

# **Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat**

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Lay summary: Meerkats live in groups in which older animals assist in rearing pups by providing food for the pups. Despite that support, increasing air temperatures over the past two decades have been associated with reduced growth and survival of pups. Climate change may threaten the continued survival of meerkats in arid zones.

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## Abstract

1. Breeding systems in which group members help to raise the offspring of co-members are associated with arid, unpredictable environments. Cooperative rearing may mitigate the effects of adverse environmental conditions on pup growth and survival. However, few studies have explored the relationship between environmental variation and breeding success, and the role of helpers.
2. Here we show that increases in daily maximum air temperatures ( $T_{\max}$ ) in the southern Kalahari over the last twenty years have been associated with reductions in the growth and survival of meerkat (*Suricata suricatta*) pups.
3. On days when  $T_{\max}$  was high, meerkat pups gained less body mass than on cooler days. Reductions in the diurnal body mass gain ( $\Delta M_b$ ) of pups on hotter days were not a consequence of reductions in the frequency with which pups were fed by adults as feeding rate increased with  $T_{\max}$ , suggesting that the reductions in  $\Delta M_b$  by pups on hot days reflected a decrease in water content of the food items or an increased water and energy cost of thermoregulation.
4. Reductions in pup  $\Delta M_b$  on hot days were smaller in larger groups, in which helper-to-pup ratios were relatively high.
5. As further increases in air temperature are predicted with climate change, further reductions in meerkat pup growth and survival seem inevitable.

Key words: Thermoregulation, Evaporative heat loss, Growth, Meerkat

## Introduction

Cooperative breeding in birds and mammals is associated with unpredictable, arid habitats (Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017). The involvement of multiple adults in provisioning young may buffer dependent young against the consequences of adverse environmental conditions, allowing cooperative species to persist better than species that do not employ cooperative breeding in hot and dry habitats (Langmore *et al.* 2016). The cooperative birds and mammals of the Kalahari provide opportunities to explore the effects of climate change on growth, reproduction and survival and the extent to which these may be modified by cooperative feeding of young by helpers. Daily maximum air temperature ( $T_{\max}$ ) in the arid zones of southern Africa has increased over the last three decades (Kruger & Sekele 2012; van Wilgen *et al.* 2016; Lukas & Clutton-Brock 2017), and is predicted to continue to increase and to be associated with an increased occurrence of droughts and reductions in food availability for many species (Joubert *et al.* 1999; Huxman *et al.* 2004). The requirement for evaporative water loss in birds and mammals increases with increasing environmental temperatures, requiring greater water intake (Smit & McKechnie 2015). In addition, higher air temperatures are associated with more frequent selection of cooler microsites, reducing foraging time (Cunningham, Martin & Hockey 2015; Van de Ven, McKechnie & Cunningham 2019). As a result, higher air temperatures may reduce the rate at which group members feed dependent young, lowering the young's food and water intake, growth, and survival (Wuethrich 2000; Visser 2008; Moses, Frey & Roemer 2012; Fuller *et al.* 2016).

The effects of increasing environmental temperatures and other adverse conditions may be ameliorated if group members increase their investment in feeding young under adverse conditions (Wiley & Ridley 2016). However, evidence that increases in feeding rate alters the effects of adverse environmental conditions is absent. For example, alloparental care by dominant adults in a population of southern pied babblers (*Turdoides bicolor*) in the Kalahari was reduced on hot days as adults prioritised their own survival over reproductive success (Wiley & Ridley 2016). In African wild dogs (*Lycaon pictus*) a progressive increase in  $T_{\max}$  was linked to a reduction in survival of pups and a decline in population density (Woodroffe, Groom & McNutt 2017).

In this paper, we describe the relationships between variation in  $T_{\max}$ , changes in pup growth and survival in meerkats over two decades and investigate the effects of variation in maximum air temperature between days on the body mass gain of pups. Meerkats are insectivorous cooperative breeders living in groups of up to 50, in which family members provision and protect young that are not their own (Emlen 1984; Doolan & Macdonald 1997). Like that of other small mammals in hot and arid environments (Schmidt-Nielsen 1997), water intake of weaned meerkat pups is obtained from ingested food items and their food intake consequently plays an important role in osmoregulation.

On hot days, which are increasing in frequency, meerkats that are actively foraging may experience rapid increases in body temperature and evaporative water loss as a result of their small size and high surface to volume ratios (Walsberg 2000), and individuals seldom continue to forage during the midday periods when air temperatures are highest (Doolan & Macdonald 1996; Russell *et al.* 2002). In meerkat groups of small size, with fewer helpers, pup growth and survival are reduced, and small groups are less likely than large-sized groups to persist through dry periods (Clutton-Brock *et al.* 1999; Ozgul *et al.* 2014). Since pup body mass ( $M_b$ ) and growth declined when  $T_{\max}$  was high (Russell *et al.* 2002), we predicted that both the frequency of pup feeding by helpers and pup diurnal body mass gain ( $\Delta M_b$ ) would be reduced on hotter days. Finally, we investigated whether the association between increased  $T_{\max}$  and  $\Delta M_b$  of pups was reduced in larger groups where helper-to-pup ratios are high, and pups receive more food from helpers.

