

RESEARCH ARTICLE

Mother–offspring conflict and body temperature regulation during gestation and lactation in a wild primate

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Abstract

1. The physiological performance of a mother during reproduction represents a trade-off between continued investment in her current offspring, and the mother's own survival and ability to invest in future offspring. Here, we used core body temperature (T_b) patterns to examine the degree to which maternal body temperatures support the infant during periods of gestation and lactation.
2. We implanted 30 wild vervet monkeys (*Chlorocebus pygerythrus*) with miniature data loggers to obtain continuous measurements of core T_b during periods of typical (i.e. non-drought periods) and limited (i.e. drought period) resource availability.
3. We tracked maternal T_b profiles across the gestation and lactation periods, associated with 23 births, and compared those with T_b profiles of non-reproductive females. This allowed us to examine the flexibility in maternal body temperatures and test whether limited resource availability shifts priority away from offspring investment and towards self-maintenance.
4. Vervet monkeys demonstrated the predicted pattern of gestational hypothermia and improved homeothermy in the gestation period during typical conditions, consistent with the maintenance of a thermal gradient to facilitate heat loss from the foetus. During periods of limited resource availability (i.e. drought), mothers were less homeothermic and more hyperthermic during the gestation period.
5. Vervet monkeys showed no evidence of lactational hyperthermia during typical conditions. During the drought, lactating mothers demonstrated hyperthermia and increased variability in body temperature, consistent with the increased metabolic demands and water requirements for milk production required to support growing infants.
6. Although a mother's degree of homeothermy during gestation and lactation was unrelated to her infant's chance of survival to weaning, mothers did show flexibility in the degree to which they prioritized the maintenance of a thermal environment that supports their infant's development. Together, our findings demonstrate that flexibility in a mother's investment in thermoregulation during gestation

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and lactation may reflect a bet-hedging trade-off between self-maintenance and offspring investment.

KEYWORDS

drought, life-history trade-off, reproduction, thermoregulation, vervet monkey

1 | INTRODUCTION

The reproductive success of female mammals is limited primarily by the high water or energetic costs associated with infant development during gestation and lactation (Brody & Lardy, 1946; Gittleman & Thompson, 1988). These costs are particularly salient for female primates, given their long gestation periods and the production of relatively precocial, large-brained infants, combined with long lactation periods, late weaning and slow postnatal growth (Emery-Thompson, 2013; Martin, 1995). Indeed, an infant's growth rate, behavioural phenotype and chances of survival, are closely tied to the performance of their mothers during both the prenatal and postnatal periods (Coe & Lubach, 2000; Emery-Thompson, 2013; Hinde, 2013; Hinde et al., 2015; Maestripieri, 2009; Rutherford, 2013; Singh et al., 2012). The physiological performance of a mother therefore represents a trade-off between continued investment in her current offspring, and the mother's own survival and ability to invest in future offspring (Charnov & Berrigan, 1993; Clutton-Brock, 1984; Stearns, 1992). This trade-off is likely to be particularly true for 'income breeders' that rely on resources acquired during reproductive periods to fulfil the energetic demands of reproduction, rather than 'capital breeders' that rely on energy stored in advance of reproduction (Brockman & van Schaik, 2005).

To maximize individual fitness, reproductive effort should be suppressed if it poses a risk to the mother's survival, or if current reproductive investment jeopardizes, or is outweighed by, future reproductive prospects (Uphouse, 2011; Wasser & Barash, 1983). During periods of limited resource availability, for example, females in poor body condition are less likely to conceive, and if they do conceive, are less likely to bring a pregnancy to full-term, compared with females in good condition (Beehner, Onderdonk, et al., 2006; Brockman & van Schaik, 2005; Stearns, 1976). Among primates, for example, wild yellow baboons were less likely to conceive during periods of drought and, if they did conceive, they were less likely to have successful pregnancies (Beehner, Nguyen, et al., 2016). Experimentally imposed energy restriction was also found to induce the termination of pregnancies in common marmosets (Tardif et al., 2004). Although severe energy depletion may well result in aborted pregnancies in favour of female survival, it is also possible that more subtle 'bet-hedging' trade-offs exist in female reproductive investment (Stearns, 1989). That is, under resource-limited conditions, selection may favour mothers who experience reduced survival prospects in order to compensate for sub-optimal offspring investment, and in doing so achieve successful pregnancies. In such

instances, mother-offspring conflict would not solely lie in the dichotomy of aborted versus completed pregnancies but would also reflect the investment of maternal resources into homeostatic regulation of physiological processes during reproduction.

To date, studies of the physiological performance of female primates during reproduction have primarily focused on energetics (Emery-Thompson, 2013, 2017), nutrient transfer (Rutherford, 2013) and hormone signalling (Coe & Lubach, 2000; Hinde et al., 2015). Given that the regulation of body temperature reflects not only the response of an individual to its external environment (Hetem et al., 2016; McFarland et al., 2015, 2020), but also the maintenance of an internal environment that supports reproduction (Kozak, 1997), there is the additional possibility that patterns of body temperature regulation might provide useful information on a mother's ability to invest in her offspring. To date, maternal thermal homeostasis during gestation and lactation has been unexplored in wild primates (but see McFarland et al., 2022 for details of maternal body temperature during birth).

The degree to which mammals maintain body temperature within a narrow homeothermic range—that is, a small amplitude of the 24-h body temperature rhythm—is closely tied to the availability of energy and water resources and is therefore considered to provide a useful index of physiological performance across varying environments (Hetem et al., 2016; Maloney et al., 2017). Despite the increased energetic demands of gestation, however, several mammalian species exhibit improved homeothermy (i.e. smaller amplitude of the 24-h body temperature rhythm) during pregnancy (e.g. brown bears: Friebe et al., 2014; lions: Trethewan et al., 2016; high Arctic muskoxen: Schmidt et al., 2020). Improved homeothermy likely accelerates foetal development because of rapid cell division under optimum temperature conditions (Farmer, 2000). A gradual and regulated decline in mean body temperature over the course of gestation, termed 'gestational hypothermia' (Kozak, 1997), has also been reported in several species (rats: Melanie et al., 1988; sheep: Laburn et al., 1992; lions: Arctic ground squirrels: Williams et al., 2011; Trethewan et al., 2016; wolverines: Thiel et al., 2019; humans: Hartgill et al., 2011), including some that do not display improved homeothermy (rabbits: Naccarato & Hunter, 1983). Foetal body temperature is generally ~0.5°C higher than maternal body temperature (Laburn et al., 1992). Consequently, it has been argued that lower mean maternal body temperature during gestation allows the foetus—which has a higher temperature than the mother—to maintain a gradient for heat loss, and a greater buffer if the mother were to reach hyperthermic and potentially teratogenic temperatures (Asakura, 2004; Fewell, 1995; Laburn, 1996).

