

The birth hour of mammals: insights from intra-specific variation in wild blue monkeys

Marina Cords^{a,b,*} and Emma Gometz^a

^aDepartment of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA

^bNew York Consortium in Evolutionary Primatology, 695 Park Avenue, New York, NY 10065, USA

*Address correspondence to Marina Cords. E-mail: mc51@columbia.edu.

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Abstract

While most mammals show birth hour peaks at times of the 24-h cycle when they are less active, there are exceptions to this general pattern. Such exceptions have been little explored, but may clarify evolutionary reasons for the diel timing of births. We investigated intraspecific variation in birth hour in wild blue monkeys *Cercopithecus mitis stuhlmanni*, a diurnal primate, to identify factors that differentiated daytime versus nighttime births. Behavioral and life history data from 14 groups over 14 years revealed that 4% of 484 births occurred during the day. Probability of daytime birth varied with mother's age, peaking at 15.7 years. Births whose annual timing deviated most from the population's peak birth months were 5 times more likely to occur during daytime than those that deviated less. There was no evidence that mother's rank or infant sex influenced birth hour, and mixed evidence that daytime births were more probable in larger groups. Survivorship did not differ significantly for infants born during the day versus night. Prime-aged mothers may be able to handle the consequences of an unusual birth hour more successfully than mothers with less experience or those weakened by age. Daytime birth may be more advantageous in the off-season because nights are colder at that time of year. These findings are consistent with hypotheses relating birth hour to the risk of losing social protection in group-living animals, but are not consistent with those emphasizing risk of conspecific harassment. Patterns of within-species variation can help in evaluating evolutionary hypotheses for non-random birth hour.

Keywords: birth timing, *Cercopithecus mitis*, circadian pattern, diel cycle, guenon, parturition

Mammalian births are generally described as non-randomly distributed across the diel cycle, peaking at hours when the animals are less active (Honnabier and Nathanielsz 1994). Much of the non-human evidence for this pattern comes from captive populations, especially from laboratory and farm animals (e.g., Rossdale and Short 1967; Lincoln and Porter 1976; Gatterman 1983; Viswanathan and Davis 1992; Hudson et al. 1999), but also from wild-caught ungulates and rodents brought into captivity (Manski 1991; McElhinny et al. 1997). Some captive ungulates also exhibit exceptions to the general pattern, which may relate to aspects of their husbandry (Langenau and Lerg 1976; Edwards 1979; Rowland et al. 1984; Kaulfuss 2002). Data on wild mammalian populations are scarce, and come mostly from primates. Among primates, the daytime births of nocturnal species and nighttime births of diurnal ones occur in both captive and wild populations. For example, in a study of 72 zoo populations, Jolly (1973) found that 85% of cercopithecoid births ($N = 488$) and 82% of diurnal ceboid births ($N = 93$) occurred during nighttime hours, their normal inactive phase. By contrast, nocturnally active strepsirrhines usually gave birth during the day (68%, $N = 45$; Jolly 1973). Wild diurnal primates appear generally to match this pattern. In wild geladas, for example, 5–6% of births ($N = 62$, Dunbar and Dunbar 1974; $N = 247$, Nguyen et al. 2017) were

witnessed during the day. In wild snub-nosed monkeys, only 1 of 14 births occurred during the day (Ding et al. 2013).

Despite the general pattern of births occurring during inactive periods, there are exceptions. In fact, in some populations of diurnal primates, most births occur during the day (94% of 18 births in captive patas monkeys *Erythrocebus patas*, Chism et al. 1978; 88% of 8 births in wild patas monkeys, Chism et al. 1983; 62% of 16 births in wild ring-tailed lemurs *Lemur catta*, Takahata et al. 2001; 57% of 7 births in wild black howler monkeys *Alouatta caraya*, Paker et al. 2009; 53% of 90 births in captive orangutans genus *Pongo*, Jolly 1973; 51% of 88 births in captive pied tamarins *Saguinus bicolor*, Price et al. 2016). Even when most births occur during the inactive period, the exceptions can represent a sizeable minority (Jolly 1973; Rowland et al. 1984; Sauter 1991). In this study, we sought to understand variation in birth hour within a single population, and asked how that variation related to existing hypotheses explaining variation in birth hour.