## Methods

We used long-term data of behaviour,  $M_b$  and life history collected between 1994 and 2018 from a meerkat population living at the Kuruman River Reserve and neighbouring properties, in the southern Kalahari, South Africa (26°85' S, 21°49' E). The meerkats at the study site were habituated to close observation, which facilitated the collection of detailed daily behavioural data, and they were trained to climb onto a scale in return for a small reward (boiled egg crumb < 1g) (Russell *et al.* 2002).  $M_b$  was measured for all meerkats each day near to sunrise, midday and sunset.  $\Delta M_b$  was expressed as a

percentage of the initial  $M_b$  and corrected for time elapsed between the weighing events of meerkats, following du Plessis *et al.* (2012). In addition to foraging for themselves, meerkats older than three months feed pups. We defined and analysed the feeding rate of individuals as the mean number of food items received by individual pups per hour during the morning and afternoon observation sessions. Behavioural data were collected during 1545 morning sessions (duration mean 2.6h, range 0.5 to 4.6h) and during 1205 afternoon sessions (duration mean 1.1h, range 0.5 to 2.3h; S 1).

Daily  $T_{max}$  and daily rainfall data from 2009 - 2018 were obtained from an onsite weather station (CR200 datalogger, Campbell Scientific, USA)(S 2). Rainfall and  $T_{max}$  data from the onsite station were used for correlation with  $\Delta M_b$  and feeding rate. We used cumulated rainfall in the preceding 2 months in our analyses; a 2-month period is used commonly as the epoch relating to food availability in Kalahari ecosystems (Ridley & Raihani 2007). Long-term weather data from the South African Weather Services (SAWS) weather station located in Van Zylsrus, about 30 km from the study site, were used to analyse the long-term trends of  $T_{max}$  in the southern Kalahari.

Analyses were conducted in the R statistical environment using R Studio (R Development Core Team 2016). Linear mixed models (LMM) were computed using the lme4 package (Bates, Maechler & Bolker 2015) and the MuMin package was used for model selection (Bartoń 2015). The variables in the models were standardised to mean zero and unit variance to allow comparison of the effect sizes. Best-fit models were chosen based on comparison of the Akaike Information Criterion between all possible nested models within the global models, using the “dredge” function in MuMin. Goodness of fit to model assumptions was assessed with residual plots, and results from the best-fit model with  $\Delta AIC < 2$  were presented.

$M_b$  between 1997 and 2017 was analysed for pups at the age of 3 months (range 2.5 to 3.5 months). A linear model (LM) with a Gaussian error structure with the predictor variable ‘year’ was used to predict annual  $M_b$  change. ‘Individual ID’ was included as a random factor. We used data from 2040 pups from 47 meerkat groups between February 1997 and December 2017. A separate LM with a Gaussian error

structure was constructed using the smaller dataset of  $T_{\max}$  to predict  $M_b$  of pups at the age of 3 months as a function of the mean  $T_{\max}$  over the 3 months after birth with 'Group ID' included as a random factor. We used data from 846 pups from 33 meerkat groups between December 2009 and December 2017.

Survival rate of pups between the age of 0 to 3 months was analysed as the proportion of survivors per litter. A combined vector of 'survivors' versus 'non-survivors' was analysed using a generalised linear mixed model (GLMM) with a binomial error distribution as a function of the predictor variable 'year of birth'. 'Group ID' was included as a random factor. Survival rate was calculated from 792 litters from 67 meerkat groups between January 1994 and January 2016. Survival rate also was analysed as a function of the mean  $T_{\max}$  over the 3 months after birth with 'Group ID' included as a random factor. Data for this analysis came from 386 litters from 52 meerkat groups between December 2009 and January 2016.

The feeding rate was analysed as a LMM with a Gaussian error structure including the predictor variables 'daily  $T_{\max}$ ', '2-month rainfall', 'helper-pup ratio', 'time of year' and 'age'. 'Group ID' was included as a random factor. 'Group size' was correlated with 'helper-pup ratio' and could therefore not be fitted in the same model. Models including 'helper-pup ratio' had a lower AIC value than those including 'group size', hence the choice to include 'helper-pup ratio'. We used data from 7031 observations on 29 meerkat groups between December 2009 and August 2017.