Following birth, maternal body temperatures increase, becoming either higher than (rats: Fewell, 1995) or no different from those of non-reproductive females (lions: Trethowan et al., 2016). Increased core body temperatures during the lactation period are likely a consequence of increased metabolic heat generation because of milk production and greater food intake (Adels & Leon, 1986; Hinde et al., 2009; Oftedal, 1984; Rosetta et al., 2011; Speakman, 2008), an inability to dissipate heat because body water is diverted to milk production (Fuller et al., 2021), and altered hormone levels, including corticosterone and progesterone (Adels & Leon, 1986; Stern et al., 1973). Chronic hyperthermia has been observed in several small lactating rodents (e.g. dwarf hamsters: Scribner & Wynne-Edwards, 1994; rats: Fewell, 1995; mice: Gamo et al., 2013). Whether gestational hypothermia and lactational hyperthermia occur in wild primates is currently unknown.

We used core body temperature measurements from wild vervet monkeys (*Chlorocebus pygerythrus*) to examine patterns of maternal body temperature across both gestation and lactation. We predicted that vervet monkeys would demonstrate hypothermia and improved homeothermy during gestation and would experience higher-than-normal body temperatures when lactating. We then examined whether the observed patterns of maternal body temperature were mediated by the availability of food and water resources. To do so, we took advantage of a 12-month drought (Young et al., 2019), which allowed us to compare the thermoregulation of reproductive and non-reproductive females during periods of typical (i.e. non-drought periods) and limited (i.e. drought period) resource availability. We tested the hypothesis that maternal body temperatures reflect prioritization of the infant (i.e. show improved homeothermy) during periods of typical resource availability, but relax this priority (i.e. show increased heterothermy), and hence reduce offspring investment, when resources are limited. Our study focused on the variability in a mother's investment in her offspring during gestation and lactation. Although the extreme of mother-infant conflict during gestation would be a terminated pregnancy, our sample involved only full-term pregnancies. Therefore, we investigated whether there was a direct link between a mothers' degree of homeothermy during gestation and her infant's chances of survival to weaning age.

2 | METHODS

2.1 | Study site and species

Data were collected between June 2012 and December 2017 from three groups of wild vervet monkey in the Eastern Cape, South Africa (32°22' S, 24°52' E). Mean adult group sizes across the five-year period, for each of the three groups, were Troop 1 = 25 ± 7 SD, Troop 2 = 45 ± 9 SD, and Troop 3 = 23 ± 4 SD. These animals were fully habituated to the presence of researchers, could be individually identified by means of natural markings, and consumed a completely natural diet. Vervet females are philopatric while males typically

leave their natal group when they reach sexual maturity (Henzi & Lucas, 1980). Vervet monkey females reach sexual maturity at approximately 3 years of age, give birth for the first time between the ages of 3 and 5 years, and produce a single offspring at each reproductive event (Turner et al., 1997). Infants typically wean at approximately 7 months (Henzi et al., 2023).

Vervet monkeys are characterized as 'income breeders' (Brockman & van Schaik, 2005; Lee, 1987). Vervets are also seasonal breeders (Rowell & Richards, 1979) and conception typically occurs in advance of resource abundance, whereas peak lactation—the most energetically expensive period in the primate reproductive cycle (Emery-Thompson, 2013; Hanwell & Peaker, 1977; Rosetta et al., 2011)—tends to coincide with the peak in resource availability (Brockman & van Schaik, 2005; Lee, 1987; Stearns, 1992). This seasonal breeding is evident in this population, whereby the mating season typically falls within the dry austral winter months (between April and June), and the birth season falls within the wet austral summer months (between October and December; McFarland et al., 2014). The gestation period for wild vervet monkeys is ~165 days and typically occurs during the austral winter and spring months whereas the lactation period of ~155 days typically occurs over the austral summer months (Rowell, 1970; Sashaw, 2012; Seier et al., 2000). Observational data collection protocols were approved by the University of Lethbridge (Animal Welfare Protocols 0702/1505). Permission to conduct fieldwork was granted by the Samara Private Game Reserve and the Department of Economic Development, Environmental Affairs and Tourism, South Africa.

2.2 | Measurement of body temperature

A variable subset of adult females across the three groups were captured by darting each year and were implanted abdominally with temperature-sensitive data loggers (2012–2013: mlog T1C, Sigma Delta Technologies, Perth, Australia; 2013–2017: DST centi-T, Star-Oddi Ltd., Gardabaer, Iceland). For full details of the capture and surgery procedure, see McFarland et al. (2015). Data loggers instantaneously recorded core body temperature (T_b) at 5-min intervals at a resolution of 0.06°C and were individually calibrated to an accuracy of at least 0.1°C. After 12 months, similar procedures were used for subject re-capture, reimplantation and the eventual removal of data loggers. Animals were weighed at the beginning of each surgery. Mean female body mass was 3.4 kg ± 0.3 SD. Normal behaviour resumed on the day after surgery, and no long-term sequelae were observed because of surgical intervention, as confirmed by regular behavioural monitoring by researchers and a veterinarian. Capture and surgical procedures were approved by the University of the Witwatersrand Animal Ethics Research Committee (2010/41/04; 2015/04/14B).

We calculated the 24-h means, maxima and minima, and amplitudes (i.e. 24-h maxima–minima) of T_b rhythm for each day a female was gestating, lactating or non-reproductive. We used these four metrics of T_b to facilitate a comprehensive evaluation of how

resource availability and reproductive status effects T_b rhythm, identifying possible occurrences of hyperthermic (increased 24-h means and maxima) and hypothermic (decreased 24-h means and minima) episodes, and the degree of homeothermy/heterothermy (24-h amplitude of T_b rhythm).

We used direct observations and distinct perturbations of T_b to identify the dates of parturition (McFarland et al., 2022) and used these dates to define the gestation (i.e. date of parturition – 165 days) and lactation (i.e. date of parturition + 155 days) periods. Lactation periods were considered terminated if the mother's infant died. Days of gestation would be missed if a pregnancy terminated prematurely, thus the identification of any differences in T_b patterns between gestating and non-gestating females can be considered conservative. We counted the number of days each female experienced particularly high 24-h T_b means (greater than 2SD above mean gestation or lactation T_b) during each gestation and lactation period. We also checked for and counted the number of fever episodes (McFarland et al., 2021) experienced by mothers during the gestation and lactation periods to investigate the possible negative effects maternal fever could have on offspring health (Dreier et al., 2014). Between 2012 and 2017, we collected T_b data across the gestation and lactation periods associated with 23 births (range: 1–3 births/female), from 14 of our 30 adult females for which we recorded T_b (Figure 1; Table S1). Of these 23 births, 14 occurred in non-drought conditions and nine occurred during drought conditions. Births ranged from 0 to 9 per year (mean = 5 per year) across the study period (Table 1).

