

RESEARCH ARTICLE

Maternal care in wild toque macaques (*Macaca sinica*) involves prolonged lactation and interbirth intervals as adaptations to reduce maternal depletion and infant mortality in harsh environments

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Abstract

Weaning age in primates has been challenging to measure and new methods, involving molecular biomarkers in feces, tissue, or teeth have contributed to a solution. Here, we used a direct approach by briefly anesthetizing 442 female toque macaques (*Macaca sinica*) of Sri Lanka (over a 17-year period) and manually testing their mammary tissue for the presence or absence of milk. Milk tests were related to known offspring ages and maternal care behaviors and indicated that older infants suckled milk well past the weaning age of 7 months that is often reported for food-provisioned primates. Mothers strongly rejected their infants' nursing attempts in two phases, the first at 7 months as an honest signal "giving notice" promoting a shift to greater independence from milk to solid food, and when "shutting down" at final weaning after 12–18 months. The shift to supplementary lactation coincided also with the cessation of mothers carrying their infants and a resumption of cycling. All infants up to 7.2 months suckled milk, 91% of them did up to 18 months, this continued for 42% of infants beyond 18 months, and normally none received milk after 22 months. Lactation extended into 2.2% of cycling and 10.7% of pregnant females (up to 50% of gestation). The interbirth interval was prolonged by factors predicted to draw on female metabolic energy reserves and included the duration of lactation, growth among primiparas, and dietary limitations. The last also increased menarche. Females offset the metabolic costs of lactation with increased foraging and catabolism, but infants died when lactation costs seemingly compromised maternal condition. The prolonged lactation and slowed reproduction are considered adaptations to promote infant survival and growth in an environment where the natural food supply limits population growth and competition for food and water impacts the mortality of the youngest the most.

KEYWORDS

interbirth interval, lactation and weaning, maternal depletion and infant survival, maternal investment and metabolic energy balance, wild primate

1 | INTRODUCTION

Maternal care behaviors among nonhuman primates are of theoretical interest for understanding primate group dynamics and the evolution of reproductive and life history strategies (Charnov, 1991; Trivers, 1974). Central to this consideration is the concept of weaning whereby the developing primate must make the major transition from a state of complete dependence on mother's milk to solid food as a source of nutrition (Martin, 1984). Nursing delays a mother's return to sexual receptivity (Charnov, 1991; Lee, 1996; Pagel & Harvey, 2002), and the age of weaning determines the length of interbirth intervals (IBI) and the number of offspring a female can bear in her lifetime (Lee, 1987). Weaning presents genetic conflicts of interest between mother and infant who are both attempting to maximize their evolutionary fitness (Martin, 1984; Trivers, 1974). The infant's interest to prolong nursing is therefore at odds with the mother's best interest to partition care between the current and future offspring (Trivers, 1972). Weaning also affects infants' vulnerability to infanticide (Crockett & Sekulic, 1984) and nursing distinguishes infants from juveniles in groups (National Research Council, 1981). The IBI is a key to population viability analyses and in formulating conservation strategies (Caro, 1999). Knowing the age of weaning is therefore critical in studies of the mother–infant relationship, primate life history with respect to maternal metabolic balance and fitness (Ellison, 2003; Lunn et al., 1984), and conservation. Identifying the age at which lactation stops and infants are fully weaned has, however, posed a practical challenge for field primatologists (e.g., Altmann, 1980; Jay, 1965; Lee, 1996; Rajpurohit & Mohnot, 1991; Smith et al., 2017). Observations of nursing behavior may be hampered by visual obstructions in the natural habitat, by unhabituated groups, and by nighttime. In addition, proxy variables of weaning such as the frequency of nursing, maternal carrying of infants, and the amount of solid food in the infant's diet cannot account for actual milk transfer (Martin, 1984). Furthermore, regardless of how long an infant appears to suckle, the behavior may be “comfort nursing” (Blass & Teicher, 1980; Cameron, 1998) by which the infant contacts the mother's nipple for months after weaning occurs as a means of reassurance rather than sustenance (Bădescu et al., 2016). The practical limitations of determining weaning through observational studies has hampered our understanding of the complex dynamic between mothers and infants (Maestripieri, 2002; Martin, 1984), and its effects on female fitness under variable environments.

To circumvent this practical limitation stable isotope analyses of soft tissues have been applied to determine weaning age in mother–infant pairs of zoo-raised François' langur (*Trachypithecus francoisi*) (Reitsemá, 2012) and among captive rhesus macaques (*Macaca mulatta*) (Reitsemá et al., 2016). Noninvasive fecal stable isotopes have been used for this purpose in wild chimpanzees (Bădescu et al., 2016). Biomarkers from barium (Ba) have left stress signatures in the development of teeth that indicate the transition from milk to solid foods in macaques and humans (Austin et al., 2013, 2016) as well as in wild orangutans (Smith et al., 2017). In this report, we

present a more direct approach that was applied in a wild population of toque macaques (*Macaca sinica*) in Sri Lanka. Instead of using proxies, lactation duration was measured directly by sampling the milk expressed manually from the mammary tissue of captured and released females that were nursing known-aged offspring. While the presence of milk from nipple stripping verifies maternal milk production and nursing suggest an infant's milk ingestion, neither is a direct measure of the amount or quality of milk transfer. The nutritional contribution of milk to the infant's diet has been reviewed for toque macaques and other primates (Goto et al., 2010; Hinde & Milligan, 2011; Milligan et al., 2008; Oftedal et al., unpublished).

The first aim of this research was to establish new information on the period of lactation and weaning age and to relate this to the trajectories of known maternal care behaviors in this wild population. Second, we wanted to test hypotheses addressing causes for variations in lactation and their influence on IBIs. For a better understanding of female reproductive schedules, it was of interest to profile the prevalence of lactation at the level of the population in relation to other female reproductive states, depletion of maternal condition, and infant survival.

1.1 | Rationale and hypotheses

Lactation outweighs all other forms of parental investment in terms of energy expenditure and its concomitants (Clutton-Brock, 1991; Ellison, 2008; Martin, 1984). The energetic cost of lactation is the primary factor influencing the duration of postpartum amenorrhea and in this way the interval between births (IBI), other effects on the IBI being variations in the durations of gestation and cycling (e.g., Pontzer et al., 2014; Valeggia & Ellison, 2001). The duration of gestation is the least variable for a given macaque species (Ardito, 1976; Kiltie, 1982), that of cycling can be more so (e.g., Garcia et al., 2008; Gesquiere et al., 2018). Given the dominant effect of lactation on the IBI or birth rate (Valeggia & Ellison, 2001), lactation ranks with survival and growth as a key determinant of female reproductive success and life history.