Several evolutionary hypotheses have been proposed to explain why mammalian births tend to occur during the inactive part of the diel cycle. One is that births are timed to minimize risk of predation, as parturient females may attract

predators through visual or olfactory cues and be less able to seek safe cover when threatened because of their limited mobility. Accordingly, selection should favor females giving birth at times when the risk of predator encounters is low. Rowland et al. (1984) compared 26 mammalian species living in zoos, and found that births were more strongly clustered in the inactive hours for those taxa facing “medium” or “high” versus “low” predation risk in their natural habitat (the authors rated risk based on a literature review). In wild wildebeest, births peak as hyena hunting winds down for the morning, allowing newborn calves to gain strength before hyena hunting activity resumes in the late afternoon or evening (Sinclair 1977). Similarly in moose, a midday birth peak was offset from the active period of wolf and bear predators, though other explanations for the peak’s timing could not be excluded (Patterson et al. 2016).

When predation risk peaks at non-active times, birth hour should be shifted. Chism et al. (1983) argued that diurnal savanna–woodland dwelling patas monkeys are exceptionally vulnerable to nocturnal predators, and use a concealment strategy to avoid them, ultimately making daytime births advantageous. These monkeys sleep in small trees individually, immobile and silent, even aggressively excluding groupmates who try to share a sleeping tree. Birthing activity at night would likely draw attention to the entire group’s resting area, and daytime births appear to predominate in this species (Chism et al. 1978, 1983).

An alternative but related hypothesis is that birthing during inactive times may also be a way for females of social species to avoid losing their group as it travels, and also the protection against predators that groupmates afford (Jolly 1972). While losing a group may be unlikely when groups are highly gregarious (Nguyen et al. 2017) or densely packed in small home ranges (Takahata et al. 2001), animals living in groups that move widely through large home ranges would face a bigger challenge. Patas monkeys have large ranges and long daily travel paths, but groups move more slowly before mid-afternoon, and daytime births seem to be concentrated in the earlier hours of the day (Chism et al. 1983). If animals do not live in groups, or move slowly, selection on birth timing to avoid losing the group could be relaxed (Jolly 1972; Sekulic 1982). Accordingly, it is interesting that captive orangutans and some solitary strepsirrhines, who are not group living in nature, have relatively many births outside their inactive period (Jolly 1973; Trevathan 2011). Similarly, diurnal births in howler monkeys, who spend considerable “active” time resting, have been noted repeatedly (Sekulic 1982; Dias 2005; Peker et al. 2009). Mothers who lose their group while giving birth may make behavioral adjustments to compensate for the associated risks: for example, African buffalos appear to give birth in the herd just before dawn, but as the herd moves off to graze, mothers hide with their newborns in dense thickets as the calf gains sufficient strength to later follow its mother back to the herd (Sinclair 1977).

Another hypothesis for birth hour posits that giving birth during the inactive phase is a way for new mothers to avoid harassment or even just intense attention from group mates, or neighboring groups (Dubocsq et al. 2008), which may interfere with the newborn’s earliest settling (Jolly 1972). Harassment of new mothers has been reported in some primates, such as wild lemurs *L. catta*: in 2 of 9 closely observed daytime births, groupmates attacked the new

mother whereas 4 mothers who temporarily lost contact with their group during daytime births experienced no harassment (Takahata et al. 2001). Gelada females sometimes move away from groupmates just before daytime births, perhaps to avoid harassment from other females, although such behavior may risk increased aggression by their leader male (Nguyen et al. 2017). Daytime births might be more likely when new mothers are unlikely to face harassment—either because they live alone (e.g., orangutans) or because harassment is rare in their species. Similarly, within-species variation may relate to the relative likelihood of individuals being harassed: for example, high-ranking mothers may be less likely to face harassment.