2.3 | Climate and drought

Given that local climate may directly affect T_b (Lubbe et al., 2014; McFarland et al., 2015, 2020), we controlled for air temperature in all our analyses. Mean 24-h air temperatures were recorded at a local weather station and ranged from 1.8 to 31.7°C during the study period. Mean 24-h air temperature was 15.5°C ± 5.4SD during periods of gestation, and 21.1°C ± 4.1SD during periods of lactation. Our study region experienced a drought during 2016 and 2017, characterized by very low level (<50% of typical) of rainfall, reduced food availability and the absence of standing (i.e. drinking) water for extended periods (Young et al., 2019). June 2016 to June 2017 was the most severely affected period and was therefore considered to represent the resource-limited drought period in the current study.

2.4 | Statistical analysis

We ran a series of Bayesian generalized linear mixed models (hereafter GLMMs) using the 'brms' package (Bürkner, 2017) in R 4.3.0. (R Core Team, 2023). We ran four chains for at least 3000 iterations, after 1000 warmup iterations, to confirm convergence (all R-hats <1.01 and ESS >400: Bürkner, 2017). This convergence and large ESS values are reassurance that autocorrelation is not an issue in our models, and that posterior outputs are reliable. We set weakly informative priors centred on zero (i.e. normal (0, 1)) for

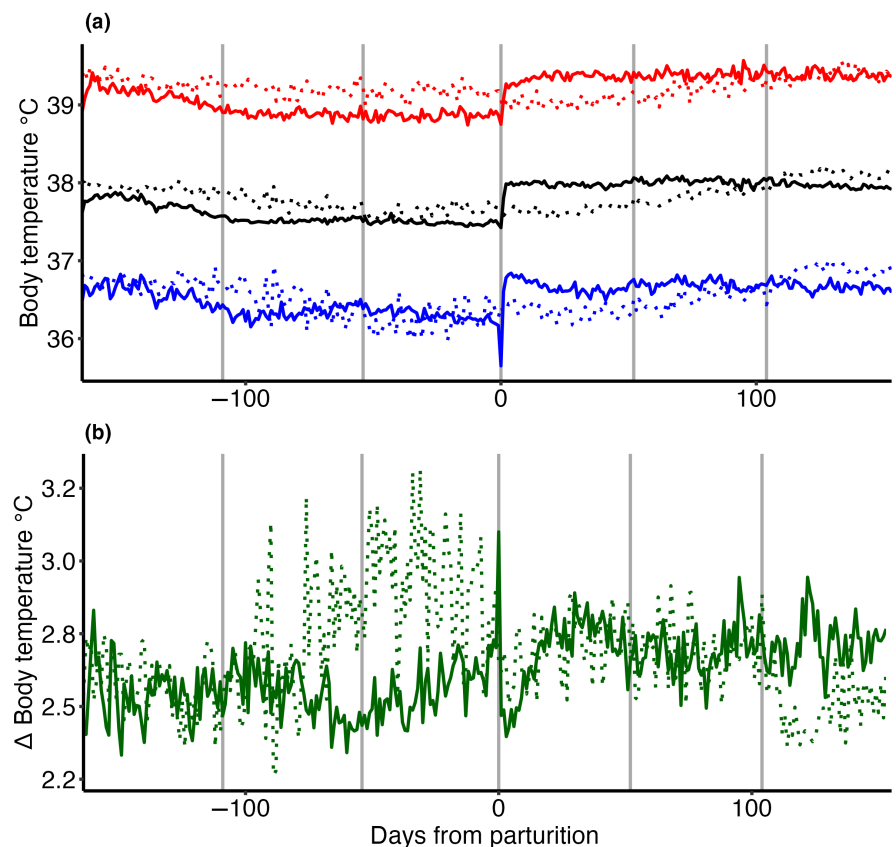


FIGURE 1 Average (a) 24-h mean (black), minimum (blue) and maximum (red), and (b) amplitude (green) of body temperature rhythm of wild vervet monkeys during reproductive (solid lines, $N=23$ births from 14 monkeys) and time-matched non-reproductive (dotted lines, $N=30$ monkeys) periods, coinciding with the 165 days of gestation and 155 days of lactation, centred on Day 0, the day of parturition. Grey lines demarcate trimesters.

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individuals (across three groups)	24-h body temperature measurements	16,497 days from 30 vervet monkeys (14 of 30 monkeys contributed 23 reproductive events)

the main effects, and used the 'posterior predictive check' (pp_check) function to confirm the suitability of our choice of priors and likelihood model distributions (McElreath, 2020). All continuous variables were scaled and centred by 1 SD (Schielzeth, 2010). We used the 'bayestestR' package (Makowski et al., 2019) to generate 'probability of direction' (p.d.) estimates for the fixed effects. We used the 'r2_bayes' function to calculate marginal and conditional R^2 values for the fixed effect and whole models, respectively (Nakagawa & Schielzeth, 2013). We used the 'loo-compare' function to compare the widely applicable information criterion (WAIC) scores of the full models, with the random-effects only models, where lower WAIC scores (i.e. $-\Delta$) indicate the better model (Vehtari et al., 2017). Full model results are provided in the supplementary material (Tables S2–S31). Here, we used a combination of random-effect model comparisons and p.d. estimates to infer meaningful effects from our models.

To examine the effect of gestation on T_b rhythm, we compared the 24-h T_b patterns of gestating females with non-reproductive females during the same period. We ran four GLMMs, specifying a Gaussian distribution, entering either 24-h (a) means, (b) maxima, (c) minima or (d) amplitudes of T_b rhythm, in turn, as the response variable. In each of the four models, we entered whether a female was gestating (no/yes), experiencing drought conditions (no/yes) and their interaction as our predictor variables. We entered mean 24-h air temperature and body mass as statistical control predictor variables because of their known effect on T_b (McFarland et al., 2015, 2020). Body mass was typically lower in the drought period compared with the preceding year. Since smaller individuals have a greater relative surface area, which will increase the rate of heat exchange with the environment (Mitchell et al., 2018), including both body mass and drought in the models allowed us to account for the influence of reduced resource availability independent of body mass. Body mass was also considered to represent a reasonable proxy for subject age (sensu, Turner et al., 2018). We entered date ID and subject ID as crossed random effects. Random effects were defined as factor variables. To examine the effect of lactation on T_b rhythms, we followed the same model structure as for the four gestation models, entering whether a female was lactating (no/yes) as the predictor variable.