What agents involve the theoretically predicted balance of maternal reserves (Ellison, 2003) that determines the IBI in this population and other energy dependent reproductive parameters? Earlier studies of reproduction in nonhuman primates have identified several factors relevant to the complex relation between lactation, the IBI, and reproduction (see reviews by Gesquiere et al., 2018; Hill, 2000; Lee & Bowman, 1995). A number of these agents were measurable in our field study of the toque macaques, namely: the duration of lactation, weaning age, the IBI, environmental food sources, female parity, female activity and body condition, and infant survival. These observations were applied to test several hypotheses relevant to lactation in this wild population. We hypothesized that the IBI is extended through lactation because it draws most on maternal reserves (Valeggia & Ellison, 2001), and that this would be evident in a comparison of the IBIs between lactating mothers and those whose energy debits

were released from lactational amenorrhea by their infants' early deaths. It has been shown that the IBI is reduced among primates that feed on a high nutritional plane (Asquith, 1989; Gesquiere et al., 2018; Lee & Bowman, 1995; Rawlins & Kessler, 1986) presumably because access to quality food supports the energy requirements for lactation and restores maternal reserves. In the Polonnaruwa population of toque macaques access to quality foods is known to enhance female growth rate (Cheverud et al., 1992) and the accumulation of body fat (Dittus, 2013). These observations suggested the second hypothesis that maternal access to high-quality human sources of food and water reduced the IBI when compared to females feeding primarily on a natural forest diet.

Young mammalian mothers face trade-offs between investing in their own growth and reproduction (Clutton-Brock, 1991; Stearns, 1989). In toque macaques, skeletal limb growth in juvenile females ceased at about 5.5 years, whereas muscle mass, body weight, and other morphological traits did not reach maturity until about 8 years (Cheverud et al., 1992). This pattern of somatic growth is similar to that reported for well-fed captive managed rhesus macaques (Turnquist & Kessler, 1989) and baboons (Coelho, 1985) as well as feral baboons (Sigg et al., 1982), although the rates of maturation of primates in their natural habitats are considerably slower than their well-fed counterparts under captive management (macaques, Turnquist & Kessler, 1989; and baboons, Altmann & Alberts, 1987; Altmann et al., 1977; Phillips-Conroy & Jolly, 1988). Focusing on investment trade-offs, growing toque macaque females had their first birth on average in their sixth year (Dittus, 1975) before attaining physical maturity, a trend that has been noted also in colony raised macaque species (Cerroni et al., 2003; Lipkin et al., 2001) and baboons (Coelho, 1985). The third hypothesis was that the additional demands on bodily reserves for physical growth during lactation would result in greater IBIs among primiparas than among mature females, a phenomenon that has been observed in several species (baboons: Altmann et al., 1988; mandrills *Mandrillus sphinx*: Setchell et al., 2002; Setchell & Wickings, 2004; and macaques: Hinde, 2009; Koyama et al., 1992). A related fourth hypothesis predicted that menarche is reached earlier in females feeding on rich food sources than among those feeding primarily on a natural diet, a consideration that is relevant to trade-offs in female survival and future reproduction (Bercovitch & Berard, 1993; Blomquist, 2009; Charnov & Berrigan, 1993; Stearns, 1989) especially in relation to environmental and social variation in resource acquisition (Altmann & Alberts, 2005; Arlet et al., 2015; Mori et al., 1997; van Noordwijk & de Jong, 1986).

Reflecting on Altmann's (1980) model of maternal time budgets a fifth hypothesis predicted that mothers meet the energy costs of lactation by increasing energy input through extended feeding time. Support for the model has been partial with a better fit being achieved by incorporating differences in food quality (Dunbar & Dunbar, 1988; Dunbar et al., 2002; Koenig et al., 1997; Lycett et al., 1998). Trade-offs with vigilance against infanticidal males have

confounded a simple relationship in baboons of South Africa (Barrett et al., 2006). In toque macaques, foraging times differ seasonally in relation to food availability as well as by age and sex, social structure, and dominance rank (Dittus, 1977a).

An alternate or additional means of meeting the cost of lactation has been suggested through catabolism (Altmann, 1980) as observed in a variety of mammals (Robinson, 1986) including baboons (Bercovitch, 1987). In a sixth inquiry, we consider whether increased feeding time together with catabolism may compromise maternal ability to support offspring survival. A perspective from humans contributes to these considerations, because like nonhuman primates and other mammals, humans also experience high metabolic costs of pregnancy and especially lactation (Butte & King, 2005). Human studies indicated that successive pregnancies with short intervals and/or poor diets may overburden the mother nutritionally leading to poor health for the mother and offspring and increased infant mortality, a phenomenon referred to as the "maternal depletion syndrome (MDS)" (Engelen & Wolf, 2011; Kozuki & Neff, 2013; Stephansson et al., 2003; Wang et al., 2022). The phenomenon has been investigated in nonhuman primates only recently by Lee et al. (2019); infant mortality was high among well-fed colony-raised rhesus mothers with short IBIs before and after pregnancy, a condition that reduces maternal resources for investment in the offspring. Winkvist et al. (1992) emphasized that maternal depletion may occur from rapid reproduction as well as extrinsic factors such as poor food quality that affect maternal nutritional status directly. We present evidence suggesting that toque macaque females lose the ability to support infant survival through lactation consistent with both causes for maternal depletion.

2 | METHODS

The methods of field observation, capture and release of macaques and milk sampling comply with all regulations regarding the ethical treatment of research subjects as prescribed by the National Institute of Fundamental Studies, Sri Lanka, and the Smithsonian Conservation Biology Institute, USA, and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2.1 | The study population

Toque macaques are endemic to Sri Lanka. They are long-tailed, relatively small-bodied (5.5 kg adult males, 3.1 kg adult females) monkeys, mostly arboreal and opportunistically terrestrial. They live in closed and cohesive matrilineal societies with one or more immigrant breeding males. Those living in the Nature Sanctuary and Archeological Reserve at Polonnaruwa have been studied continuously for over five decades (1968–2023). The natural dry

evergreen forest at the site is typically diverse and comprises dense layers of shrubs overlain with a continuous tree canopy up to 15–20 m and scattered emergent trees up to 30 m (Dittus, 1977b). Shrubs and some trees have been cleared in restricted areas to expose archeological structures in a parkland setting. The area is highly seasonal transitioning from excess rain in winter (October to January) to drought in summer (May to September). The birth season is from December to May with a peak in March. The natural diet of the macaques includes a diversity of ripe fruit, young leaves, insects, and the occasional small vertebrate (Dittus, 1974; Hladik & Hladik, 1972). The standing population for this study involved up to 1100 individuals distributed among 39 independent social groups; many of which were established through group fissions (e.g., Dittus, 1988a). Toque macaque population size in general is closely attuned to the availability of natural food and water in their habitat (Dittus, 1977a, 1977c). In undisturbed natural forest environments net population growth is near zero, but the introduction of anthropogenic food sources has stimulated growth in a few affected groups (Dittus, 2012; Dittus et al., 2019). Seven groups, labeled: A, B1, D1, D2, D3, M, and M1 had regular access to anthropogenic food sources, the remaining 32 groups had occasional or no such access. We distinguished the diets of the females in these groups as “enriched” and “natural,” respectively.

2.2 | Demographic census

All macaques in the population of 39 groups were individually identified by their natural markings and tattoos (Dittus, 1990; National Research Council, 1981). Individuals in all groups were subject to a regular census about once per month. During the birth season females were checked once per week or more to pin-point infant birth dates. Such data were the basis for monitoring individual life-histories from birth to death (Dittus, 2004). The chronological ages of nearly all individuals in this sample were based on known birth dates; those of a few individuals that were born before 1968, were estimated from morphological development. IBIs were estimated in days but expressed here in terms of months, where days were divided by the mean duration of a calendar month (30.438 days).

