis. **Graham J. Alexander:** Writing – review & editing, Supervision. **Thilo F. Beck:** Writing – review & editing, Data curation. **Robin A. Maritz:** Writing – review & editing, Visualization, Validation, Supervision, Formal analysis. **Bryan Maritz:** Writing – review & editing, Supervision.

Data availability

Datasets and R code used in this study are available on Figshare.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2025.105398.

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