Although avoiding conspecifics may reduce harassment, being near them could also benefit a birthing female by facilitating birth assistance. Such behavior has been described rarely in diurnal births of colobine monkeys, in which group members may help pull the infant from the mother’s birth canal (Ding et al. 2013; Pan et al. 2014; Yang et al. 2016; Li et al. 2020). However, little is known about this behavior’s prevalence and whether it is limited to births during the active period. Assistance could be especially valuable for certain individuals, such as the most inexperienced mothers; it is noteworthy that the 3 of the 4 reports above involved assistance to a first-time mother. In humans, where birth attendance and assistance are the norm (Trevathan 2011), there is evidence that primiparous mothers spread their spontaneous births (without medical intervention) more evenly across the diel cycle, whereas multiparous mothers have a sharper peak of births at night (Charles 1953; Erhardt et al. 1967; Glatte and Bjerkedal 1983).

Finally, some primate researchers attribute births during the active period to “evolutionary disequilibrium,” a mismatch between the selective pressures of the species’ nocturnal evolutionary origins and the selective pressures they currently face as diurnal animals (van Schaik and Kappeler 1996). This explanation was offered specifically for diurnal ringtail lemurs, which show a large proportion of daytime births (Sauter 1991; Takahata et al. 2001), but it is not able to explain variation within a species so we do not consider it further.

In this study, we aimed to understand how daytime births differed from those at night in a single population of a wild diurnal blue monkeys (*Cercopithecus mitis stuhlmanni*), and see whether any such differences relate to hypotheses for specific birth timing. Blue monkeys are arboreal forest-dwelling African cercopithecines that live in female-philopatric groups with only 1 adult male most of the time (Lawes et al. 2013). Adult females have stable dominance hierarchies (Klass and Cords 2015), but high rank does not predict energy or nutrient intake, survival, or fertility (Roberts and Cords 2013; Thompson and Cords 2018; Takahashi et al. 2019). Births are seasonal, with about 64% occurring within a 3-month period during the dry season (Cords and Chowdhury 2010). Interbirth intervals are typically either 2 or 3 years (Cords and Chowdhury 2010). One daytime birth was previously described in the study population, with the female engaging in social interactions and responding to predator alarm calls during labor (Brogan and Cords 2010). Two daytime births have been reported previously in captive individuals (Jolly 1972).

We examined whether the likelihood of daytime birth reflected the mother’s age and dominance rank, infant’s sex,

and the degree to which the birth month deviated from the population's annual peak. We predicted that daytime births would be more likely in older females, whose experience might allow them to cope better with the predation risks associated with daytime births. We also predicted that higher ranking females would be more likely to give birth during the day as they should be less vulnerable to conspecific harassment (or even simply unwanted attention) than low-rankers. There is no evidence that blue monkeys experience birth assistance, which otherwise might have favored daytime births for younger mothers. Our analysis included sex as a control variable, and infant birthdate relative to peak birth month because a preliminary visualization of the data suggested this might be an important variable.

We also examined whether infant survival differed after daytime versus nighttime births. Greater mortality following daytime births would support the adaptive benefits of giving birth at night (Honnebier and Nathanielsz 1994); however, if daytime births are more likely for mothers who can handle the concomitant risks, then there may be no difference in survival outcomes.

Materials and Methods

Study population

The study population inhabited the Kakamega Forest (0°19 N, 34°52 E, 1,580 m) in western Kenya, a rain forest averaging ca. 2,000 mm of annual rainfall (Mitchell et al. 2009) where blue monkeys occur at a high density (192 km⁻², Fashing et al. 2012). The population had been monitored since 1979 (Cords 2012), but births came from a period of 14 years (January 2006–March 2020) when the study groups were observed on a near daily basis. During this period, there were 4–10 study groups at any 1 time, and 14 overall, because of 5 group fissions. When a group split, the 2 daughter groups were considered new groups.