2.3 | Estimating infant survival in relation to the IBI

Dates and ages of death were available from regular census logs. We wished to measure whether infants survived to the dates of conception and birth of the next sibling. The statistics were not available if a mother bore no further infants owed to her death or transition to postreproduction in old age. For these cases, therefore, we chose infant survival to at least 18 months, which encompassed the mean IBI for the population.

2.4 | Estimating gestation and pregnancy

The duration of gestation in toque macaques was not measured; however, in the most closely related species, the bonnet macaques (*M. radiata*) of southern India, the mean period of gestation was 166 ± 5 days or (5.45 ± 0.17 months) (Rao et al., 1998), the same as in rhesus (*M. mulatta*) (Silk et al., 1993) and other congeners (Ardito, 1976). Accepting these statistics as applicable to toque macaques as well, the dates of conception and the status of pregnancy were estimated by subtracting 166 days from the known dates of birth.

2.5 | Cross-sectional sampling of females for lactation analyses

The study population comprised 39 independent social groups for which the sum of their home ranges occupied an area of approximately 8.5 km² with a perimeter of 18 km. These groups were sampled during 13 different years over a span of 17 years (125 group sampling events) between 1986 and 2002. Months of sampling were distributed from March to December. There were 814 tests for milk among females of which 14 were rejected owed to abnormalities (twins, miscarriage, and kidnaping). Some females were tested more than once, each time with a different infant, year, and season. Mother–infant pairs were tested only once per lactation. The reproductive condition of females (see Definitions), their body weights, morphometry (e.g., Cheverud et al., 1992), and body fat indices (e.g., Dittus & Gunathilake, 2015) were recorded on sampling dates. To eliminate the potential influence of female individual-specific qualities a random numbers generator was applied to select each female only once in analyses; this left 442 unique females among which independent milk tests were analyzed (Table 1). All test data, and random selections, were repositied (Dittus, 2023). The removal of female duplicates did not alter the patterns described here because we had large sample sizes. The age of the youngest female in the population that had milk was 4.08 years. Therefore, the females considered in this report were >4.0 years old. Most females experienced their first birth in the sixth year.

2.6 | Sampling milk

Procedures for the capture and release of macaques had been described earlier (Hoelzer et al., 1994). Macaques were habituated to enter steel mesh box traps (ca. 1 × 1 × 1.5 m) which were baited with food for several days before the capture date. Upon capture, mothers and their young were separated, and the mother tranquilized with a single dose of IM injection of ketamine hydrochloride (Ketalar, Park-Davis Co.). The dose tranquilized the mother for less than 40 min and in pregnant mothers was far below the threshold for toxicity in the mother or in fetal development (Paule et al., 2011; Zou et al., 2009).

TABLE 1 Population cross-sectional frequency distribution of different reproductive phases among 442 unique wild female toque macaques in the period 1986–2002 at Polonnaruwa.

Reproductive condition of females	Number observed
Lactating	
Lactating only	236
Lactating and cycling	6
Lactating and pregnant	29
All lactating	271
Dry, infant weaned	
Weaned and cycling	4
Weaned and pregnant	12
Weaned and quiescent	5
Total dry and weaned	21
Dry, infant died	
Dry and cycling	5
Dry and pregnant	18
Dry and quiescent	31
Total dry and infant died	54
Total parous and reproductively active	346
Postreproductive	24
Sterile	0
Nulliparous	
Cycling	3
Pregnant	6
Nonreproductive	63
Total nulliparous	72
Total sample of females age > 4.0 year	442

Notwithstanding, as a precaution, a few females were not sampled if they appeared in the late stage of pregnancy as evident from a well-swollen abdomen.

All test for the presence or absence of milk considered in this report involved manually palpating the mammary tissue of anesthetized females irrespective of their reproductive status. Earlier work, based in 72 females (1986–1994), involved the IM injection of oxytocin (0.20 cc, 4 IU) to induce milk letdown of small volumes of milk for nutritional analyses (Goto et al., 2010; Milligan et al., 2008; Oftedal et al., unpublished). Oxytocin was not applied, however, in the tests for the mere presence of milk because the earlier and present work showed that no milk was released with or without oxytocin in nulliparas and nonnursing parous mothers. The mammary tissue in such females also was not swollen. In contrast, in nursing mothers the mammary tissue was swollen and manual nipple stripping alone easily yielded small amounts of milk in the absence of oxytocin. Coincidentally only, oxytocin had been applied

for three tests for mothers with infants aged 0.36, 2.33, and 14.17 months.

2.7 | Mother–infant behaviors and analyses

In an independent study, two groups of macaques, A and D, were selected for behavioral observations of mother–infant relationships in the period 1977–1983 (Baker-Dittus, 1985). The home ranges of these two groups overlapped and included both intact natural forest and parkland. The macaques had access to both natural and occasional anthropogenic food sources. The study groups were well habituated to an observer, and approached, and permitted an observer to approach, to within two meters without apparent disruption to their behavior. Data were recorded only when the observer was in direct visual contact with the focal study animal. The focal animal's general activity states were recorded every minute (see Dittus, 1977a). The activity states most relevant in this report were nursing, carrying, and foraging (see Definitions). A total of 59 different infants distributed among 20 different mothers were observed for approximately 64 h each on the following schedule: Infants were observed for a minimum of 8 h each month during their first 6 months of life. For the next 6 months of life, infants were observed for a minimum of 8 h during the 6-month period. Older offspring were observed for 8 h two to three times a year. Each 8-h sample was conducted over a period of 4 consecutive days. Days were divided into four sampling periods of 2.5 h each, and each animal was observed for a different sampling period each day. The behavioral data presented here represent over 3500 h of direct observation.

In addition to activity states, all interactions between the focal animal and other group members were recorded ad libitum (Altmann, 1974). Frequencies were scored with which infants were successful in their nursing attempts and with which mothers refused an infant's attempt to nurse. Mothers refused infants access to the nipple by turning their backs to the infant, by covering the nipple with their upper arm, by lying with their ventrum pressed against a branch, or by threatening the infant. Threats ranged from mild upjerks and raised eyebrow threats to more severe hitting and biting. An upjerk involved a rapid straightening of the mother's back which caused the nipple to be suddenly pulled out of the infant's mouth.

Observation times were not equal for all animals. Therefore, behaviors (durations of activities and frequencies of events) were calculated as rates per hour of observation and were expressed as means and their standard errors (Altmann, 1974).

2.8 | Female activity budgets

Independently, Dittus (1977a) recorded the temporal distribution of daily activity states of all group members that included lactating and nonlactating parous females of social groups A and D. The present objective was to compare foraging durations in relation to female

lactational status. Focal animal samples of females' activities were taken on 24 different days between January and December 1971. Daily observations were dawn to dusk for a daily mean of 11.3 h (10.2–12.9 h) for a total of 159.2 h (14 female lactation days) compared to 112.6 h (10 female nonlactation days). The ages of infants of nursing mothers were (Mn = 5.3 months, range: 0.7–8.0 months) and that of nonnursing mothers was (Mn = 16.1 months, range: 5.7–22.9 months).

2.9 | Definitions of reproductive states and behaviors

Engaged mother, a female caring for her most recent living infant in the period between successive births. Maternal behaviors included nursing (lactation), carrying, grooming, closely associating, and social support.

Lactating mother, an engaged mother for which milk was expressed from the mammary tissue.

