

## Research



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## Physiology

# The thermal consequences of primate birth hour and its evolutionary implications

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Most primates, including humans, give birth during the inactive phase of the daily cycle. Practical constraints therefore limit our knowledge of the precise timing of nocturnal birth in wild diurnal primates and so limit our understanding of selective pressures and consequences. We measured maternal core body temperature ( $T_b$ ) across 24 births in a population of wild vervet monkeys using biologgers. We identified distinct perturbations in  $T_b$  during the birth period, including declining  $T_b$  during labour and the rapid recovery of  $T_b$  post-parturition. Vervet monkeys typically gave birth during their inactive phase in synchrony with the nadir of the maternal nychthemeral  $T_b$  rhythm but also showed remarkable inter-individual variability in their absolute  $T_b$  during birth. Our findings support the view that selection may have favoured a nocturnal timing of primate birth to coincide with lower night-time  $T_b$  and environmental temperatures, which improve thermal efficiency during birth.

## 1. Introduction

Most primate births occur during the inactive phase, with diurnal species generally giving birth at night, and nocturnal species during the day [1–3]. This conserved timing is argued to benefit new mothers by reducing predation risk, conspecific harassment and the need to keep up with a travelling group [1,4–8]. While there are data from captive animals, the obvious practical challenges mean that we know little about the precise timing of nocturnal parturition in wild diurnal primates, and the extent to which this might contribute to our understanding of the selection pressures promoting inactive-phase birth. Mammalian births are characterized by a decrease in maternal body temperature ( $T_b$ ) over the hours of labour and a precipitous increase in  $T_b$  in the hours immediately post-parturition [9–12]. These distinct perturbations in  $T_b$  suggest a means whereby the timing of birth can be accurately gauged in the absence of direct observation.

In mammals, melatonin release at the end of the active phase appears to signal the timing of birth [3,13,14]. Although the role of melatonin in regulating  $T_b$  during parturition has not been investigated [3], its role in influencing the nychthemeral fall in  $T_b$  [15,16] suggests that a common factor may regulate the maternal and environmental thermal conditions to best support birth. The

maternal thermal environmental is important to the birthing process [9] and irregular birth conditions can have negative consequences for neonatal survival and development [17,18]. Low maternal  $T_b$  during labour can help protect the fetus from neuronal injury during hypoxic birth conditions [19,20].

We investigate the possibility that evolution of primate birth hour may have favoured synchronization with both the maternal nychthemeral  $T_b$  rhythm to maximize thermoregulatory efficiency and environmental conditions that reduce the costs of  $T_b$  regulation. We confirm the perturbations in core  $T_b$  associated with the birth process in wild vervet monkeys (*Chlorocebus pygerythrus*) and assess the degree to which hour of birth aligns with the light–dark cycle and the maternal nychthemeral  $T_b$  rhythm [21,22]. Finally, we discuss the possible thermal costs associated with atypical birth following our direct observation of two daytime births.

## 2. Methods

### (a) Data collection

Data were collected between September 2010 and December 2017 from three troops of wild vervet monkeys on the Samara Private Game Reserve, South Africa. Monkeys were fully habituated to researchers and could be individually identified. Daily censuses of troop membership were recorded. Vervet females reach sexual maturity at approximately 3 years and produce a single offspring at each reproductive event [23,24]. Vervets are seasonal breeders and our population's birth season falls in the austral summer [25,26]. The birth season coincides with increasing resource abundance, to support the energetically expensive lactation period [26,27], but also with higher environmental temperatures [28]. Mean hourly air temperatures were recorded at a local weather station and ranged from  $-8.1^\circ\text{C}$  to  $41.6^\circ\text{C}$  (mean =  $17.2^\circ\text{C} \pm 8.3$  s.d.).

In a longitudinal study of vervet monkey thermal physiology, 30 adult females (mean body mass =  $3.4 \text{ kg} \pm 0.3$  s.d.) were implanted with temperature-sensitive biologgers over a 7-year period [28–30]. Biologgers instantaneously recorded intra-abdominal  $T_b$  at five-minute intervals. Normal behaviour resumed on the day after surgery, and no long-term sequelae were observed because of surgeries. For details of the capture and surgery procedure, see McFarland *et al.* [29].