To examine changes in T_b rhythms across the gestation period, we ran four GLMMs, specifying a Gaussian distribution, entering either 24-h (a) means, (b) maxima, (c) minima or (d) amplitudes of T_b rhythm, in turn, as the response variable. We entered the day of gestation (i.e. 1–165) as the predictor variable. Mean 24-h air temperature and body mass were entered as control variables. We entered

date ID, and gestation event ID nested inside subject ID, as random effects to deal with repeated measures. We specified the random slope of the day of gestation on the random-effect event ID/subject ID (Barr, 2013). The four models were run at the level of the subject day. We ran these same four models replacing day of gestation with gestation trimester (with the second trimester as the base variable) to examine whether any change in T_b across gestation was gradual or whether it shifted across certain trimesters. To examine changes in T_b rhythms across the lactation period, we followed the same model structure used for the day of gestation models, instead entering day of lactation (i.e. 1–155) as the predictor variable. We ran these same four models replacing day of lactation with 'lactation trimester' (with the second trimester as the base variable) to examine whether any change in T_b across lactation was gradual or whether it shifted across certain trimesters.

Finally, to examine whether a mother's degree of homeothermy during gestation had an effect on their infant's chances of surviving to weaning, we ran five GLMMs, specifying a Bernoulli distribution, entering whether the infant survived to weaning (no/yes) as the response variable, and either average 24-h (a) means, (b) maxima, (c) minima or (d) amplitudes of T_b rhythm, and (e) the number of 'high' 24-h T_b means, during gestation, in turn, as the predictor variables. We also entered drought (no/yes) and fever (no/yes) as further predictor variables. To examine whether a mother's degree of homeothermy during lactation influenced her infant's chances of surviving to weaning, we followed the same model structure used for the gestation infant survival models, instead entering comparable T_b parameters extracted from the lactation period. We entered subject ID as a random effect in all 10 weaning models to deal with repeated measures.

3 | RESULTS

3.1 | Gestation period

Female vervet monkeys became increasingly hypothermic during the gestation period, returned to typical T_b immediately post-parturition, and maintained relatively typical T_b during the lactation period (Figure 1). Gestating females had lower 24-h T_b means, maxima, minima and amplitudes, compared with non-reproductive females (Table 2). As gestation advanced, females had progressively lower 24-h T_b means, minima and maxima, but showed no change in 24-h T_b amplitudes (Table 3; Figure 1). Further analyses revealed that a downward shift in 24-h T_b mean, maxima and minima occurred between both trimesters one and

TABLE 2 Results of the Bayesian generalized linear mixed models estimating the effect of reproductive state, drought and their interaction on vervet monkey 24-h body temperatures (T_b) during periods of gestation and lactation. T_b parameter ~ Gestation or Lactation × Drought + Mean Ambient Temperature + Body mass + (1|Calendar Date) + (1|Subject ID).

Model	Reproductive (no/yes)			Drought (no/yes)			Interaction			Whole model		
	Estimate	Probability of direction %	Estimate	Probability of direction %	Estimate	Probability of direction %	Estimate	Probability of direction %	R ²	R ² marginal	R ² conditional	Full model results
Gestation period												
T_b means	-0.20	100	-0.06	100	0.09	100	0.09	100	0.28	0.28	0.60	Table S2
T_b maxima	-0.33	100	0.09	100	0.04	99.56	0.04	99.56	0.23	0.23	0.46	Table S3
T_b minima	-0.04	100	-0.16	100	0.14	100	0.14	100	0.12	0.12	0.52	Table S4
T_b amplitudes	-0.28	100	0.26	100	-0.09	99.94	-0.09	99.94	0.10	0.10	0.46	Table S5
Lactation period												
T_b means	0.02	99.90	-0.04	100	-0.01	72.12	-0.01	72.12	0.24	0.24	0.55	Table S14
T_b maxima	-0.03	99.90	0.10	100	0.10	100	0.10	100	0.10	0.10	0.41	Table S15
T_b minima	0.05	100	-0.14	100	-0.06	99.05	-0.06	99.05	0.13	0.13	0.53	Table S16
T_b amplitudes	-0.08	100	0.25	100	0.13	100	0.13	100	0.07	0.07	0.51	Table S17

Note: All full models performed better than the random-effects only model: T_b parameter ~ (1|Calendar Date) + (1|Subject ID).

two, and two and three, but the magnitude of this decline was greatest between the former (Figure 1; Tables S10 and S13). There was no change in 24-h T_b amplitude between trimesters one and two, but 24-h T_b amplitudes increased in trimester three compared with trimester two because of a larger reduction in 24 T_b minima than maxima.

The interaction between gestation and drought had a meaningful effect on 24-h T_b means, maxima, minima and amplitudes (Table 2; Figure 2). Gestating females consistently had lower 24-h T_b means compared with non-reproductive females, but whereas non-reproductive females reduced their 24-h T_b means during the drought, compared with non-drought periods, gestating females had increased 24-h T_b means during the drought (Figure 2). Both gestating and non-reproductive females had higher 24-h T_b maxima during the drought compared with the non-drought period, but this increase was exaggerated for gestating females (Figure 2). Gestating females showed a smaller reduction in 24-h T_b minima in the drought period, such that non-reproductive females had lower 24-h T_b minima than gestating females during the drought (Figure 2). Gestating females had consistently narrower 24-h T_b amplitudes compared with non-reproductive females and showed a smaller increase in amplitudes during the drought compared with non-reproductive females (Table 2; Figure 2).

3.2 | Lactation period

Lactating females had higher 24-h T_b means and minima, lower 24-h T_b maxima and narrower 24-h T_b amplitudes, compared with non-reproductive females (Table 2). As lactation advanced, females had progressively higher 24-h T_b maxima, but showed no change in 24-h T_b means, minima or amplitudes (Table 3; Figure 1). Further analyses of 24-h T_b changes across lactation trimesters revealed there was no change in 24-h T_b parameters between trimesters one and two, but an upward shift in 24-h T_b mean, maxima and minima occurred between trimesters two and three (Tables S22–S24). There were no changes in 24-h T_b amplitude across lactation trimesters (Table S25).

The interaction between lactation and drought did not have a meaningful effect on 24-h T_b means (Table 3; Figure 3). All females had lower 24-h T_b means in drought conditions compared with non-drought conditions (Table 2). The interaction between lactation and drought did, however, have a meaningful effect on 24-h T_b maxima, minima and amplitudes (Table 2; Figure 2). Both lactating and non-reproductive females had higher 24-h T_b maxima during the drought compared with the non-drought period, but this increase was bigger for lactating females (Figure 3). Both lactating and non-reproductive females had lower 24-h T_b minima during the drought compared with the non-drought period, but this decrease was bigger for lactating females (Figure 3). Both lactating and non-reproductive females had wider 24-h T_b amplitudes during the drought compared with the non-drought period, but this increase was bigger for lactating females (Figure 3).