$\Delta M_b$  of meerkats was analysed as a LMM with a Gaussian error structure including the predictor variables 'daily  $T_{\max}$ ', '2-month rainfall', 'helper-pup ratio', 'time of year' and 'age'. 'Time of year' was made up of the four categorical values 'wet hot', 'wet cool', 'dry cool', and 'dry hot' to assess seasonal effects (S 1). Again, 'Group size' was correlated with 'helper-pup ratio', therefore we included the variable 'helper-pup ratio' since this model had a lower AIC value than the model including 'group size'. 'Individual ID' and 'Group ID' were used as random factors to account for non-independence due to repeated measures of individuals within groups. Diurnal  $\Delta M_b$  per age category as a function of

daily  $T_{\max}$  was furthermore analysed using Davies' test to test for a non-constant regression parameter in the linear predictor using the segmented package (Davies 2002). We classified animals into age categories as pups (0 to 3 months), juveniles (3 to 6 months), sub-adults (6 to 12 months), yearlings (12 to 24 months), and adults (24 months and older). We used data from 1140 individuals from 45 meerkat groups between December 2009 and June 2018.

## Results

Weather data from Van Zylsrus confirmed an increasing trend in daily  $T_{\max}$  since 1995 (estimate  $0.08 \pm 0.01$ , 95% CI 0.06 - 0.10; Figure 1a). Environmental conditions in the Kalahari were marked by high summer air temperatures ( $> 40$  °C) from October to March and seasonal rainfall from December to April (S 2). The  $M_b$  of pups at 3 months of age decreased annually after 1997 (estimate  $-0.97 \pm 0.21$ , 95% CI -1.38 to -0.57, t value -4.70; Figure 1b) and was correlated negatively with mean  $T_{\max}$  over the 3 months after birth (estimate  $-1.64 \pm 0.35$ , 95% CI -2.33 to -0.94, t value -4.63; Figure 1c). Survival rate of pups before the age of 3 months declined annually after 1994 (estimate  $-0.08 \pm 0.01$ , 95% CI -0.10 to -0.05, t value -9.15; Figure 1b) and was correlated negatively with mean  $T_{\max}$  over the 3 months after birth (estimate  $-0.10 \pm 0.02$ , 95% CI -0.12 to -0.07, t value -4.77; Figure 1c).

During the study period  $T_{\max}$  ranged between 11.7 °C and 44.2 °C. A segmented regression model per age category showed that diurnal  $\Delta M_b$  was correlated positively with  $T_{\max}$  in all meerkat age categories when daily  $T_{\max}$  was less than 25.8 °C (estimate  $0.043 \pm 0.009$  °C, 95% CI 0.025 - 0.061, t value 4.63). However, on days when daily  $T_{\max}$  exceeded 25.8 °C, a decrease in diurnal  $\Delta M_b$  was observed with increasing daily  $T_{\max}$  for all meerkat age categories (estimate  $-0.275 \pm 0.004$  °C, 95% CI -0.283 to -0.267, t value -71.15; Figure 2).

The single best-fit model explaining the variation in the pup feeding rate in meerkats had a model weight of 0.67 and contained all the predictor variables of the global model. The parameter estimates of this model indicated that daily  $T_{\max}$ , helper-pup ratio and the 'dry cool' time of year were associated

positively with feeding rate. Cumulative rainfall in the preceding 2-months and age were associated negatively with feeding rate (Table 1).

$T_{\max}$  had a strong association with the frequency with which pups received food items from helpers, as well as with pup  $\Delta M_b$ . The average pup feeding rate during the morning observation sessions (estimate  $0.05 \pm 0.01$ , 95% CI 0.01 - 0.07, t value 2.97; Figure 3a) and during the afternoon observation sessions (estimate  $0.03 \pm 0.01$ , 95% CI 0.01 - 0.04, t value 3.92; Figure 3b) was correlated positively with daily  $T_{\max}$ . This positive correlation arose primarily as a result of changes in feeding rates by adults, with pups receiving the highest number of food items from adults at high temperatures, during both the morning and afternoon sessions. The average number of food items received per pup per hour was significantly higher during the morning observation session than during the afternoon observation session (AM session: 2.54, 95% CI 2.44 – 2.54, PM session: 1.54, 95% CI 1.46 – 1.61, t value = 5.34).

In parallel with the increased feeding rate on the mornings and afternoons of hotter days,  $\Delta M_b$  of the pups during the morning observation session was correlated positively with daily  $T_{\max}$  (estimate  $0.03 \pm 0.01$  °C, 95% CI 0.01 - 0.05, t value 2.60; Figure 3c). During the afternoon session,  $\Delta M_b$  of the pups was correlated negatively with daily  $T_{\max}$  (estimate  $-0.25 \pm 0.01$  °C, 95% CI -0.27 to -0.23, t value -24.90; Figure 3d). As a result,  $\Delta M_b$  declined by 0.8 g (0.25 % of mean initial mass of 322.6 g) for every one degree increase in daily  $T_{\max}$  and pups had a negative diurnal  $\Delta M_b$  (lost  $M_b$  over the afternoon) on days where air temperature exceeded 41.2 °C.