We ran three Bayesian generalized linear mixed models (GLMMs), specifying a Gaussian distribution, to compare the (i) minimum night-time  $T_b$  of birthing and non-birthing females (between-subject), (ii) number of hours from sunset that birthing and non-birthing females took to reach their minimum night-time  $T_b$  and (iii) minimum night-time  $T_b$  of birthing females on the night of birth and seven days prior (within-subject). We entered minimum night-time  $T_b$  and number of hours after sunset, in turn, as the outcome variable. We entered whether each female gave birth that night as a predictor variable. Body mass was entered as a predictor variable to control for its influence on  $T_b$  [29]. GLMMs were run using the 'brms' package in R v. 3.5.0. [31,32]. Full model descriptions, code and results are provided in the electronic supplementary material.

## 3. Results

Twenty-four infants were born to 16 mothers implanted with  $T_b$  biologgers. Two of these births were directly witnessed during routine daytime field observations (figure 1; electronic supplementary material, Video). For the two daytime births, we observed an identifiable drop in maternal  $T_b$  before

parturition, immediately followed by a precipitous rise in  $T_b$  (table 1 and figure 1). For 17 of the 22 unwitnessed births, we were able to identify the same distinct post-parturition increase in maternal  $T_b$  that could not otherwise be explained by the nychthemeral  $T_b$  rhythm or activity that might take place at night (table 1). Fifteen of these 17 births occurred at night, and two occurred within 1 h of sunset when the mother was inactive at her sleep site (figure 2). We were unable to identify the timing of birth for the remaining five births. We excluded these five births from our analyses, focusing on the 17 inactive-phase births from 14 females.

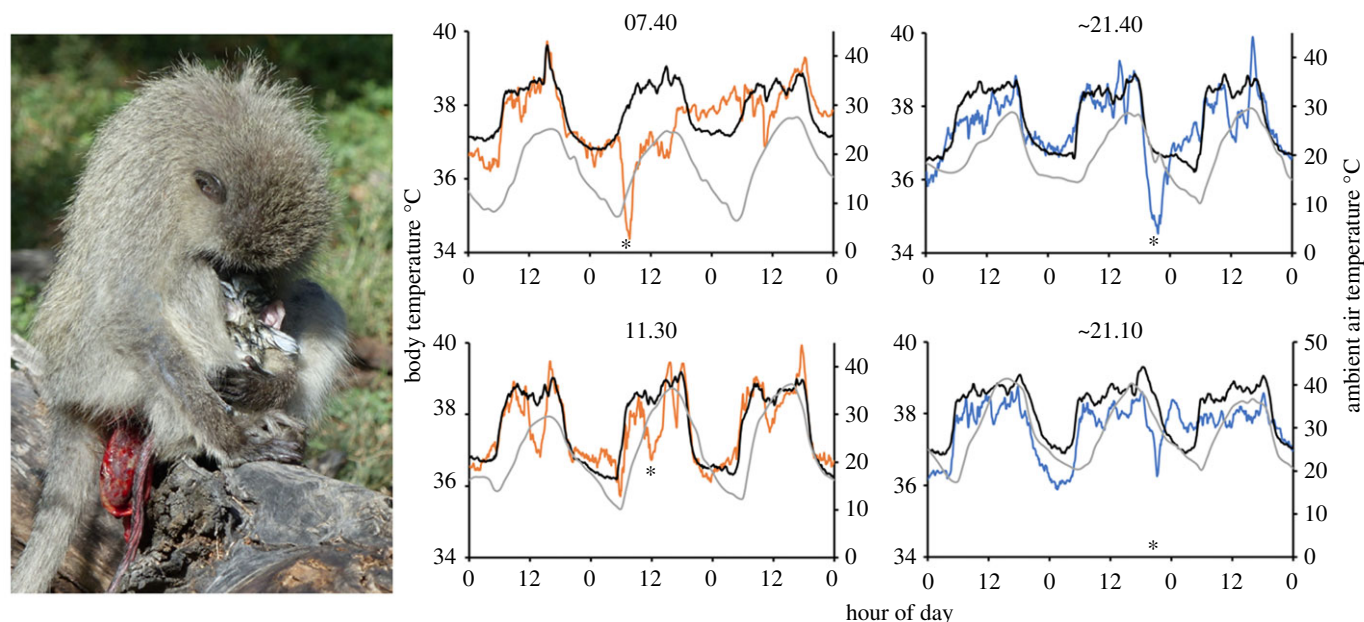
Birthing females experienced lower night-time  $T_b$  minima than non-birthing females and reached those temperatures earlier in the night (table 1 and table 2). Birthing females also experienced lower  $T_b$  minima during birth than they did on a night 7 days prior (tables 1 and 2). For the 17 typical inactive-phase births, maternal  $T_b$  reached a mean low of  $35.9^\circ\text{C}$  approximately 2.5 h after sunset (table 1). Maternal  $T_b$  then increased precipitously to a mean of  $37.2^\circ\text{C}$  after 1.7 h, whereafter  $T_b$  stabilized and followed the normal nychthemeral rhythm. By contrast, non-birthing females—over all birth seasons—reached a mean minimum of  $36.6^\circ\text{C}$ , 7.7 h after sunset. These females then gradually increased their  $T_b$  over 6.5 h to  $38.3^\circ\text{C}$ .