Model	Estimate	Probability of direction %	R ² marginal	R ² conditional	Full model results
Day of gestation					
T _b means	-0.12	100	0.43	0.67	Table S6
T _b maxima	-0.12	100	0.14	0.54	Table S7
T _b minima	-0.16	100	0.31	0.58	Table S8
T _b amplitudes*	0.04	84.94	0.02	0.51	Table S9
Day of lactation					
T _b means	0.02	79.59	0.12	0.66	Table S18
T _b maxima	0.05	98.86	0.10	0.49	Table S19
T _b minima*	0.01	58.04	0.03	0.64	Table S20
T _b amplitudes	0.05	79.08	0.03	0.65	Table S21

*The full model being no better than the random-effects only model: T_b parameter ~ (1|Calendar Date) + (1 + Day of Gestation or Lactation|Subject ID/Reproductive Event ID).

3.3 | Infant survival to weaning

Of the 23 births, 14 infants (61%) survived to weaning, with six of the nine infant deaths occurring during the drought. Infants died on average 81 ± 68 SD days after birth (range: 1–213 days). All models performed better than their respective random-effects only models except one gestation (number of high T_b days) and two lactation (T_b means and maxima) models (Table 4). A mother's average 24-h T_b mean, maxima, minima and amplitude during gestation did not have a meaningful effect on their infant's chance of surviving to weaning, nor did the number of days (mean = 5.3 ± 3.5 SD) they experienced high T_b means during gestation (Table 4). Similarly, a mother's average 24-h T_b means, maxima, minima and amplitude during lactation did not have a meaningful effect on their infant's chance of surviving to weaning, nor did the number of days (mean = 2.3 ± 1.8 SD) they experienced high T_b means during lactation (Table 4). In all 24-h gestation and lactation T_b infant survival models, where the full model performed better than the random-effects only model, the drought had a meaningful negative effect on infant survival to weaning (Tables S26–S35). One gestation period and seven lactation periods involved a febrile mother but, across all the infant survival models, including a fever (no/yes) predictor did not improve model fit, nor yield meaningful effects. Similarly, excluding the predictor variable drought also had no effect on the T_b predictor variable contributions to each model.

4 | DISCUSSION

We observed the predicted pattern of gestational hypothermia in wild vervet monkeys, supporting the notion that the maternal thermal environment serves to provide an optimal temperature for development and protect the foetus from potential heat-induced teratogenic effects (Asakura, 2004; Edwards, 1986; Fewell, 1995; Laburn, 1996). The vervet monkey gestation period includes the austral winter, a period typically associated with cool ambient temperatures and low resource availability, and more variable T_b (Henzi

et al., 2017; Lubbe et al., 2014; McFarland et al., 2015). However, gestating females demonstrated improved homeothermy (i.e. narrower 24-h T_b amplitudes) during gestation, which suggests the prioritization of thermoregulation to maintain a thermal gradient for heat loss from the developing foetus (Farmer, 2000). Similar to observations in smaller mammals (e.g. dwarf hamsters: Scribner & Wynne-Edwards, 1994; rats: Fewell, 1995; mice: Gamo et al., 2013), we found evidence of increased body temperature maxima during lactation, particularly in late lactation and when resources were limited during a drought.

We demonstrate that the regulation of maternal T_b is tied to both reproductive processes and the availability of resources. Female vervet monkeys maintained more homeothermic T_b during gestation which progressively decreased over the course of gestation. An increasing magnitude of gestational hypothermia throughout gestation allows dissipation of metabolic heat generated by the foetus, which increases progressively as the foetus grows (Laburn, 1996). When females faced limited resources and harsh climatic conditions (i.e. the drought period), 24-h T_b amplitude increased, although this increase in T_b amplitude was smaller for gestating females compared with non-reproductive females.

Data from other species show that there appears to be a limit to which a reduction in body temperature is beneficial for foetal development. Both pregnant high Arctic muskoxen (Schmidt et al., 2020) and hibernating bears (Friebe et al., 2014; Shimozuru et al., 2013; Tøien et al., 2015), for example, displayed higher and more stable body temperatures than their non-pregnant counterparts during periods of resource scarcity. In species with shorter gestational periods (e.g. Arctic ground squirrel), conception occurred after hibernation and coincided with spring snow melt (Williams et al., 2011). Although pregnant vervet females appeared to prioritize the maintenance of a more constant thermal environment for the developing foetus, foetuses conceived during drought years were exposed to a warmer and more variable maternal thermal environment compared with the non-drought periods. The degree of homeothermy of a female during gestation may therefore represent a trade-off between offspring investment (i.e. improved homeothermy) and the prioritization of the

TABLE 3 Results of the Bayesian generalized linear mixed models estimating the effect of day of gestation or lactation on female vervet monkeys 24-h body temperature (T_b). T_b parameter ~ Day of Gestation or Lactation + Mean Ambient Temperature + Body mass + (1|Calendar Date) + (1 + Day of Gestation or Lactation|Subject ID/Reproductive Event ID).