The best-fit model explaining the variation in the diurnal  $\Delta M_b$  in meerkats had a model weight of 0.46 and contained the predictor variables daily  $T_{\max}$ , rainfall of the preceding 2-months, age, and time of year. A second competing model additionally included the predictor variable helper-pup ratio and had a model weight of 0.37. The averaged parameter estimates of these two best-fit models indicated that cumulative rainfall in the preceding 2-months and daily  $T_{\max}$  were associated negatively with diurnal  $\Delta M_b$  in meerkat pups. Helper-pup ratio, age and time of year were associated positively with diurnal  $\Delta M_b$  in meerkats (Table 2).



## Discussion

Our research shows that, both across years and between days, increases in daily  $T_{\max}$  were associated with reduced  $\Delta M_b$  and survival in our meerkat pups. As the average daily  $T_{\max}$  at the study site increased by 1.5 °C over two decades, pup  $M_b$  at the age of 3-months declined by 5.7 % and pup survival rate before the age of 3-months decreased by 3.1%. Comparisons of body mass gain between days showed that diurnal  $\Delta M_b$  was lower on days when  $T_{\max}$  exceeded 25.8 °C, and it decreased progressively as  $T_{\max}$  increased beyond that threshold. The rate at which pups received food was higher during the morning compared to the afternoon period, but in both periods the feeding rate was higher on days that reached higher  $T_{\max}$ . All age classes of meerkats above the age of 3 months provided food for pups, but adults contributed most to the increased frequency with which pups received food at higher air temperatures. Pups gained on average 3.6 g h<sup>-1</sup> during the morning session and  $\Delta M_b$  increased more on the mornings of hotter days. In contrast, in the afternoons, average  $\Delta M_b$  by pups was about 5-fold lower and, even though rate at which pups received food from other group members was higher on hotter days, pup  $\Delta M_b$  declined with increasing  $T_{\max}$ .

The observed reduction in  $\Delta M_b$  of all meerkats on days when  $T_{\max}$  exceeded 25.8 °C may have resulted from either by a reduction in energy intake, reduced energy conversion into growth, an increase in energy expenditure, or body water loss during the hottest time of the day (13:00-15:00; S 1). Like many other animals living in arid environments (Walsberg 2000; Fick *et al.* 2009; Moses, Frey & Roemer 2012), meerkats usually cease feeding as temperatures increase in the midday period. Extended resting periods over midday on hotter days may explain the decrease in pup body mass gain on hot days despite higher rates of provisioning when groups were active. We did not have data on total foraging time per day; a shorter duration of feeding over the full day may have offset the effects of increased feeding rate on hot days. However, prey items were more abundant in summer, when temperatures were highest, and  $\Delta M_b$  was higher in meerkats of all age categories during the summer months than in winter (Clutton-Brock & Manser 2016).

An alternative explanation for the reduction in pup body mass gain on hot days is that pups lost mass as a consequence of increases in evaporative water loss. Meerkats in the Kalahari typically are exposed to high air temperatures in combination with high soil surface temperatures and high solar radiation, particularly between 12:00 and 15:00 (when heat load usually is highest; S 1). Under such conditions, the high surface area to mass ratio resulting from their small body size could lead to rapid heat gain from the environment (Mitchell *et al.* 2008). A higher body temperature on hotter days and associated higher metabolic rate, as a consequence of the Q10 effect, also may contribute to higher energy expenditure (Tattersall *et al.* 2012). Small desert mammals have lower heat storage capacity than do larger mammals and typically move into cooler microclimates to prevent excessive rises in body temperature (Walsberg 2000; Fick *et al.* 2009; Moses, Frey & Roemer 2012; Tattersall *et al.* 2012). When heat exchange by radiation, convection and conduction imposes a net heat gain on the body, the only mechanism available for heat loss is via evaporative water loss (Schmidt-Nielsen 1997). However, mammals routinely implement evaporative heat loss at lower environmental temperatures, in which dry heat loss is still possible (Mitchell *et al.* 2018). In slender mongooses (*Herpestes sanguineus*) in a controlled laboratory environment, heat loss by cutaneous and respiratory evaporation increased at air temperatures above 26 °C, such that all metabolic heat could be lost by evaporation at an air temperature of 37 °C (Kamau, Johansen & Maloiy 1979). Similarly, meerkats exposed to heat in the laboratory dissipated heat effectively by evaporative cooling, with marked increases in evaporative water loss at air temperatures above 33 °C (Müller & Lojewski 1986). At air temperatures of 40 °C meerkats lost 5 ml water kg  $M_b^{-1}$  h<sup>-1</sup> on average (Müller & Lojewski 1986). Given the need to dissipate the additional heat load from solar radiation and high surface temperature in the outdoor Kalahari environment, as well as metabolic heat generated by activity, evaporative water loss may have been even higher in our meerkats and may explain most of the  $M_b$  loss on hot days. As a result of their larger size, adult meerkats will dehydrate more slowly than younger meerkats (Fuller *et al.* 2016), an effect that may explain why food provisioning to pups was undertaken primarily by meerkats in the adult age class (rather than younger meerkats of smaller  $M_b$ ) on the hottest days (Figure 3a and b).