Data collection

Field data were collected by MC and a team of trained assistants, who were able to identify all group members individually based on natural characteristics. Typically, 1 observer followed each group on a given day. After locating the group, they began a daily census, recording the identity of each group member they observed. If they detected a female with a new infant (whether alive or dead), its condition was described, including signs of recent birth such as fur that was wet with blood or other fluids, and/or a still-attached umbilical cord. We coded births as daytime births (while sun was up) if any of these signs were evident when the infant was first seen ($N = 11$ daytime births). The earliest such sighting was at 8:48 AM, whereas sunrise occurs at 6:21–6:51 AM at this site, depending on the month. Births were also coded as daytime births if a mother seen with no infant earlier in the day was later seen with a newborn that same day ($N = 10$). Young infants are always with their mothers in this species. All other births were coded as nighttime births. In most cases, new infants were first detected by 9–10 AM, and showed no signs of recent birth. In some cases, the mother of a new infant was not located until later in the day, but she was nevertheless classified as giving birth at night if her infant showed no signs of recent birth. Infants were sexed opportunistically after birth when field observers were able to see the

genitals clearly and repeatedly (5 repeat confirmations), which sometimes took several months to confirm. Some infants died before sexing was completed.

We calculated the mother's age at each birth by subtracting the date of the infant's birth from the mother's own date of birth, both known from long-term study. Specifically, the mother's date of birth was known to the day for 400 births, to 2–5 days for 27 births, to a period of 2–6 months for 14 births, to a period of 1–2 years for 31 births, and to a period of up to 6 years for 12 births. The infant's date of birth was known to the day for 350 births, to a period of 2–4 days for 119 births, to 5–7 days for 12 births, and 3–8 weeks for 3 births. For date ranges, we generally assigned the midpoint as the birth date, unless signs of very recent birth (see above) or more distant birth (infant active and alert, fluffy fur) were evident.

The data set also included information on the infant's survival, extracted from the long-term records. If an infant disappeared, we assumed it had died. The data set included cases in which the infant was dead when first seen. The full data set is available at Dryad (<https://doi.org/10.5061/dryad.q2bvq83kt>).

Data analysis

We used logistic regression (implemented in Stata 15.0) to assess how mother's dominance rank, mother's age, infant sex (binary), and deviation from the population's peak birth month were related to the probability of a daytime birth. "Deviation from peak birth month" was binary, with a value of 1 for large deviations (birth in either July or August, exactly 6 months offset from the January–February peak), and 0 otherwise. We did not have a priori expectations about how birth hour would relate to annual birth peaks, but initial graphical inspection of the data suggested that this might be an important variable. We standardized continuous variables (rank, mother's age) before fitting the model, and included a quadratic term for mother's age in case effects of age waned for the oldest mothers.

Mother's rank was based on the outcomes of dyadic agonistic interactions among females of reproductive age, that is, at least 5 years old, which is the earliest age at first birth. Data on such interactions were recorded during focal follows of females and ad libitum (Klass and Cords 2015). We included only those interactions in which there was a clear winner and loser (i.e., one and only one contestant showed submissive behavior). We compiled interactions for each group and each calendar year, and used the I&SI method implemented in "DomiCalc" (Schmid and de Vries 2013) to derive a rank ordering for females in each group. These ranks were rescaled to values of 0–1 (lowest to highest), so that rank represented the proportion of adult and large juvenile females a mother outranked in a given year. A follow-up analysis, to check if rank effects might be limited to larger groups, also incorporated the number of females in the hierarchy in the year of the infant's birth.