Dry mother, an engaged mother for which no milk could be expressed from the mammary tissue. Mothers were dry because either the infant had died, or it had been weaned.

Parous. The active reproductive phase of a female that has experienced at least one birth and is capable of pregnancy, lactation, and cycling.

Nulliparous. The nonreproductive state of a juvenile or adolescent female before the first birth.

Postreproductive. A formerly parous female, usually older than 22 years, that has not given birth again after her last infant despite living through one or more annual birth seasons before dying of old age.

Quiescent. The status of a parous female when she was neither pregnant, lactating, nor showing external signs of cycling in the interval between births and may or may not have weaned offspring that were subject to other forms of maternal care. It corresponds loosely to the "recuperative interval" described in humans (Dewey & Cohen, 2007).

Sterile. The status of a female of reproductive age that has not given birth despite mating and cycling over several years. Permanently sterile females were not observed in this population.

Menstruation was scored when a female had traces of blood on her vagina that was not related to parturition or injury.

Cycling was manifested by menstruation and/or the secretion of copious amounts of mucous from the vagina (Hill, 1939) that is typically associated with mating consorts and probable ovulation. Toque macaques do not have conspicuous edematous swellings of the vulva and neighboring skin as is typical of many other macaque species (Dixon, 1983). The formation of consort relations, which involved female soliciting mating, was a good indication of cycling whereas copulations often initiated by males was less so.

Nursing. The infant has the mother's nipple in the mouth. It was not always determined if the infant was also suckling, that is, pumping its cheeks in sucking motions. It was never possible to ascertain if the infant was receiving milk.

Foraging. The macaque was actively searching for and consuming food from the environment.

Carrying. The infant was transported by clinging with its limbs to the ventrum of the mother in locomotion. Toque macaque infants very rarely ride their mother's back, even when moving on the ground.

2.10 | Data collection and analysis pertaining to individual differences in lactation and reproduction

All data were tied to the identities of the individual female, her offspring, and date of sampling. Relevant variables pertaining to the female, the infant, capture and release, anesthesia, milk sampling, and remarks were entered into handwritten data sheets in the field and were then transcribed onto EXCEL spreadsheets. Additional and derived information from demographic records were integrated. These detailed records and methods of analyses were documented in a publicly available repository (Dittus, 2023).

2.11 | Statistical tests

Differences in the distributions of age and IBIs were portrayed with boxplots where outliers were represented by the 5th and 95th percentiles. Differences in these distributions were tested with the Kaplan–Meier Log-rank test using SigmaPlot version 14.5 software. Data were cited as medians (Md) and means with their standard deviations (Mn ± SD).

3 | RESULTS

3.1 | Changes in the behavior of mothers and infants over the first 16 months of infant life

Focal animal studies of the behavior of mothers and their infants by Baker-Dittus (1985) involved two groups of toque macaques and indicated the changes in the mother-infant relationship as infants grew. These changes were measured in terms of infants' rates of nursing and foraging as well as maternal rates of carrying infants and rejecting infants' attempts to suckle (Figure 1).

Mothers were observed to nurse their infants from birth to 16 months old, but the rate of nursing declined gradually (Figure 1a). During their infants' first month of life mothers did not reject infants' attempts at suckling (Figure 1c) and none of these infants foraged (Figure 1d). A low rate of maternal rejection was observed from the second to fifth month of infant age, it doubled by 6 months and peaked at 7 months when variance in maternal rejection rates was also the greatest. A second peak in maternal rejection occurred between the 11th and 13th months of infancy (Figure 1c). Maternal rejection rates were accompanied by a decline in nursing rates that dropped by about half during the first 4 months of infancy and then continued to decline more gradually until nursing stopped altogether

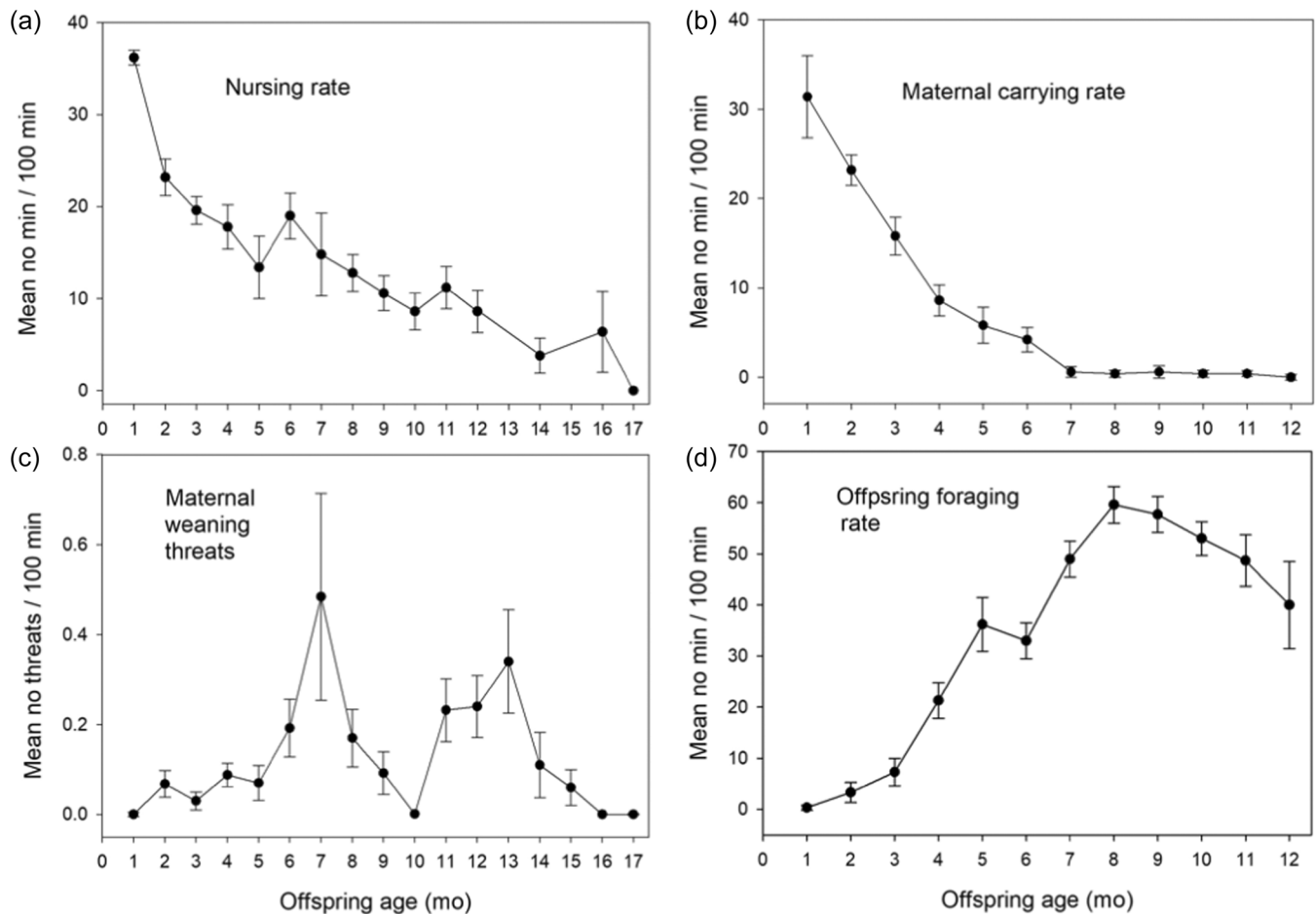


FIGURE 1 Behavioral changes in the mother–infant relationship from infant birth to weaning in wild toque macaques: (a) nursing rate, (b) maternal carrying rate, (c) maternal weaning threats, and (d) offspring foraging rate. Plotted values are means and their standard error bars (compiled from Baker-Dittus, 1985).

after 16 months of age. Infants in their second month of life began foraging but at very low rates until, by 5 months of age, infants spend more time searching for their food than suckling. Foraging rates in infants reached a plateau by about 7 months when foraging rates matched that of much older offspring. The rates at which mothers carried their infants declined steadily in synchrony with the changes noted above; infants at 7 months and older were carried <1% of observation time and none were carried after 12 months of age (Figure 1b).