In addition to its direct effects in reducing diurnal  $\Delta M_b$ , loss of body water may impair growth. In response to dehydration, mammals increase protein oxidation and catabolism of muscle (Bintz & Mackin 1980; McCue *et al.* 2017). Low rates of diurnal  $\Delta M_b$  also will have subsequent consequences for the development and survival of meerkat pups (Clutton-Brock *et al.* 2001; Russell *et al.* 2002). Meerkats in the Kalahari rarely drink, so water is obtained mainly via prey items and metabolic water production, making increased food intake necessary to maintain body water balance in hot environments. It is possible that water intake may have been lower in hot periods if prey items contained less water as a consequence of dehydration, however previous work has found that meerkat prey size does not differ seasonally or across the day (Doolan & Macdonald 1996).

The potential vulnerability of the same Kalahari meerkat population has been revealed recently in a study projecting population responses under future climate scenarios (Paniw *et al.* 2019). Our study provides evidence that in the past 22 years, an increase of 1.7 °C in  $T_{max}$  (from an average of 29.3 °C in 1995 to 30.9 °C in 2017) has been associated with an annual  $M_b$  decrease of 0.9 g in meerkat pups (at the age of 3 months). Climate change is expected to increase air temperatures in the Kalahari further (Kruger & Sekele 2012; van Wilgen *et al.* 2016).

Long-term body mass declines have been observed in other species facing climate change, and have been attributed to a combination of lower food availability, shorter foraging periods (Mason *et al.* 2014) and high air temperatures (Gardner *et al.* 2011). Following Bergmann's rule, smaller body sizes evolve in the lower latitudes where air temperatures are warmer (Bergmann 1847). Smaller body size is proposed to be advantageous in a warming climate as a larger surface area to body mass ratio favours heat loss (Gardner *et al.* 2011). However, when air temperature exceeds body temperature, as is happening more often in the Kalahari (Figure 1a), smaller mammals will gain heat more rapidly than larger mammals, and they will dehydrate more rapidly if evaporative water loss is obligatory (Fuller *et al.* 2016) and sufficient water intake cannot be obtained through their diet.

It is believed that cooperative breeding systems provide advantages for mammals living in unpredictable and arid habitats, which is where cooperative breeders are more likely to be found. Nevertheless, despite the ratio of helpers to pups being associated positively with pup  $\Delta M_b$  in hot as in cooler environments, and adults increasingly supporting the feeding of pups at higher air temperatures, we show here that cooperative systems in themselves were not sufficient to buffer meerkat pups against the effects of climate change in the Kalahari. The forecast for a continued warming of the Kalahari is likely to have an increasingly detrimental impact on the growth and survival of meerkat pups.

### **Ethics**

All procedures were approved by the Northern Cape Department of Environment and Nature Conservation (permit no. 1020/2016) and the Animal Ethics Screening Committee of the University of the Pretoria (project no. EC047-16).

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### **Data availability statement**

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5dv41ns2m>, (Van de Ven, Fuller & Clutton-Brock 2019).

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## Tables

*Table 1 Factors affecting feeding rate (food items received per hour per pup) in meerkats; estimates of effect sizes, standard error, t values and 95% confidence intervals.*

<b>Variable</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>95% CI</b>	
Daily T <sub>max</sub>	0.031	0.015	2.100	0.002	- 0.059
Rainfall 2 months	-0.075	0.015	-4.868	-0.104	- -0.044
Age	-0.207	0.011	-19.706	-0.228	- -0.186
Helper : pup	0.374	0.011	33.292	0.352	- 0.396
Time of year:					
Wet hot	0.052	0.056	0.918	-0.060	- 0.163
Wet cool	-0.052	0.057	-0.908	-0.165	- 0.061
Dry cool	0.174	0.063	2.748	0.049	- 0.299
Dry hot	0.064	0.058	1.111	-0.050	- 0.179

n = 7031 observations on 29 groups between 12/2009 and 08/2017.

*Table 2 Factors affecting diurnal body mass gain in meerkat pups; estimates of effect sizes, standard error, standard error, z values and 95% confidence intervals.*

<b>Variable</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>Adjusted SE</b>	<b>z value</b>	<b>95% CI</b>	
Daily T <sub>max</sub>	-0.193	0.016	0.016	12.219	-0.224	- -0.162
Rainfall 2 months	-0.055	0.016	0.016	3.392	-0.088	- -0.023
Age	6.177	0.324	0.324	19.043	5.542	- 6.813
Helper : pup	0.062	0.023	0.023	2.705	0.017	- 0.106
Time of year:						
Wet hot	5.029	0.258	0.258	19.491	4.523	- 5.534
Wet cool	5.360	0.257	0.257	20.862	4.856	- 5.863
Dry cool	5.425	0.261	0.261	20.792	4.913	- 5.936
Dry hot	5.061	0.264	0.264	19.157	4.543	- 5.579

n = 973 pups from 30 groups between 12/2009 and 06/2018.