We initially inspected the data in bivariate plots to see if there were any patterns in relation to birth year (2006–2020) or group identity, but no such patterns were apparent. We also checked whether a mixed-effects model including random factors of group identity and mother's identity led to a better model fit, as at least 1 previous study suggested that individual female rats show consistent birth hours in successive births (Rowland et al. 1991). However, adding these random factors did not significantly change the model

Table 1. Number and percentage of daytime births per group, ordered by mean group size

Group (mean size)	Mean group size	Number of daytime births	Number of nighttime births	% of all daytime births	% group's births that occurred in daytime
Tws	54.6	7	109	33	6
Tpa	48.0	1	12	7	8
Gns	47.9	4	24	31	14
Gs	47.0	0	23	0	0
Gn	45.6	2	65	22	3
Gsaa	37.1	3	72	43	4
Tpax	33.8	0	4	0	0
Gsa	32.6	0	5	0	0
Gsc	30.0	1	60	25	2
Twn	28.6	3	58	100	5
Tpay	18.5	0	2	0	0
Tpb	12.1	0	5	0	0
Gnn	11.0	0	9	0	0
Gsb	9.1	0	15	0	0

(likelihood ratio test, $\chi^2 = 1.27$, $P = 0.130$), and the variance they explained was tiny; therefore, we present a model that does not include random factors. We used a likelihood ratio test to assess whether the entire set of predictors in this model influenced the odds of daytime birth. We also checked for collinearity of predictors by examining variance inflation factors, all of which were ≤ 1.01 .

To evaluate whether birth timing (day vs. night) influenced the probability of survival to 365 days (yes/no), we used a mixed-effects logistic model. We entered group and mother's identity as random factors, as a likelihood ratio test suggested that their inclusion significantly improved the model ($\chi^2 = 7.82$, $P = 0.020$).

Results

The complete data set included 484 births from 136 mothers over 14 years. A given mother averaged 4.5 births, and could have as few as 1 birth ($N = 33$ mothers) and as many as 12 ($N = 1$ mother). Twenty-one of the 484 births (4.3%) were known to have occurred during the daytime, whereas there was no evidence that the remaining births occurred during daylight hours. Of the 136 mothers, 17 had 1 daytime birth each, and 2 mothers had 2 daytime births. Of the 14 total groups, 7 experienced between 1 and 7 daytime births, with 1 group accounting for 33% of total daytime births (Table 1). Larger groups generally had a higher proportion of daytime births ($r = 0.61$, $df = 12$, $P = 0.020$).

The logistic model predicting daytime versus nighttime births differed significantly from a null model with no predictors (likelihood ratio test: $\chi^2 = 20.65$, $P = 0.0009$). There was no evidence that mother's dominance rank affected the odds of a daytime birth (Table 2). However, the quadratic term for mother's age did influence the odds of a daytime birth (Table 2). Specifically, the probability of daytime birth was lowest for the youngest and oldest females and peaked for females at 15.7 years of age (Figure 1). The odds of daytime birth were also 4.6 times greater for infants born in the months of July and August, maximally offset from the population's annual birth peak of January–February, relative to those born closer

Table 2. Logistic regression model of daytime versus nighttime birth ($N = 415$ births)^a

Independent variable	Odds Ratio	SE	z	$P > z $	95% CI
Mother's rank	0.90	0.22	-0.44	0.660	0.56–1.44
Mother's age at birth	3.09	1.47	2.38	0.017	1.22–7.84
Mother's age at birth ²	0.32	0.14	-2.59	0.010	0.14–0.76
Infant born 5 mos off peak: yes ^b	4.56	3.43	2.01	0.044	1.04–19.92
Infant sex: male ^c	2.09	1.07	1.44	0.151	0.76–5.72

^aMother's age and rank were standardized. Model diagnostics: C-statistic: 0.78; Hosmer–Lemeshow $\chi^2 = 2.75$, $df = 8$, $P = 0.95$; McFadden's $R^2 = 0.13$.

^bReference class: no, that is, infant born within 4 months of or during the peak birth months of January–February.

^cReference class: female.

to the peak (i.e., all other months; Table 2). Infant sex had no significant effect on the odds of daytime birth (Table 2).

To check the possibility that rank might influence the odds of daytime birth only for mothers in larger groups, we re-ran the model including as additional predictors both the number of females in the hierarchy and an interaction of this variable with mother's rank (Table 3). Neither new term had a significant effect on the odds of daytime births, while odds ratios for other terms closely resembled the original model. The 2 models did not differ significantly (likelihood ratio test, $\chi^2 = 0.79$, $P = 0.675$), suggesting that there was no evidence for rank effects contingent on group size.