In the following section, we supplement information about the mother–infant relationship in toque macaques from the perspective of a cross-sectional population profile for the evidence of lactation and its effects on maternal condition and infant survival.

3.2 | The population distribution of female reproductive states

Among the 442 independent tests for the presence or absence of milk among females aged >4.0 years old, 72 (16.3%) involved

nulliparous females and 24 (5.4%) were postreproductive ones; none of these had milk. Among the parous subset ($n = 346$), 271 (78.3%) females were lactating, and 75 (21.7%) had no milk because either they had weaned their infant ($n = 21$) or the infant had died ($n = 54$) (Table 1).

Twin births were rare (about one per thousand) and all IBIs were measured between singleton births. The overall IBI was ($n = 320$, median = 19.8, mean = 18.6 ± 4.6 months, range 10.3–28.5 months, with bimodal peaks at the 13th and 22nd months). Females nursed only the most recent single offspring unlike rhesus macaques *M. mulatta* under food provisioning where mothers may simultaneously nurse two infants from successive birth cohorts (Lee et al., 2019)

3.3 | The evidence for lactation and its relation to offspring age

The presence of manually expressed milk from the teats of captured (and released) females was taken as indicative of lactation (see Section 2.6). All engaged mothers had milk for

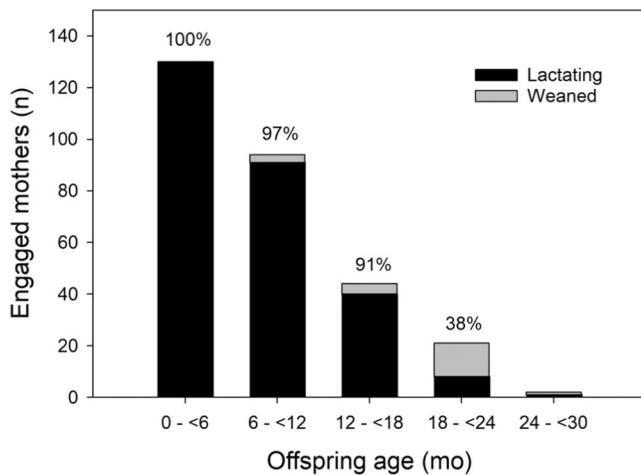


FIGURE 2 The distribution of engaged mothers that were lactating (suckling offspring, $n = 271$) and not lactating (weaned live offspring, $n = 21$) in relation to offspring age, and the proportion of females lactating within each offspring age range.

infants aged less than 7.2 months; thereafter the frequency of lactating mothers decreased with increasing infant age (Figure 2). Of all engaged mothers, approximately 74% were lactating with infants 1 year and older, 42% had milk for infants at 18–22 months, and normally no mothers had milk for infants greater than 22 months old. Two exceptional cases included offspring that nursed at 24.2 and 26.4 months old and were the last before their mothers died of old age (>27 years). A third unusual case, excluded from the sample, involved a 28.2-month-old juvenile that suckled milk destined for its miscarried younger sibling.

Among the 21 mothers that had weaned their infants the age distribution of weanlings was manifest in two periods (Figure 3). A minority of infants (10%) were subject to full weaning at an early age (7–8 months), whereas most (86%) were not fully weaned until well past 15 months old. The observed ages of weaning were maxima because it is unknown exactly how long before sampling dry mothers had weaned their offspring.

3.4 | Maternal reproductive schedules and overlap of states

The overall distribution of the different reproductive states among parous females indicated that only a small proportion of them ($n = 36$, 10.4%) were in a quiescent state providing only nonreproductive care for weaned offspring if any. Most parous females ($n = 310$, 89.6%) were either pregnant, lactating, cycling, or lactation co-occurred with cycling or pregnancy. Among the 271 lactating mothers, six (2.2%) were also cycling, and 29 (10.7%) were pregnant (Table 1). The frequency of lactating and cycling mothers peaked when offspring were at 6–9 months old. The frequency of lactating and pregnant mothers peaked at offspring ages 5–9 months and again between 14 and 20 months (Figure 4). The number of pregnant mothers that were

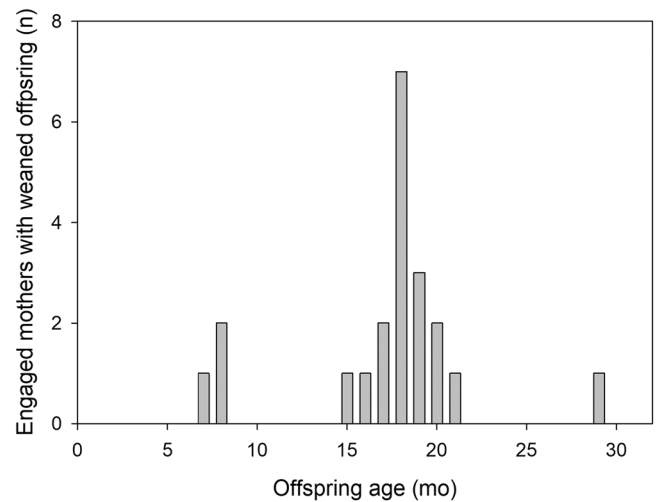


FIGURE 3 The distribution of engaged mothers ($n = 21$) with live weaned offspring in relation to offspring age.

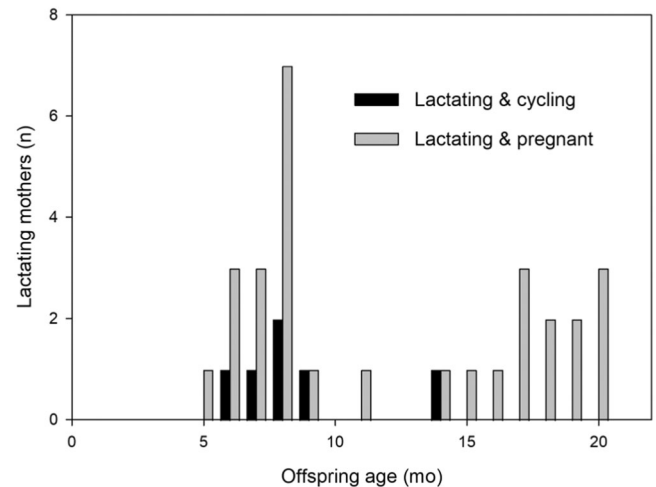


FIGURE 4 The frequency of lactating mothers that were also cycling ($n = 6$) and pregnant ($n = 29$).

lactating decreased in relation to the age of the fetus up to 84 days into gestation (Figure 5).