The distinct perturbations of  $T_b$ —declining temperatures during labour and post-parturition recovery—were observed during both typical inactive-phase and atypical active-phase births (figure 1). Given that the active-phase births were not synchronized with the nychthemeral  $T_b$  rhythm, the decline in  $T_b$  during labour was more pronounced due to its decline from a higher active-phase level. Active/diurnal birth 1 took place in the early morning (7.40 h; figure 1) and coincided with the coldest time of day when the mother was close to her  $T_b$  bathyphase. The large gradient for dry heat loss to the environment at this time might explain why this mother became particularly hypothermic during birth, reaching a  $T_b$  low of  $34.4^\circ\text{C}$ . This female was observed eating her placenta at 07.45, and her post-parturition  $T_b$  profile was consistent with that of nocturnal births. Active/diurnal birth 2 took place in the middle of the day (11.30; figure 1), coinciding with the warmest time of the day when the mother was approaching her  $T_b$  acrophase. The challenges associated with regulating  $T_b$  at this time likely explain why this mother reached a hyperthermic  $T_b$  ( $39.5^\circ\text{C}$ ) post-parturition.

## 4. Discussion

Vervet monkeys typically gave birth during their inactive phase, with most births occurring at night, consistent with observations in other diurnal primate species [1–9]. While there were consistencies in both the timing of birth and the patterns of maternal  $T_b$  during parturition, there was also substantial inter-individual variability in absolute  $T_b$ , suggesting flexibility in the 'typical' thermal conditions of a successful birth.

Giving birth during the inactive phase facilitates the critical establishment of the mother–infant link with respect to nursing, bonding and heat retention, without interference by conspecifics or troop movements [8,33]. Post-parturition is a critical period for the infant, when heat lost via the evaporation of amniotic fluid poses a significant risk of hypothermia [17,34,35]. To combat the risk of hypothermia,



**Figure 1.** Maternal 72 h body temperature ( $T_b$ ) rhythms across two diurnal (orange lines) and two nocturnal (blue lines) vervet monkey births. Asterisks denote time of birth. Black lines denote the average non-birthing female time-matched 72 h  $T_b$ , and grey lines denote ambient air temperature. Top-left birth was photographed and video recorded (electronic supplementary material, Video).

neonates engage in non-shivering thermogenesis [36] and gain heat through maternal body contact as the mother's  $T_b$  returns to normal [17,37]. Following relatively hypothermic birth conditions, maternal resources are needed to re-establish the nychthemeral  $T_b$  rhythm. Placentophagia has previously been argued to replenish nutritional losses from pregnancy, enhance pregnancy-mediated analgesia and prevent the placenta from attracting predators [38]. We suggest that, in addition, the specific dynamic action of placentophagia may also provide the heat needed to recover  $T_b$  post-parturition [39]. Variation in maternal nutritional and energetic demands at the time of birth could potentially explain the variation in a tendency for nonhuman primates to eat the placenta [7].

Our observation of two daytime births provides preliminary insight into possible thermal costs, for both mother and infant, when the timing of birth deviates from the inactive phase. We directly witnessed two active-phase births, the first of which took place in the cool early morning, and the second which took place in the heat of the day. The distinct perturbations of  $T_b$  during typical births were similarly observed during these atypical births, supporting the view that low  $T_b$  during labour is not a by-product of the low nychthemeral  $T_b$  rhythm at night, but rather a distinct phenology associated with labour. Whereas low  $T_b$  during labour is facilitated by the natural nychthemeral fall of  $T_b$  and low environmental temperatures during night-time births, no such benefits are experienced during daytime births. The physiological costs of maternal  $T_b$  regulation are therefore likely to be greater during daytime births, when the mother needs to dissipate heat at a time of day when she is closer to her acrophase in nychthemeral  $T_b$ , and when the environmental heat load is higher. Furthermore, when recovering from birth during warm daytime temperatures, both mother and infant are at greater risk of post-parturition hyperthermia and dehydration [21,22]. Infants use evaporative water loss soon after birth, and given their small body size and relatively high surface area to volume ratio, are particularly vulnerable to dehydration [40].