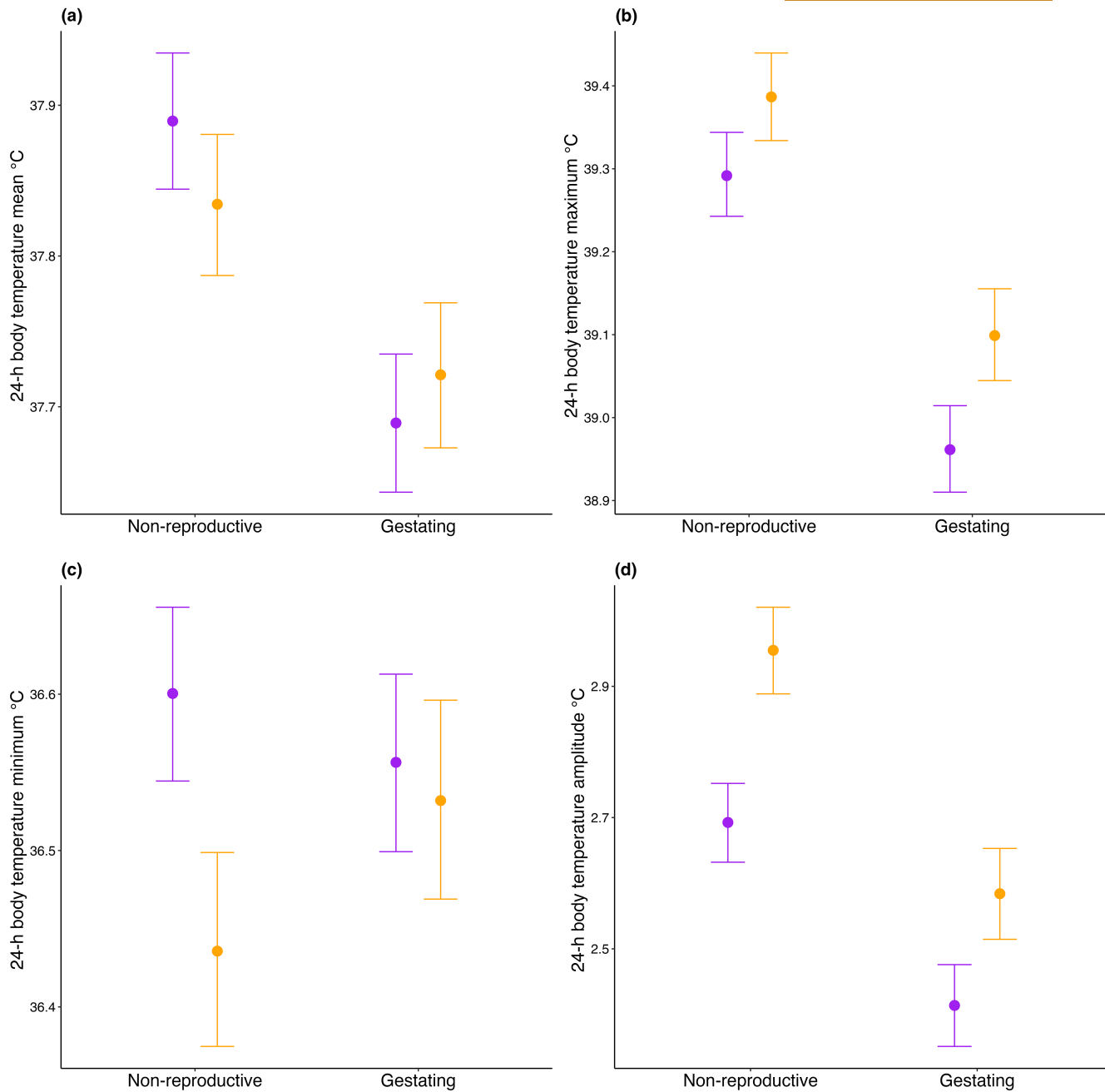


FIGURE 2 Conditional effects plots showing the meaningful interaction effects between gestation and drought on female vervet monkey 24-h body temperature (a) means, (b) maxima, (c) minima and (d) amplitudes. Purple = non-drought period. Orange = drought. $N = 23$ gestation periods (14 non-drought/9 drought) from 14 monkeys compared with non-reproductive periods of 30 monkeys. Credible intervals set at 95%.

mother's other homeostatic systems that ensure her own survival. That is, when resources are limited, gestating females are less likely to demonstrate the low and narrow amplitudes of T_b that are likely to be most beneficial to the foetus.

While pregnant monkeys attempted to defend a narrow rhythm of body temperature during the drought, lactating females displayed a larger increase in the amplitude of T_b rhythm than their non-reproductive counterparts during the drought. The latter likely reflects the increased energetic and water demands of lactation (Emery-Thompson, 2013), which may have put additional strain

on body water and energy reserves when resources were limited. Indeed, lactating grey mouse lemurs increased the frequency and depth of torpor bouts in response to food restriction (Canale et al., 2012). In more typical years, vervet monkeys appear to have sufficient access to water and food resources to maintain a narrow rhythm of body temperature throughout lactation.

Lactating females also experienced higher T_b means compared with non-reproductive females, but T_b maxima was highest in non-reproductive females. One implication of this finding is that the increased T_b maxima observed in small mammals during lactation

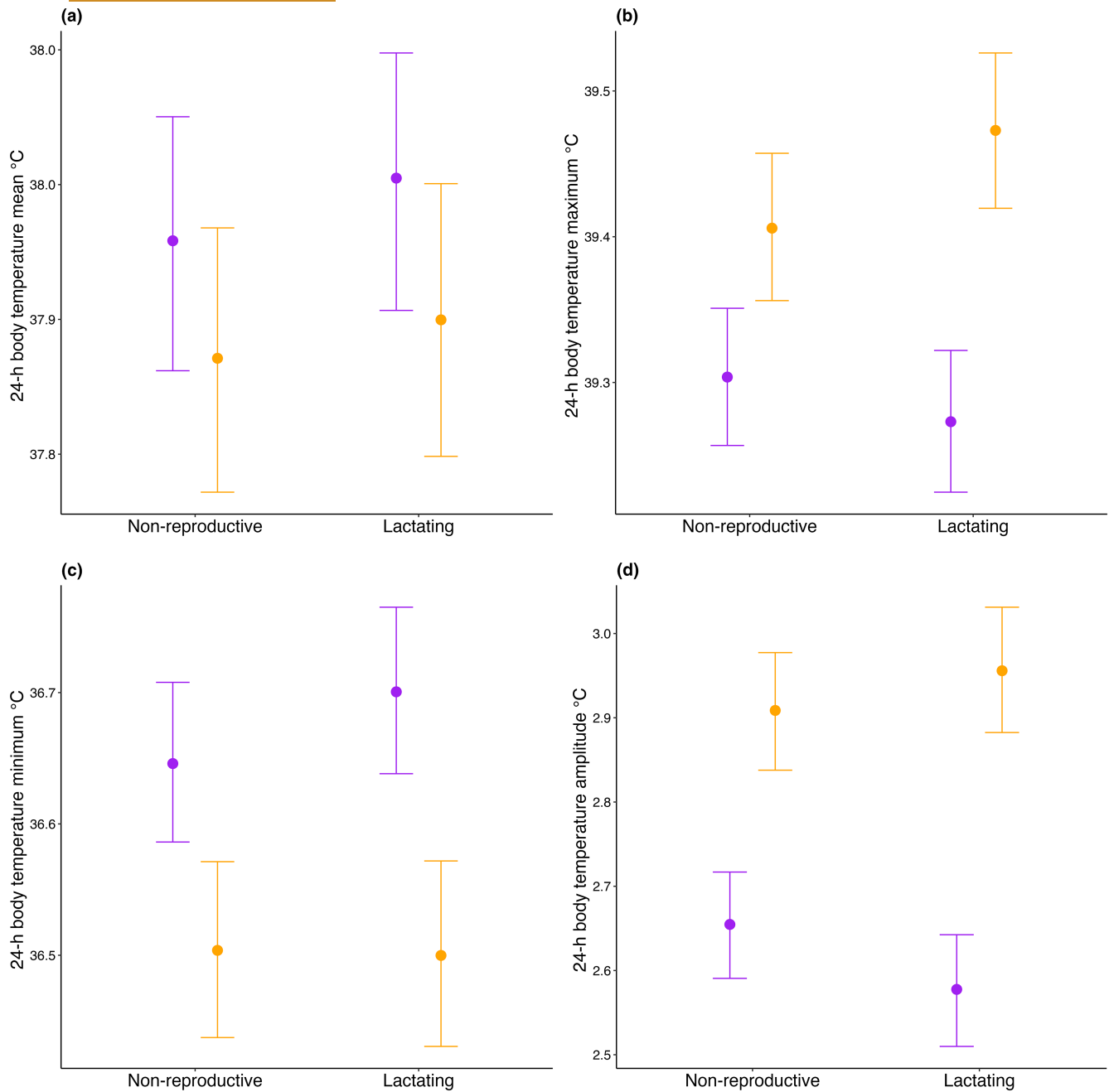


FIGURE 3 Conditional effects plots showing the meaningful interaction effects between lactation and drought on female vervet monkey 24-h body temperature (a) means, (b) maxima, (c) minima and (d) amplitudes. Purple = non-drought period. Orange = drought. $N = 22$ lactation periods (14 non-drought/8 drought) from 14 monkeys compared with non-reproductive periods of 30 monkeys. Credible intervals set at 95%.