3.5 | Lactation, menarche, and the IBI in relation to maternal reserves

The balance of female energy reserves (Ellison, 2003) was never measured directly in this population of toque macaques but was assumed to impact the measurable IBI (Valeggia & Ellison, 2001) and both variables to be affected by the factors as hypothesized below.

Hypothesis #1, Lactation extends the IBI. Focusing only on the years 1986 to 2002 and excluding dry mothers that had weaned their infants, the IBIs among lactating mothers irrespective of diets and whose infants survived to the birth of the next infant ($Md = 20.2$

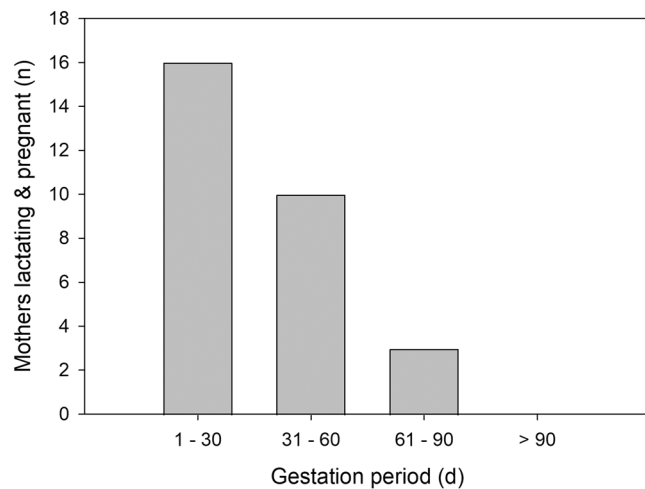


FIGURE 5 The numerical distribution of lactating mothers that were nursing their current infant and pregnant with the next infant in relation to the age of the fetus.

months, $Mn = 19.1 \pm 4.4$ months, $n = 221$) was significantly greater by 3–6 months than the IBIs among dry mothers whose infants had died early ($Md = 13.7$ months, $Mn = 16.0 \pm 4.6$ months, $n = 51$) (Log-rank test = 18.662, $df = 1$, $p < 0.001$) (Figure 6a).

Hypothesis #2. Rich diet shortens the IBI. Among lactating mothers whose infants did and did not survive to the birth of the next infant, the IBI among females with access to a rich diet was significantly less ($Md = 17.6$ months, $Mn = 18.0 \pm 4.4$ months, $n = 83$) by 1–3 months than that among females on a natural diet ($Md = 20.1$, $Mn = 19.3 \pm 4.5$ months, $n = 169$) (log-rank statistic = 6.742, $df = 1$, $p < 0.009$) (Figure 6b).

Hypothesis #3. Maternal physical growth during lactation extends the IBI. Considering lactating females under all diets whose infants did and did not survive to the next birth, the IBI among growing primiparous mothers ($Md = 21.8$, $Mn = 20.4 \pm 3.9$ months, $n = 78$) was significantly greater by 2–4 months than that among mature multiparous ones ($Md = 17.8$, $Mn = 18.2 \pm 4.6$ months, $n = 174$) (Log-rank statistic = 4.118, $df = 1$, $p = 0.042$) (Figure 6c).

Hypothesis #4. Rich maternal diet promotes menarche. The age of first birth of females feeding on a rich diet ($Md = 5.4$ year, $Mn = 5.4 \pm 0.8$ year, $n = 41$) was significantly less by about 1 year than that of females restricted to mostly a natural diet ($Md = 6.2$ year, $Mn = 6.4 \pm 0.9$ year, $n = 69$) (Log-rank statistic = 39.383, $df = 1$, $p < 0.001$) (Figure 7).

Hypothesis #5. Females increase foraging time to contribute to the metabolic costs of lactation. Lactating females expended a significantly greater proportion of a day foraging ($Md = 34.3\%$, $Mn = 35.4 \pm 1.3\%$, $n = 14$) than nonlactating ones ($Md = 26.2\%$, $Mn = 28.7 \pm 1.8\%$, $n = 10$) (Log-rank = 5.797, $df = 1$, $p = 0.016$) (Figure 8). The effects of maternal qualities and seasons that might have influenced foraging time were not parsed in these comparisons.

Hypothesis #6. The cost of catabolism and increased foraging time to support lactation may exceed maternal ability to support infant survival. Comparing rates of mortality among infants between dry and lactating mothers, and arbitrarily not counting ($n = 7$) potential neonatal deaths, ($n = 42/47$, 89.4%) of infant deaths among dry mothers occurred during

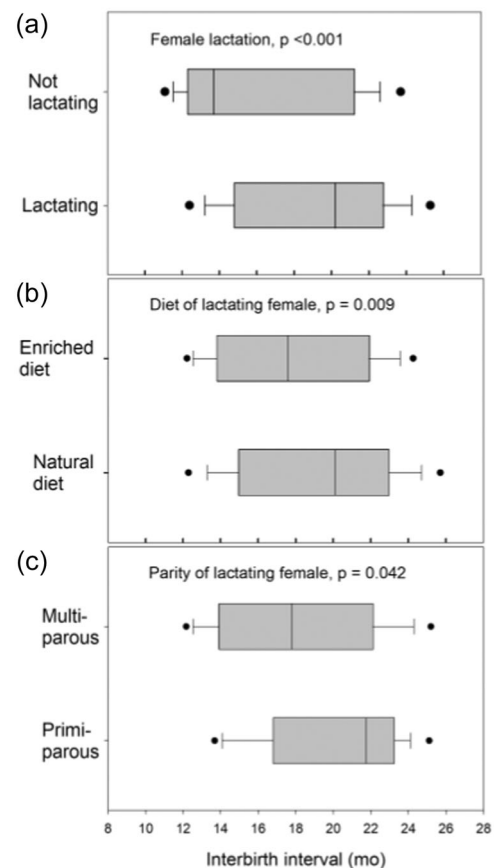


FIGURE 6 Interbirth intervals in relation to: (a) the state of lactation; (b) diet richness of lactating females, and (c) parity of lactating females.

the period of peak lactation from birth to 8 months (Figure 9a), whereas most offspring deaths among lactating mothers ($n = 33/38$, 86.8%) occurred after peak lactation (8 months) coinciding with weaning during supplemental lactation (Figure 9b). The difference in these distributions was significant ($\chi^2 = 49.360$, $df = 1$, $p < 0.001$). The frequency of quiescent females reflected those recovering their energy balance for their own survival and future reproduction following the high cost of pregnancy and lactation for their most recent reproductive effort. The proportion of quiescent mothers (Table 1) among mothers whose infants died ($n = 31/54$, 57%) was significantly greater than among mothers whose infants survived ($n = 5/21$, 24%) ($\chi^2 = 6.838$, $df = 1$, $p = 0.009$), suggesting that the depletion of maternal bodily reserves contributed to the cause of infant death as well as to the greater prevalence of recovery among the females whose infants died.