## Figure legends

*Figure 1a* Daily maximum air temperature per year from 1995 to 2017. Data were obtained from the weather station at Van Zylsrus, Northern Cape, South Africa (~ 30 km from the study site), South African Weather Service, SAWS. *Figure 1b* Pup body mass at the age of 3 months per year from 1997 to 2017 (left y-axis) and survival rate of pups younger than 3 months per year from 1994 to 2016. *Figure 1c* Pup body mass at the age of 3 months as a function of mean  $T_{max}$  ( $^{\circ}C$ ) over the 3 months after birth (left y-axis) and survival rate of pups younger than 3 months as a function of mean  $T_{max}$  ( $^{\circ}C$ ) over the 3 months after birth (right y-axis). The black dashed lines represent the best fit models. Values shown are means with standard error of the mean.

*Figure 2* Diurnal body mass gain (% initial mass) as a function of daily maximum air temperature per meerkat age category (pups in red, juveniles in green, sub-adults in blue, yearlings in purple and adults in orange). The black dashed line represents the best fit model. Values shown are means with standard error of the mean.

*Figure 3a* Feeding rate measured as food items received per pup per hour from meerkats of different age classes (juveniles in green, sub-adults in blue, yearlings in purple and adults in orange), and all meerkats (linear model in black), during a morning foraging session (AM) and b) during an afternoon foraging session (PM) as a function of daily maximum air temperature ( $^{\circ}C$ ). *Figure 3c* Pup body mass gain ( $g\ h^{-1}$ ) over a morning foraging session (AM) and d) over an afternoon foraging session (PM) as a function of daily maximum air temperature ( $^{\circ}C$ ). The black dashed lines represent the best fit models and the grey horizontal dashed lines indicate 0% mass change. The Values shown are means with standard error of the mean.

Fig 1.