(Fewell, 1995; Gamo et al., 2013; Scribner & Wynne-Edwards, 1994) is perhaps more related to an increase in thermogenesis to support altricial neonates that are typically born hairless and incapable of thermoregulation (Lezama-García et al., 2022). Despite the high thermogenic costs to support altricial neonates soon after birth, body temperatures of lactating Arctic ground squirrels increased progressively throughout lactation, peaking at the time of weaning (Williams et al., 2011). Our female vervet monkeys also experienced higher body temperatures as lactation progressed—especially in the third trimester—most likely a consequence of the increased

energetic requirements of milk production and foraging effort (Adels & Leon, 1986; Hinde et al., 2009; Oftedal, 1984; Rosetta et al., 2011; Sashaw, 2012; Speakman, 2008). These changes in body temperature throughout lactation may also reflect changes in milk composition. Initially, primates produce dilute milk that is high in sugar (lactose) to support on demand feeding by the infant and maintain infant hydration (Hinde & Milligan, 2011). This high milk yield of low energy quality allows a low daily cost of investment (Oftedal & Iverson, 1995) and ensures that the mother can produce milk even if available resources fluctuate (Oftedal, 1984). Fat and

TABLE 4 Results of the Bayesian generalized linear mixed models estimating the effect of female vervet monkey average 24-h body temperature (T_b) during gestation and lactation on the survival of their infants to weaning. Weaning $\sim T_b$ parameter + Drought + (1|Mother ID).

Model	T_b parameter		Drought (no/yes)		R^2 marginal	R^2 conditional	Full model results
	Estimate	Probability of direction %	Estimate	Probability of direction %			
Gestation period							
T_b means	-9.29	77.68	-6.32	99.69	0.38	0.45	Table S26
T_b maxima	-1.73	59.32	-4.47	99.58	0.34	0.40	Table S27
T_b minima	-16.42	85.83	-11.83	99.81	0.41	0.52	Table S28
T_b amplitudes	4.74	76.95	-4.81	99.74	0.35	0.41	Table S29
Number of high T_b days*	-0.27	89.27	-3.61	99.22	0.36	0.40	Table S30
Lactation period							
T_b means*	-2.04	58.56	-4.06	98.86	0.30	0.39	Table S31
T_b maxima*	1.43	60.38	-4.22	96.67	0.30	0.38	Table S32
T_b minima	-3.35	67.53	-5.59	98.78	0.32	0.42	Table S33
T_b amplitudes	3.04	70.12	-5.65	97.74	0.32	0.40	Table S34
Number of high T_b days	-0.87	83.53	-6.84	99.35	0.35	0.44	Table S35

*The full model being no better than the random-effects only model: Weaning \sim (1|Mother ID).

protein composition of milk then increase as the infant ages (Hinde et al., 2009), which increases the energy density of milk and presumably the energetic cost of production. If resources are particularly limited, a mother will increasingly rely on mobilization of fat reserves, which increase the energy density of the milk but decrease yield (Hinde & Milligan, 2011). When resources were limited, lactating vervet females experienced increasingly high 24-h maxima T_b and lower 24-h minima T_b . This pattern of T_b regulation is consistent with the response of other mammals to periods of limited resources (Hetem et al., 2016; Maloney et al., 2017), suggesting that, in the absence of adequate food and water resources, thermoregulation was not prioritized in lactating females, resulting in a trade-off between maternal condition and offspring growth during the lactation period (Fairbanks & McGuire, 1995; Hinde et al., 2009).

The finding that a mother's degree of homeothermy during gestation is unrelated to her infant's chance of survival to weaning, however, suggests that, in the current study, all mothers maintained a thermal environment that adequately supported their foetus. Similarly, a mother's degree of homeothermy during lactation did not seem to impact on an infant's survival to weaning. While reduced survival would suggest a trade-off between higher infant mortality against a lowered risk of their maternal mortality and future reproduction, the lack of any such effect seems to indicate that maternal investment remained above a terminal threshold and that bet-hedging may work to the benefit of both mothers and offspring. The focus of the current study was to examine whether there was a direct link between a mother's thermal performance during gestation or lactation and her infant's chances of survival to weaning; we did not conduct a full examination of the social and ecological variables that predict infant survival. Given the size of our sample ($N=23$ infants born from females with T_b data), we were restricted in the number of predictors that could be included in our infant survival analysis. However, it has recently been shown—using a much larger dataset, including animals that did not have body temperature data loggers—that maternal dominance rank, social network degree and resource availability predict infant survival to weaning in our population (Bleresch et al., 2023). Taken together, these findings support the view that resource availability plays a central role in supporting a maternal environment that supports successful reproduction (Gittleman & Thompson, 1988), and that flexibility in maternal body temperature regulation may facilitate successful reproduction in sub-optimal conditions.

Some of our models revealed small marginal R^2 values (<10%), suggesting our fixed effects explained relatively little variation. However, these small R^2 values are perhaps unsurprising given these were relatively large models ($N \sim 13,000$) and we only included main effects that were directly relevant to our study predictions, namely reproductive stage and drought. That is, one would expect a reasonable amount of unexplained individual (i.e. conditional) variation in these models. Indeed, it has been published elsewhere that vervet monkey core body temperature patterns are influenced by a range of microclimate variables (Lubbe et al., 2014; Mathewson et al., 2020; McFarland et al., 2020), individual differences in activity and

microclimate selection (e.g. resting, shade use, huddling, swimming: McFarland et al., 2015, 2020; Henzi et al., 2017), prevalence of fever (McFarland et al., 2021) and patterns of parturition (McFarland et al., 2022).