3.6 | Maternal depletion, nutritional quality, and infant mortality

The predicted link between maternal depletion, lactation, and infant mortality was investigated further. Ideally, we would want to know maternal condition on the date of infant death, but that information

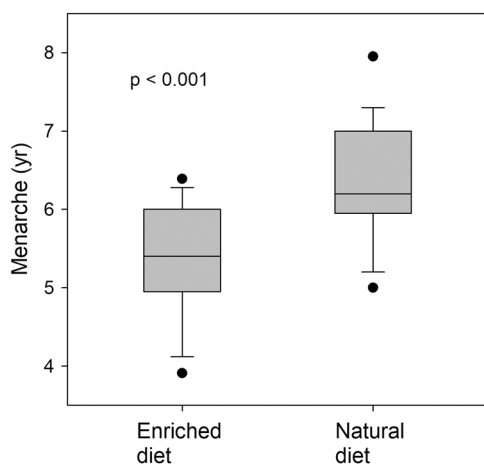


FIGURE 7 The relation between menarche and female diet quality.

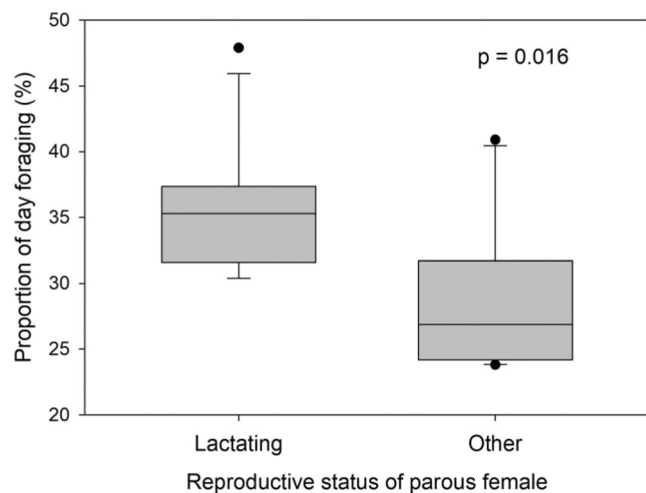


FIGURE 8 Comparison of the proportions of foraging time expended per dawn to dusk activity by parous females lactating ($n = 14$) and not lactating ($n = 10$) over 24 days of observation between January and December 1971.

was not available because sampling dates of mothers in this cross-sectional study did not coincide with the dates of infant mortality. Alternately, a combination of related measures shed light on the predicted relationship.

Hypothesis #7. The nutritional quality of the environmental food supply promotes maternal body condition and in turn infant survival. Maternal body condition was estimated by skinfold thickness that has been shown to be proportional to the mass of dissected adipose tissue or body fat in toque macaques (Dittus & Gunathilake, 2015) and similar regressions have been shown in humans (Durnin & Rahaman, 1967; Womersley & Durnin, 1977) and baboons (Rutenberg et al., 1987). The skinfold thickness of toque macaque mothers on a rich diet (Md = 2.2 mm, Mn = 2.5 ± 0.6 mm, $n = 94$; corresponding to 4.3% mean body fat) was significantly greater than that (Md = 1.9 mm, Mn = 1.9 ± 0.4 mm, $n = 207$; corresponding to 2.2% mean body fat) of mothers on a natural

diet (Log-rank = 57.587, $df = 1$, $p < 0.001$) (Figure 10). The proportion of infants surviving to the date of conception of the next sibling was significantly greater (86.2%) among mothers feeding on a rich diet ($n = 109$) and in better body condition than the proportion of infants surviving (76.9%) among mothers of lesser fatness and feeding on a natural diet ($n = 238$) ($\chi^2 = 4.057$, $df = 1$, $p < 0.05$). The combined observations underscore the importance of maternal body condition (and of the environmental food base) to maternal ability to support infant survival.

Hypothesis #8. Maternal depletion from rapid reproduction by lactating mothers is associated with higher infant mortality. Was maternal depletion from short intervals between births also a factor driving infant mortality among lactating mothers of toque macaques as has been noted in humans (Wang et al., 2022) and well-fed rhesus macaques (Lee et al., 2019)? To examine this possibility, we focused more narrowly on infant survival up to the birth of the next sibling under different conditions. Among lactating females on a natural diet, infant death was associated with significantly shorter IBIs by about 3 months (Md = 17.8, Mn = 16.8 ± 4.4 months, $n = 19$) than the IBIs among infants that survived (Md = 20.6 months, Mn = 19.7 ± 4.4 months, $n = 146$) (Log-rank = 7.778, $df = 1$, $p = 0.005$) (Figure 11). The same comparison among lactating mothers on an enriched diet lacked a significant relationship between the duration of the IBI and infant survival (Md = 17.5 months, Mn = 18.0 ± 4.2 months, $n = 71$ surviving infants, and Md = 20.5, Mn = 18.5 ± 5.5 months, $n = 12$ dead infants) (Log-rank = 0.719, $df = 1$, $p = 0.396$).

4 | DISCUSSION

4.1 | Lactation (nutrition vs. comfort) and weaning

Studies of maternal investment in primates have been inconclusive about the age at which infants are weaned because observations of suckling behavior by themselves cannot determine whether infants are drawing milk from the mother or are deriving merely comfort and reassurance (Blass & Teicher, 1980; Cameron, 1998; Jay, 1965; Lee, 1987; Martin, 1984). This study has shown that milk is indeed available for all infants up to 7.2 months old, for 91% of them up to 18 months and for a few even older (Figure 2), although the quantity of milk transferred is unknown. The extended period of lactation is therefore nutritional, at least to some degree, even among older offspring. The psychological comfort that infants may derive from suckling (Blass & Teicher, 1980; Cameron, 1998) was not tested, and may be an additional benefit as observed in wild chimpanzees that suckled after lactation ceased (Bădescu et al., 2016).

4.2 | Transition from primary to supplemental lactation

All mothers had milk for infants up to 7.2 months (Figure 2). A coincidence of developments among several parameters indicated

FIGURE 9 The distribution of offspring death ages among: (a) nonlactating or dry mothers, and (b) lactating mothers.