It has long been argued and has since become the consensus, that the nocturnal timing of primate births serves primarily to reduce the risk of predation, conspecific harassment and group-fission, all of which would be more likely if births occurred during the active phase [1–8]. Our findings suggest that there may also be important thermal consequences linked to the timing of primate birth. Together with these socio-ecological factors, selection may have favoured a nocturnal birth hour that is synchronized with both the nadir of the maternal nychthemeral rhythm of  $T_b$  and the environmental conditions that enhance thermoregulatory efficiency across birth. Coordinating the timing of birth with both the low nychthemeral  $T_b$  rhythm and cool night-time temperatures reduces the physiological costs of lowering maternal  $T_b$  during labour. Furthermore, a mother doesn't need to implement evaporative cooling at night to lower  $T_b$  and can instead rely on less costly dry heat loss. At a time when maternal resources are at a premium [41], any means by which resources can be conserved, and physiological processes made less costly, are likely to improve the welfare of both mother and infant.

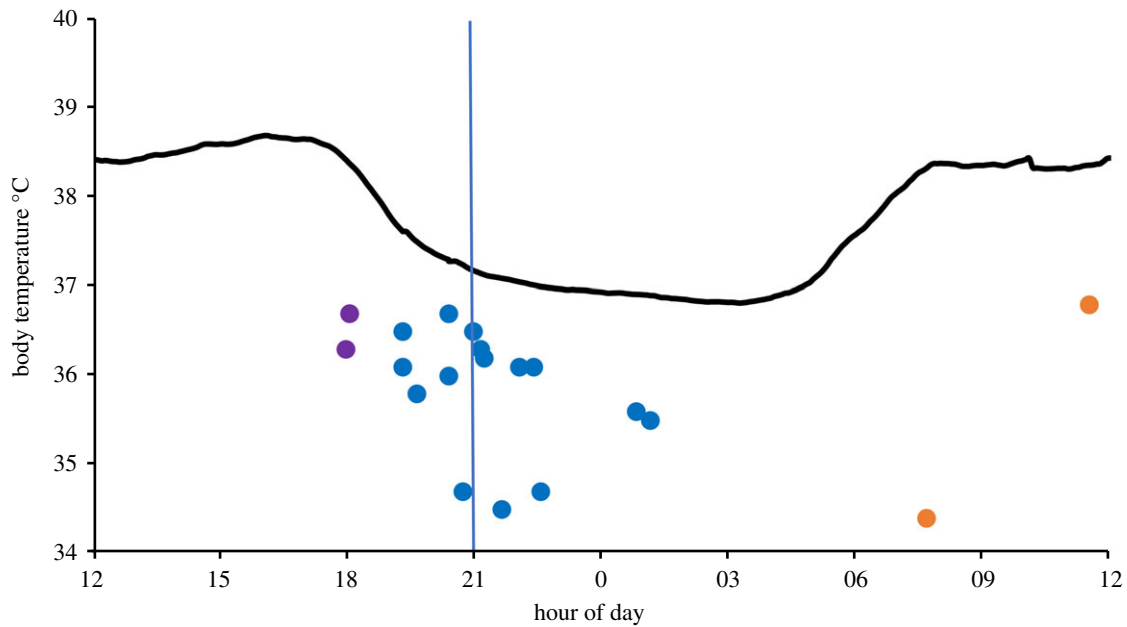
If so, then it seems reasonable to suggest that the timing of birth will be particularly important for smaller, more thermally labile species, where birth should be more synchronized to the most thermally advantageous time. Larger-bodied apes appear to be less constrained to nocturnal births compared to monkeys [1]. Furthermore, given that the pelvic inlet to neonatal head ratio is much tighter, and births are longer and more challenging in monkeys compared to apes [42,43]—it is possible that apes (excluding humans) may be less constrained by the thermal challenges of birth compared to monkeys. Species that experience more variable climates (i.e. temperate climates and/or high-elevation) are likely to have come under greater environmental selective pressure for the timing of birth, as they have for reproductive seasonality [27,44]. For seasonal breeders, the birth season coincides with resource abundance when environmental temperatures also tend to be high [28]. For these species, the risk of maternal or neonatal hypothermia