The model of infant survival to 365 days as a function of day versus nighttime birth provided no evidence of differential infant mortality (odds ratio for dying in first year [$N = 484$]: $0.76 \pm SE 0.39$, $z = -0.53$, $P = 0.60$, 95% confidence interval [CI]: 0.28–2.09; random effects variances [95% CI], mother ID: 0.10 [0.01–1.94], group ID: 0.15 [0.03–0.88]). A likelihood ratio test comparing this model to a null model (random factors only) was not significant ($\chi^2 = 0.28$, $P = 0.594$).

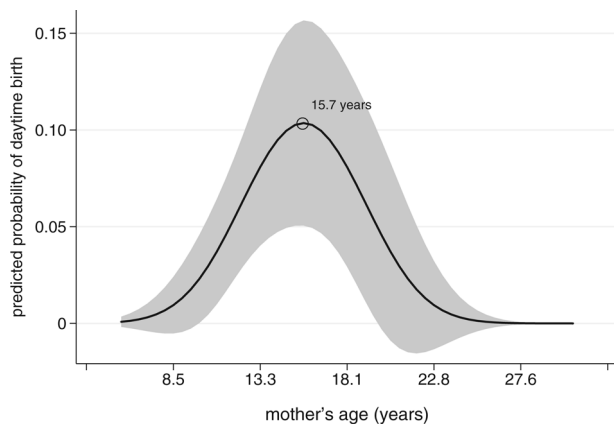


Figure 1. Predicted likelihood of daytime birth as a function of maternal age at birth (in years). Gray shading indicates 95% CI.

Table 3. Logistic regression model of daytime versus nighttime birth ($N = 415$ births)

Independent variable	Odds ratio	SE	z	$P > z $	95% CI
Mother's rank	0.89	0.22	-0.47	0.637	0.55–1.44
Number of females in hierarchy (NFem)	1.16	0.30	0.57	0.569	0.70–1.91
Mother's rank * NFem	0.85	0.22	-0.65	0.518	0.51–1.40
Mother's age at birth	2.97	1.42	2.29	0.022	1.17–7.57
Mother's age at birth ²	0.32	0.14	-2.59	0.010	0.13–0.76
Infant born 5 mos off peak: yes ^b	4.92	3.74	2.10	0.036	1.11–21.82
Infant sex: male ^c	2.03	1.05	1.38	0.169	0.74–5.57

^aMother's age and rank were standardized. This model is identical to the model in Table 2 except that it includes 2 additional predictors: number of females in the hierarchy (standardized) and an interaction of that variable with mother's rank. Model diagnostics: C-statistic: 0.78; Hosmer-Lemeshow $\chi^2 = 9.72$, $df = 8$, $P = 0.285$; McFadden's $R^2 = 0.13$.

^bReference class: no, that is, infant born within 4 months of or during the peak birth months of January–February.

^cReference class: female.

Discussion

We identified 2 factors that were associated with the likelihood of a daytime versus nighttime birth in blue monkeys. First, the odds of daytime birth peaked for prime-aged females at 15.7 years and were lower for younger and older females (Figure 1). Second, births were almost 5 times more likely to occur during the day if the birth was maximally offset (in July–August) from the population's birth peak in January–February versus other times of year (Table 2).

With regard to maternal age, previous studies have generally failed to find differences between primiparous versus multiparous mothers in the likelihood of active-period births (Lincoln and Porter 1976; Gatterman 1983; Price et al. 2016; but see Rowland et al. 1991). Analyses with a binary predictor are, however, not fully comparable to our analyses in which age was coded continuously. Our findings raise the question of why prime-aged females are more likely than younger and