Females that demonstrate more homeothermic T_b during gestation are more likely to produce healthier offspring, and factors that assist in T_b regulation, such as foraging success (Altmann, 1980; Sashaw, 2012), water intake (Brain & Mitchell, 1999; Hetem et al., 2016) and social thermoregulation (McFarland et al., 2015, 2020), are likely to be favoured by natural selection. In a previous study of climate-induced mortality in this population of vervet monkeys, female deaths typically occurred shortly after giving birth, supporting the view that over-investment in reproductive events can result in mother mortality (Young et al., 2019). This was likely the case for one female in the current sample, when the mother (and infant) died on the day of parturition. In cases where a mother does survive a compromised pregnancy, additional long-term costs associated with maternal physiological performance during reproductive events may also affect infant growth and development, including for example, nutrient and hormone transfer to the infant in vivo, or via breast milk (Coe & Lubach, 2000; Hinde et al., 2009, 2015; Rutherford, 2013; Singh et al., 2012). It seems reasonable to assume, therefore, that terminated pregnancies might be a consequence of reduced homeothermy, to the point that the internal thermal environment no longer supports foetal development. In baboons, for example, foetal loss during the first trimester was associated with high ambient temperatures (Beehner, Onderdonk, et al., 2006). Flexibility in a mother's degree of homeothermy during gestation may therefore reflect a bet-hedging trade-off between offspring investment and self-maintenance, following the prioritization of other homeostatic systems when resources are limited (Stearns, 1989). These findings also suggest that there is flexibility, both within and across, income and capital breeding strategies, especially when individuals are exposed to the selective pressure of unpredictable conditions (Jönsson, 1997; Stearns, 1989).

While maternal nutrition and body water balance will influence the degree of homeothermy, it is also possible for mother and foetus to come into conflict over maternal physiology. In the context of pre-eclampsia, for example, it appears that the foetus exerts control over maternal blood pressure to increase the delivery of nutrients through the placenta (Haig, 1993). Could a similar battle for control occur surround maternal T_b ? In other words, we would speculate that, under harsh environmental conditions, the foetus works to wrest control from the mother to ensure that thermal conditions are regulated as near to optimal as possible for its own development, resulting in higher energetic costs for the mother. If a mother invests too heavily in the current offspring at the expense of her own survival, however, this can also have long-term consequences for the fitness of her offspring (Zipple et al., 2021).

Climate change is predicted to increase the frequency and intensity of droughts throughout the arid and semi-arid regions of sub-Saharan Africa (Engelbrecht et al., 2015; Mirzabaev et al., 2019).

These changing climates will reduce species' access to the food and water resources needed to sustain costly reproductive processes, namely gestation and lactation, for placental mammals. There is increasing evidence for a direct effect of increasing temperature and reduced resource availability on the physiological performance and tolerance thresholds of individual free-living mammals (Fuller et al., 2016, 2021), with drought having a clear potential to inflict mass mortality (Rey et al., 2017; Young et al., 2019). However, there may also be more subtle and currently unexplored population-level changes in survivability. Some of these changes might be underpinned by reduced reproductive outputs when current bet-hedging trade-offs between offspring survival and self-maintenance fail. Such failure may not only result in terminated pregnancies or compromised parturition events (McFarland et al., 2022), but may also culminate in compromised maternal condition that may have more long-term costs to individual- and population-level reproductive success.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas, designed the methodology and contributed to the collection of data; RM analysed the data and led the writing of the manuscript. All authors contributed substantially and critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used in the current analyses are openly available on Figshare at <https://doi.org/10.6084/m9.figshare.25053314> (McFarland et al., 2024).

STATEMENT ON INCLUSION

Our study brings together authors from several different countries, including scientists based in South Africa where the study was carried out. Collaboration between South African and international researchers was forged before this study commenced in 2012, to the point that all authors were engaged early on with the research and study design, ensuring that the diverse sets of perspectives they represent were considered from the onset.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Summary of female body temperature (T_b) measurements over the reproductive and non-reproductive periods.

Table S2: Bayesian GLMM parameter estimates for the body temperature (T_b) means during gestation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S3: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima during gestation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S4: Bayesian GLMM parameter estimates for the body temperature (T_b) minima during gestation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S5: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitudes during gestation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S6: Bayesian GLMM parameter estimates for the body temperature (T_b) mean across gestation model, specifying a Gaussian distribution.

Table S7: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima across gestation model, specifying a Gaussian distribution.

Table S8: Bayesian GLMM parameter estimates for the body temperature (T_b) minima across gestation model, specifying a Gaussian distribution.

Table S9: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitude across gestation model, specifying a Gaussian distribution.

Table S10: Bayesian GLMM parameter estimates for the body temperature (T_b) mean across gestation trimesters model, specifying a Gaussian distribution.

Table S11: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima across gestation trimesters model, specifying a Gaussian distribution.

Table S12: Bayesian GLMM parameter estimates for the body temperature (T_b) minima across gestation trimesters model, specifying a Gaussian distribution.

Table S13: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitudes across gestation trimesters model, specifying a Gaussian distribution.

Table S14: Bayesian GLMM parameter estimates for the body temperature (T_b) means during lactation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S15: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima during lactation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S16: Bayesian GLMM parameter estimates for the body temperature (T_b) minima during lactation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S17: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitudes during lactation versus non-reproductive periods model, specifying a Gaussian distribution.

Table S18: Bayesian GLMM parameter estimates for the body temperature (T_b) mean across lactation model, specifying a Gaussian distribution.

Table S19: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima across lactation model, specifying a Gaussian distribution.

Table S20: Bayesian GLMM parameter estimates for the body temperature (T_b) minima across lactation model, specifying a Gaussian distribution.

Table S21: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitudes across lactation model, specifying a Gaussian distribution.

Table S22: Bayesian GLMM parameter estimates for the body temperature (T_b) mean across lactation trimesters model, specifying a Gaussian distribution.

Table S23: Bayesian GLMM parameter estimates for the body temperature (T_b) maxima across lactation trimesters model, specifying a Gaussian distribution.

Table S24: Bayesian GLMM parameter estimates for the body temperature (T_b) minima across lactation trimesters model, specifying a Gaussian distribution.

Table S25: Bayesian GLMM parameter estimates for the body temperature (T_b) amplitudes across lactation trimesters model, specifying a Gaussian distribution.

Table S26: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) mean during gestation model, specifying a Bernoulli distribution.

Table S27: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) maxima during gestation model, specifying a Bernoulli distribution.

Table S28: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) minima during gestation model, specifying a Bernoulli distribution.

Table S29: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) amplitudes during gestation model, specifying a Bernoulli distribution.

Table S30: Bayesian GLMM parameter estimates for survival to weaning and the number of days a mother's mean 24 h body temperature (T_b) exceeded the mean gestation temperature +2SD, specifying a Bernoulli distribution.

Table S31: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) means during lactation model, specifying a Bernoulli distribution.

Table S32: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) maxima during lactation model, specifying a Bernoulli distribution.

Table S33: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) minima during lactation model, specifying a Bernoulli distribution.

Table S34: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) amplitudes during lactation model, specifying a Bernoulli distribution.

Table S35: Bayesian GLMM parameter estimates for the survival to weaning and the mother's average 24 h body temperature (T_b) amplitudes during lactation model, specifying a Bernoulli distribution.

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