**Table 1.** Maternal body temperatures across vervet monkey births.

female ID	phase at birth	date of birth	time of observed birth				labour				post-parturition						
			time of observed birth	hh:mm	hh:mm	hh:mm	time at start of $T_b$ decline	h	hh:mm	hh:mm	time at end of $T_b$ decline	h	hh:mm	hh:mm			
			hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm	hh:mm			
Penelope	active/diurnal	20 Nov 2014	7:40	19:04	5:10	5:45	7:50	37.5	34.4	-3.1	1.5	12.06	10.00	36.9	2.10	2.5	14.1
Coco	active/diurnal	26 Oct 2016	11:30	18:42	5:28	10:20	12:05	38.1	36.8	-1.3	0.7	17.23	15:40	39.5	3.35	2.7	30.6
Ocean	inactive/nocturnal	23 Oct 2010	—	18:39	5:32	18:00	19:20	38.7	36.5	-2.2	1.7	0.41	21:40	38.1	2.20	1.6	12.8
Uma	inactive/nocturnal	5 Nov 2010	—	18:56	5:15	17:05	20:25	38.8	36.7	-2.1	0.6	1.29	22:20	37.6	1.55	0.9	16.0
Dottie	inactive/nocturnal	13 Nov 2012	—	18:57	5:14	17:10	1:10	38.6	35.5	-3.1	0.4	6.13	2:35	37.9	1.25	2.4	13.6
Wokbox	inactive/nocturnal	10 Dec 2014	—	18:31	5:44	16:50	19:40	38.9	35.8	-3.1	1.1	1.09	22:40	37.7	3.00	1.9	17.4
Dori	inactive/nocturnal	21 Oct 2014	—	18:38	5:34	16:20	20:45	38.7	34.7	-4.0	0.9	2.07	22:55	36.7	2.10	2.0	18.5
Iyvara	inactive/nocturnal	31 Oct 2014	—	18:46	5:24	17:15	19:20	37.9	36.1	-1.8	0.9	0.34	20:35	37.1	1.15	1.0	11.9
Arwen	inactive/diurnal	2 Nov 2014	—	18:48	5:22	15:55	18:00	38.4	36.3	-2.1	1.0	-0.48	19:10	36.7	1.10	0.4	16.4
Carmella	inactive/nocturnal	6 Nov 2014	—	18:51	5:18	16:50	21:15	38.8	36.2	-2.6	0.6	2.24	23:10	36.9	1.55	0.7	19.4
Lisa	inactive/nocturnal	5 Dec 2014	—	19:17	5:07	20:20	21:00	37.1	36.5	-0.6	0.9	1.43	21:30	37.0	0.30	0.5	14.8
Daffy	inactive/nocturnal	18 Dec 2014	—	19:25	5:10	18:35	0:50	38.4	35.6	-2.8	0.4	5.25	2:10	36.6	1.20	1.0	14.1
Arwen	inactive/nocturnal	21 Nov 2015	—	19:04	5:10	17:40	20:25	38.4	36	-2.4	0.9	1.21	21:30	36.7	1.05	0.7	10.2
Dori	inactive/nocturnal	12 Nov 2015	—	19:21	5:08	18:35	22:35	38.3	34.7	-3.6	0.9	3.14	0:55	36.4	2.20	1.7	15.6
Flo	inactive/nocturnal	5 Jan 2016	—	19:32	5:22	18:15	21:10	38.6	36.3	-2.3	0.8	1.38	0:20	38.4	3.10	2.1	31.9
Ubuntu	inactive/nocturnal	19 Oct 2016	—	18:38	5:35	17:45	22:05	38.2	36.1	-2.1	0.5	3.27	23:30	37.5	1.25	1.4	18.5
Dori	inactive/nocturnal	30 Oct 2016	—	18:45	5:24	17:40	21:40	38.7	34.5	-4.2	1.1	2.55	23:15	36.3	1.35	1.8	20.1
Cyclops	inactive/diurnal	14 Nov 2016	—	18:59	5:13	17:10	18:05	38.1	36.7	-1.4	1.5	-0.54	18:40	37.1	0.35	0.4	22.1
Priscilla	inactive/nocturnal	4 Jan 2017	—	19:32	5:21	20:30	22:25	37.8	36.1	-1.7	0.9	2.53	0:20	37.3	1.55	1.2	22.8
mean birthing female (inactive phase)						17:45	21:04	38.4	35.9	-2.5	0.9	2.28	22:46	37.2	1.42	1.3	17.4
mean non-birthing female (across all birth seasons)						17:15	03:15	38.6	36.8	-1.8	0.2	14.45	—	—	—	—	—

\*Estimated time of parturition for unwitnessed births. Body temperature ( $T_b$ ).