older females to give birth during the day. Primate mothers with birth experience may be better able to cope with some of the challenges of birthing during unusual daytime hours because their peri-parturitional behavior is more efficient and skillful (Timmermans and Vossen 1996; Yao et al. 2012). In wild geladas, parous mothers were more likely to give birth while at a distance from groupmates, to aid their infant manually out of the birth canal and to eat the placenta (Nguyen et al. 2017). Such behaviors may facilitate the birth process, and minimize the degree to which it disrupts daytime behavior such as keeping up with the group and avoiding predator threats. While older parous females would not lack experience, their body condition may be declining, which might contribute to added risk were they to give birth during daylight hours in terms of responding quickly to predator threats or keeping up with troop movement. We have no direct measures of age-related change in body condition, but note that female fertility peaks at the age of 13 years and declines thereafter (Roberts and Cords 2013). In short, daytime births may be least costly for the prime-aged mother, who is most able to respond readily and adaptively to unexpected circumstances during the birth process because she is both experienced and in prime condition. Accordingly, there may be less selective pressure on prime-aged females to avoid daytime births. Although our results are consistent with this hypothesis, it clearly merits further investigation in diverse taxa.

To our knowledge, a seasonal effect on the likelihood of daytime births has not been reported previously. The fact that daytime births were more common during the months most offset from the population birth peak could relate to ambient temperature, which might affect the thermoregulation needs of the newborn infant. In the study population, most births take place during the driest (and warmest) months of January and February (Cords and Chowdhury 2010). In our data set, only 3.5% of all births ($N = 484$, or 3.4% of sexed births, $N = 415$) took place in July or August, which are wetter months, with temperatures that are lower than the dry months of the birth peak (Mitchell et al. 2009; Campos et al. 2017). In addition, the pattern of rainfall at this time, with frequent late afternoon and overnight rain, means that monkeys are more likely to be both wet and cold at night, when temperatures are especially low. Monthly rainfall influenced fecal glucocorticoid levels in adult females in this population, possibly because of thermoregulatory stress (Foerster et al. 2012). In both human and non-human primates, cold temperatures can have a negative effect on infant health and survival (Richard et al. 2002; Isbell et al. 2009; Strand et al. 2011). Accordingly, when giving birth during a colder and wetter time of year, there may be thermoregulatory advantages for mothers giving birth during the day, when morning or midday sunshine may keep the neonate warm. Further investigation in taxa with strong seasonal and diurnal shifts in temperature would be valuable for confirming this idea.

The overall frequency of daytime births (4.3%, Table 1) for wild blue monkeys resembles most other cercopithecoids. This figure could be a slight under-estimate, given that we may have missed the transient signs of recent birth under field conditions. In Jolly's (1973) zoo survey, only 15% of diurnal cercopithecoid births ($N = 488$) occurred during the day, with figures varying from 5% (*Cercocebus*, $N = 19$) to 27% (*Presbytis*, $N = 9$) across genera. In most wild populations, the proportion of daytime births falls at the lower end

of this range (3–7%, Dunbar and Dunbar 1974; Duboscq et al. 2008; Ding et al. 2013; Nguyen et al. 2017). In some diurnal primates, however, considerably higher rates of daytime births have been reported: 88% in patas monkeys ($N = 8$; Chism et al. 1983), 57% in howler monkeys ($N = 7$; Peker et al. 2009), and 62% in ringtailed lemurs ($N = 16$; Takahata et al. 2001). These percentages are significantly higher than that of blue monkeys (Fisher's exact test, $P < 0.0001$ for patas, $P < 0.05$ for howlers, $P < 0.001$ for ringtailed lemurs) but the small sample of births may not be representative of these other taxa.

There was no evidence that the timing of births in the day versus night influenced the odds of surviving to 1 year. These results could be interpreted as evidence that there was no survivorship cost associated with daytime birthing. If so, daytime births might reflect specific situational factors, perhaps related to the length of labor, that are unconnected to the infant's fitness when born. Alternatively, if females who give birth during the day are those who with the lowest risk of infant loss after daytime birth, then one might expect not to see evidence that birth hour influences infant survival. Zoo-housed pied tamarins that were raised by their parents also did not show statistically significant differences in fitness measures, in this case parental rejection, as a function of births occurring during the day- versus nighttime (Price et al. 2016).