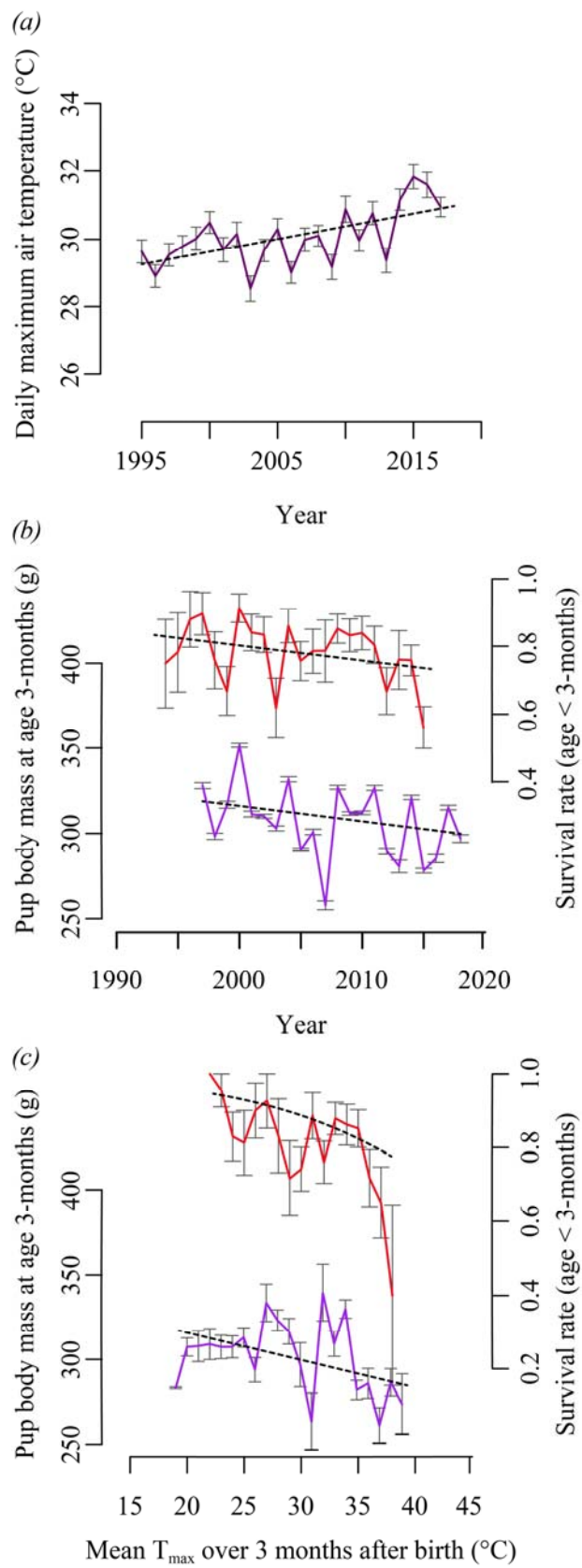
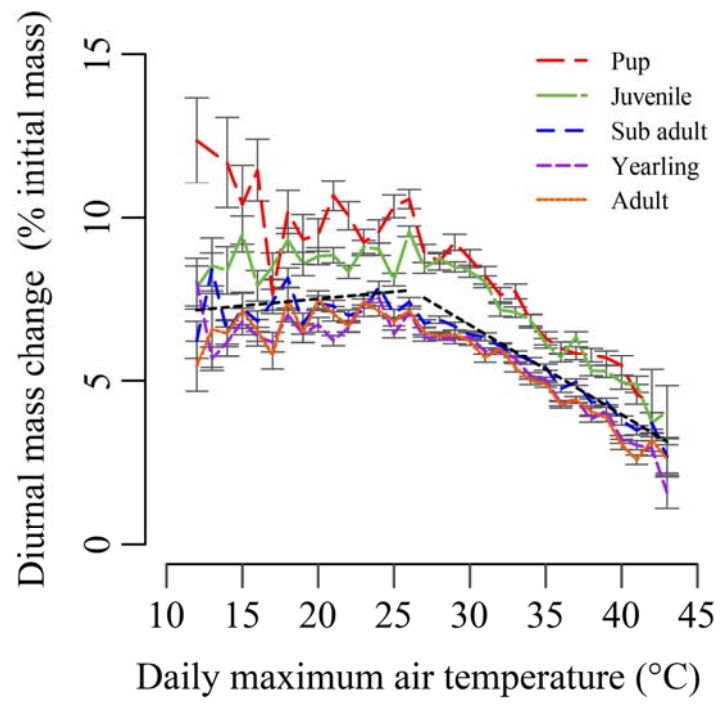
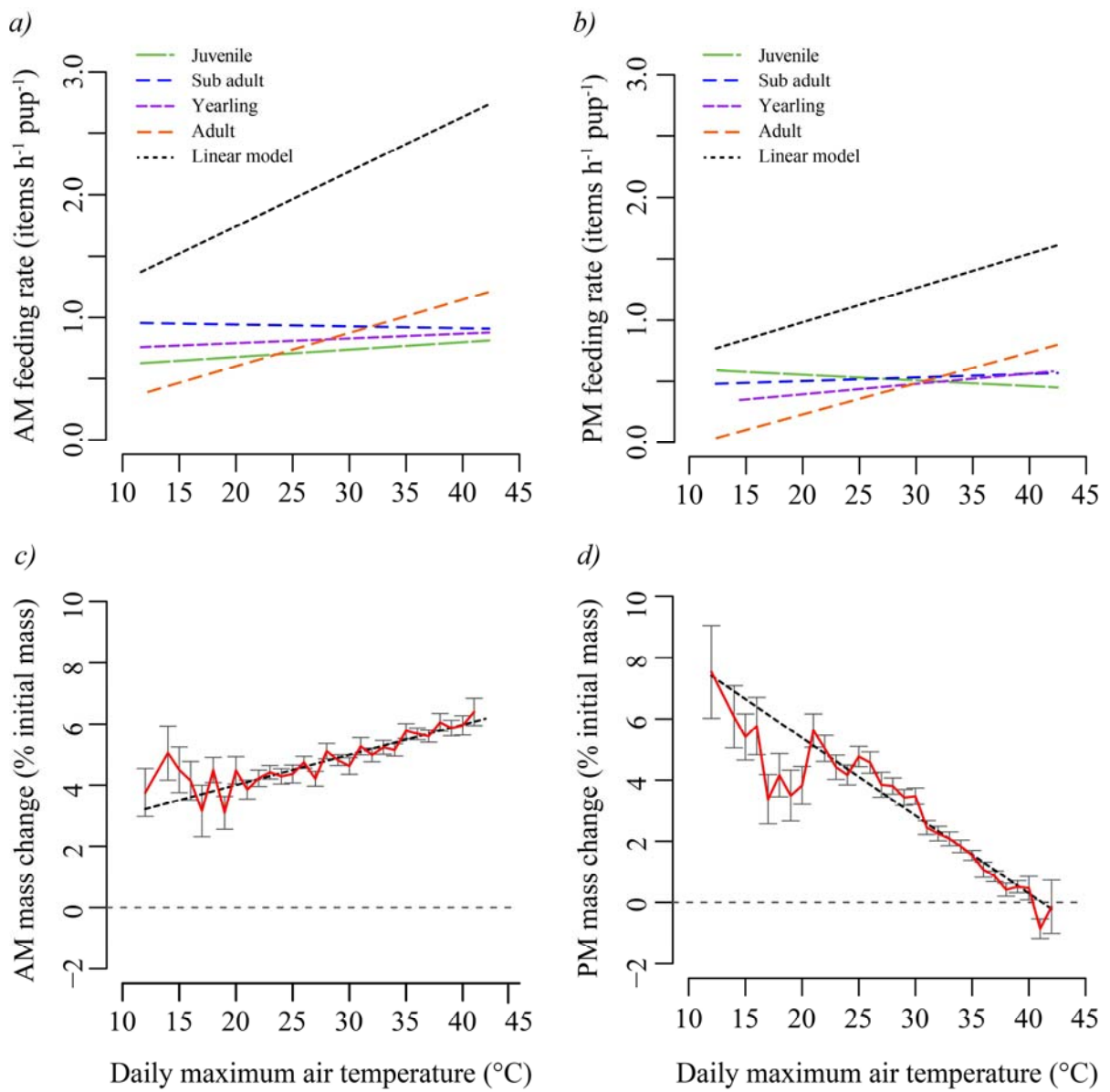