**Figure 2.** Maternal body temperature at the time of vervet monkey birth (dots) and the average female nychthemeral 24 h body temperature rhythm during the birth season (black line). Blue dots represent inactive-phase nocturnal births, purple dots the inactive-phase diurnal births and orange dots the observed active-phase diurnal births. Blue line denotes the average timing of typical inactive-phase births.

**Table 2.** GLMM results estimating the effect of birth on minimum night-time 24 h body temperature, and the time it took for females to reach that temperature after sunset.

model	estimate $\pm$ error	95% credible interval	probability of direction %	$R^2$ marginal	$R^2$ conditional	full model output
<i>minimum body temperature (between-subject)</i>				0.14	0.63	electronic supplementary material, table S1
intercept	36.38 $\pm$ 0.58	35.21, 37.50	—			
gave birth (no/yes)	−0.68 $\pm$ 0.09	−0.86, −0.50	100			
body mass (kg)	0.08 $\pm$ 0.17	−0.25, 0.41	68.45			
<i>time of minimum <math>T_b</math> (hours from sunset)</i>				0.29	0.39	electronic supplementary material, table S2
intercept	11.99 $\pm$ 2.51	7.11, 16.84	—			
gave birth (no/yes)	−4.79 $\pm$ 0.60	−5.95, −3.61	100			
body mass (kg)	−1.25 $\pm$ 0.73	−2.67, 0.18	95.78			
<i>minimum body temperature (within-subject)</i>				0.28	0.46	electronic supplementary material, table S3
intercept	37.98 $\pm$ 1.28	35.45, 40.47	—			
gave birth (no/yes)	−0.44 $\pm$ 0.15	−0.74, −0.14	99.67			
body mass (kg)	−0.49 $\pm$ 0.37	−1.20, 0.23	91.08			

during night-time births is relatively low, while the risk of post-parturition hyperthermia during daytime births is relatively high. If birth seasonality has selected for periods of food abundance [44], selection for inactive-phase births might reflect the avoidance of higher daytime heat.

Human births can occur year-round, at all times of the day, yet still tend to occur more frequently at night [3,21,45], which may reflect the diurnal ancestry of anthropoid primates [2] and the nychthemeral timing of births. The importance of the thermal environment for human birth is well recognized, and the World Health Organization has established guidelines for the maintenance of a ‘warm-chain’ thermal environment that

minimizes the risk of neonatal hypothermia [46,47]. These guidelines include keeping the delivery room warm, drying the infant of amniotic fluid and maintaining skin-to-skin maternal–neonatal contact. The uncoupling of the ancestral relationship between birth hour and the maternal nychthemeral  $T_b$  rhythm in humans is likely a consequence of the typically cool artificial environments of birth places, a greater reliance on hospital births and medical intervention and the relative infrequency of non-intervened vaginal delivery [48–50]. Nonetheless, the risk of neonatal hypothermia remains a significant cause of infant morbidity and mortality, especially in developing countries and during winter months [51,52]. Our findings

therefore not only offer new insights into the thermal consequences of birth and the evolution of primate birth hour, but also may provide an evolutionary explanation for some of the health risks associated with human birth.

**Ethics.** Observational data collection protocols were approved by the University of Lethbridge under the terms of reference of Animal Welfare Protocol 0702 and followed the Association for the Study of Animal Behaviour guidelines for the use of animals in research. All capture and surgical procedures were approved by the University of the Witwatersrand Animal Research Ethics Committee (2010/41/04; 2015/04/14B). All protocols conformed to the legal requirements of South Africa.

**Data accessibility.** All data, R code and full model results are available in the electronic supplementary material.

**Authors' contributions.** R.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, visualization, writing—original draft and writing—review and

editing; A.F.: conceptualization, funding acquisition, investigation, methodology, resources, writing—review and editing; S.P.H.: conceptualization, data curation, funding acquisition, investigation, methodology, resources and writing—review and editing; R.S.H.: conceptualization, funding acquisition, investigation, methodology, resources and writing—review and editing; C.Y.: investigation, visualization and writing—review and editing; L.B.: conceptualization, data curation, funding acquisition, investigation, methodology, resources and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

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