Our findings relate to several hypotheses that have been proposed to explain birth hour in mammals. With regard to the risk of losing a moving group while birthing during the day, the greater likelihood of daytime births for prime-aged females is consistent with this hypothesis if greater experience and condition facilitate keeping up with a moving group. Other evidence comes from the way in which group size relates to daily travel distance in this population. Both Cords (2012), studying group paths, and Takahashi (2018), studying the paths of individual females, found that daily travel distances were shorter for larger groups. This pattern suggests that females in larger groups may experience less risk of losing their group when birthing during the day. The percentage of daytime births was higher in larger groups when we aggregated data across the study (Table 1); however, in models predicting the timing of individual births, it was not statistically clear that female group size predicted the odds of daytime birth (Table 3). In addition, adding Group ID as a random factor did not improve this model. We were not able to examine whether daytime births were more likely on days when the group's movement was lower than usual, which would be a more fine-grained and conclusive test of this hypothesis.

Blue monkeys provide no evidence for the idea that the threat of conspecific harassment drives births in the inactive period. If this were so, one might expect low-ranking females, who receive aggression at higher rates generally (Klass and Cords 2015), to avoid giving birth during the day; however, there was no evidence that rank affected the likelihood of daytime births. In addition, in a closely observed daytime birth, Brogan and Cords (2010) reported no harassment by the mother's groupmates, only passive or affiliative social behavior such as sniffing and groom presentation. Together, these observations suggest that conspecific harassment is not likely to explain the rarity of daytime births in blue monkeys.

Our data also argue against the idea that the risk of conspecific threat drives between-species differences in birth hour in cercopithecoïd primates. In geladas, a relatively despotic

species, daytime births are rarer (5%) than in (wild) patas monkeys (88%), which are not despotic (Chism et al. 1983; Isbell and Pruettz 1998; Nguyen et al. 2017). Multiparous female geladas did not give birth near conspecifics, whereas primiparous females did so more often. During births near conspecifics, other females threatened the mother during her labor (Nguyen et al. 2017). In contrast, patas mothers that were closely observed giving birth during the day (both multiparous) did not avoid conspecifics, and no group members showed interest in the births beyond watching from a distance (Chism et al. 1983). Although differences in behavior between wild geladas and patas align with the conspecific threat hypothesis for birth timing, blue monkeys do not fit the pattern. Their rate of daytime births was as low as that of despotic geladas, but their non-despotic social structure is more comparable to that of patas monkeys, to whom they are more closely related.

Our findings could not directly address the effects of predation risk or birth assistance on the pattern of daytime births in the study population. With regard to predation, however, it may be worth highlighting that in the 1 observed daytime birth, the laboring female responded to predator alarm calls in her group more awkwardly and with slower movement than usual (Brogan and Cords 2010). Potentially, prime-aged females may react more quickly and adaptively to signs of heightened predation risk than less experienced or older females, again allowing them to face this aspect of increased risk during daytime births. As a more direct test, future studies could investigate whether exposure to predators and/or the frequency of alarm responses relates to the frequency of daytime births. As for birth assistance, such behavior is very rarely reported in non-human primates, and we do not even know if it occurs in blue monkeys, and thus whether it could plausibly explain variable birth timing.

In conclusion, while this study suggests that female age and the degree to which the birth month deviates from the population peak are associated with the likelihood of daytime births in a diurnal primate, further research focusing on intraspecific variation in birth timing would be valuable (Brecht et al. 2021). To our knowledge, only 1 other study has taken this approach, but results were inconclusive in terms of identifying variables that differentiated day- and nighttime births (Price et al. 2016). Additional studies could act as independent replications, or may serve to identify other factors that explain variation, with such factors differing by taxon. Either way, an examination of within-species variation has potential for evaluating evolutionary hypotheses for birth timing in the diel cycle.

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Conflict of interest

The authors declare no conflict of interest related to this work.

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