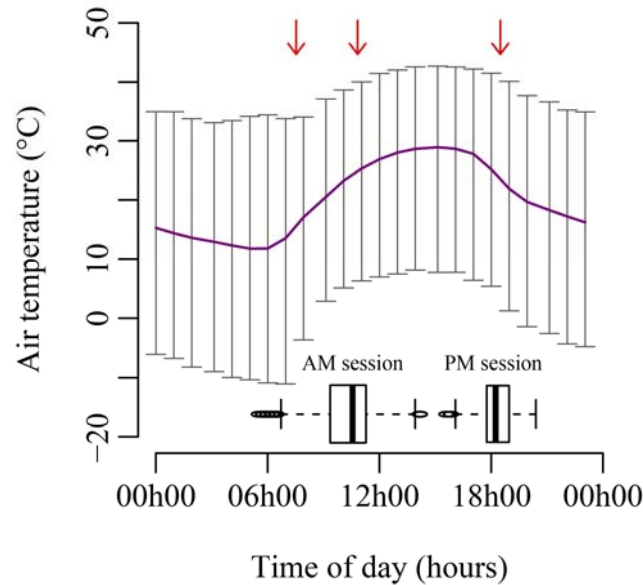
Fig 2.



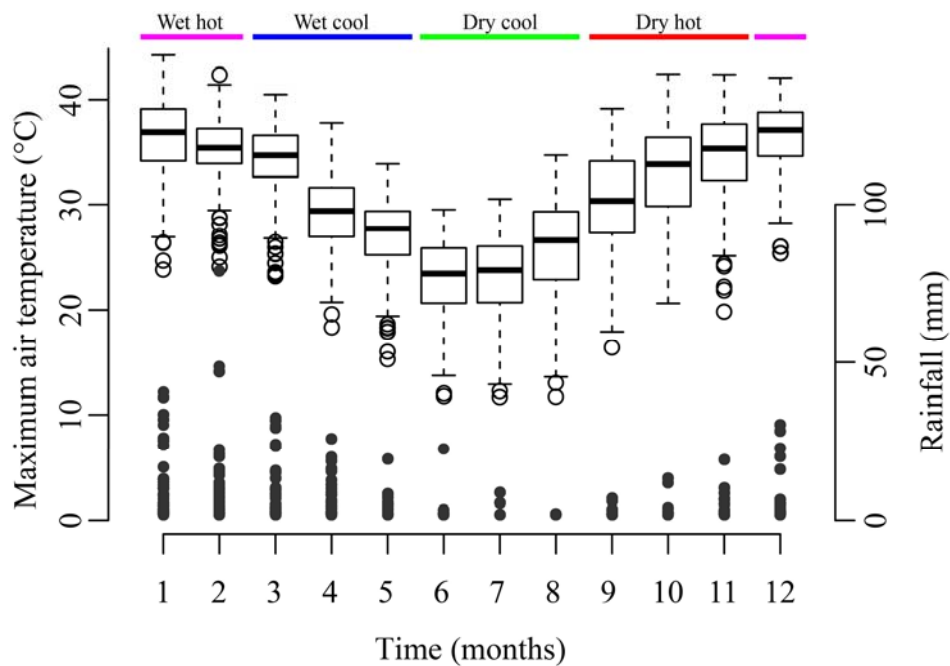
**Fig 3.**



Supplementary material



S 1 The interquartile range and median of the duration of morning (AM session) and afternoon (PM session) observations (boxplots), mean sunrise, midday and sunset time of body mass data collection (indicated by the red arrows) and the mean, minimum and maximum air temperature across the day (purple line and error bars) at the Kuruman River Reserve (26°58' S, 21°49' E) between 2009 and 2018.



S 2 The interquartile range and median of daily maximum air temperature and rainfall per month (grey symbols) at the Kuruman River Reserve (26°58' S, 21°49' E) between 2009 and 2018.