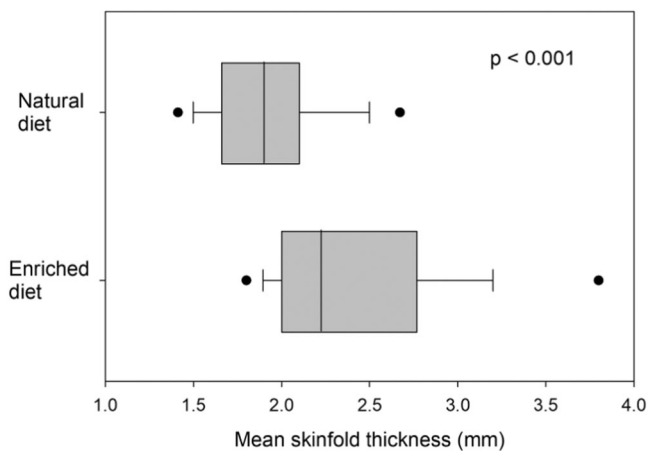
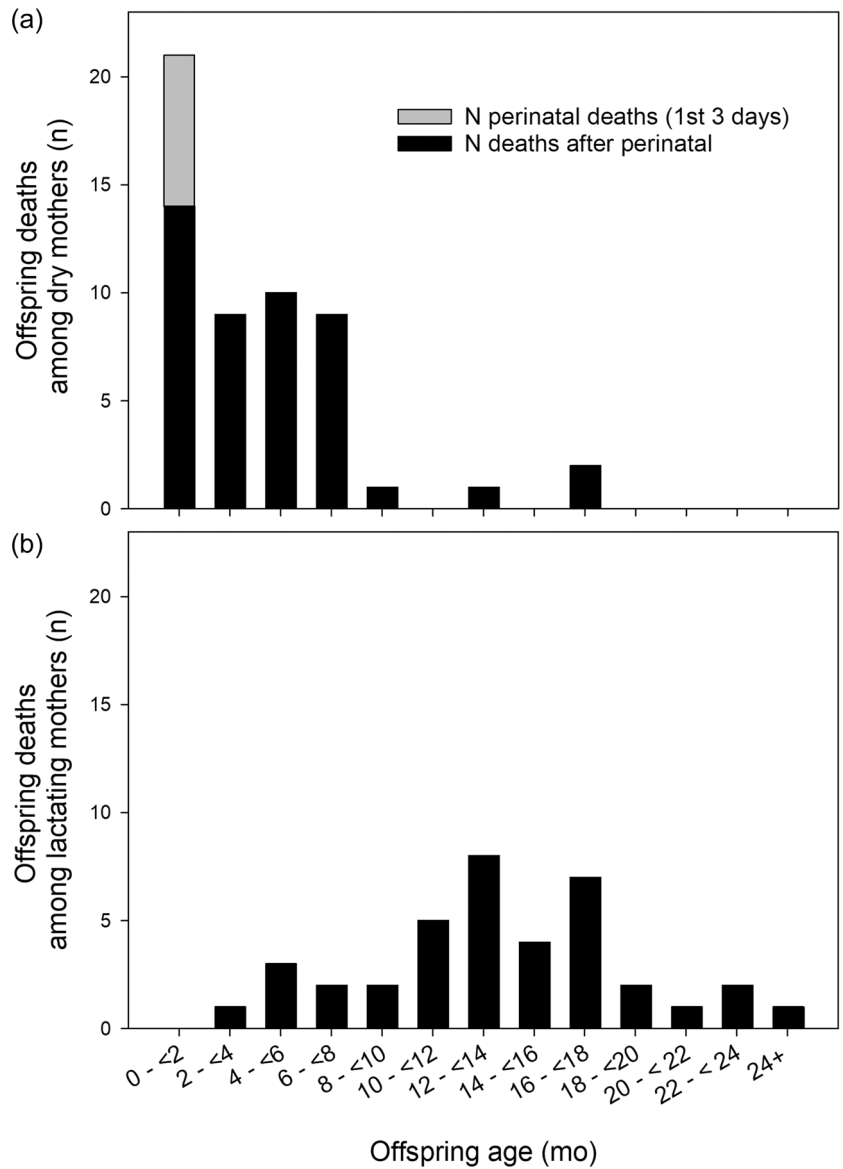


FIGURE 10 Comparison of mean skinfold thickness among parous females feeding on enriched and natural diets, corresponding to 4.3% and 2.2% mean body fat in toque macaques, respectively.

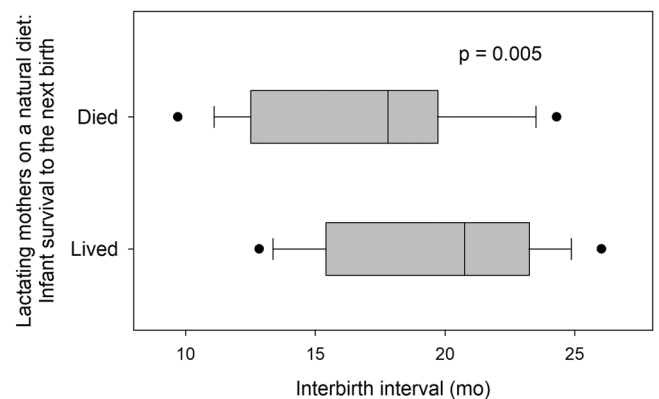


FIGURE 11 The association between the survival of infants to the birth of the next offspring and the interval between births among lactating females feeding a natural diet.

a pivotal change in the mother-infant relationship at about 7 months postpartum. This was marked by a peak in maternal rejection of infants' nursing attempts (Figure 1c), a near cessation of infant carrying by mothers (Figure 1b) and infants foraging at rates typical of older offspring (Figure 1d). Five to 8 months postpartum also coincided with the first peak in the resumption of sexual cycling among lactating mothers and their subsequent new pregnancy (Figure 4). The onset of cycling involved the formation of consorting mating pairs during which mothers shifted for several hours to the periphery or at some distance away from the social group to avoid aggressive interference for mating rights (Dittus, 1977a). During their mothers' consort excursions infants were left to fend for themselves among the core members of the group, infant stress levels were high at such times as reflected by their frequent contact and lost calls (Bayart & Dittus, 1987; Dittus, 1988b). The shift in maternal reproductive priorities accentuated weaning. Notwithstanding these pivotal developments, following the first weaning case at 7.2 months, most mothers (82.4%) continued to nurse their infants for almost another year until 16 months in the behavioral study (Figure 1a), and beyond that age in the broader demographic sample (Figure 2) where females had been tested for the presence of milk. Such prolonged lactation extended into the next pregnancy for 11% (29/271) of lactating mothers (Figure 5).

These relationships point to two phases in lactation: primary, up to about 7 months followed by supplementary lactation, or late-lactation (Ofstedal, 1984; Tanaka et al., 1970). During primary lactation, the neonate is wholly dependent upon mother's milk and gradually shifts to independent foraging such that by 4 months of age infants spend as much time in foraging as nursing, and by 7 months infants forage for durations typical for older offspring (Figure 1d). The maternal rejection for suckling at 7 months (Figure 1c) functioned primarily as an honest maternal signal "giving notice" to spur an infant's greater independence from milk towards self-reliance for finding food in the environment (Figure 1d). The efficiency of foraging by infants at that age is, however, low in terms of both the quality and quantity of food intake because of age-related priority of access relationships as was shown earlier in an independent study (Dittus, 1977a).

It is noteworthy that although maternal rejection of their infants' nursing attempts peaked (Figure 1c) when mothers returned to cycling at 6–9 months and later and assumed the additional burden of pregnancy with their next offspring at those times (Figure 4), there was no equivalent sharp discontinuity in nursing rates (Figure 1a) and milk provided (Figure 2). Instead, the withdrawal from nursing followed gradual trajectories in these parameters from birth to final weaning at ages up to 16 months and older (Figures 1a and 2). These changes were in synchrony with infants' gradually improving abilities to locomote (Figure 1b), drink and feed from the environment (Figure 1d). The enhanced maternal weaning efforts after about 1 year (Figure 1c) effected a final "shutting down" of lactation as progressively more infants were weaned (Figures 2 and 3).

4.3 | Early and late weaning in other primates

The end of lactation or weaning at 7 months of infant age was common to 16 species of cercopithecoid primates that Langer (2003) related to the anatomy of the alimentary tract in this taxon compared to that of other primate taxa and eutherian mammals. But where these primates have been investigated in the wild, or under food-restricted conditions, periods of suckling were prolonged as in vervets *Chlorocebus aethiops* (Cheney et al., 1988; Lee, 1984), Japanese macaques *M. fuscata* (Takahashi, 2002; Takahata et al., 1998), long-tailed macaques *M. fascicularis* (van Noordwijk & van Schaik, 1999), rhesus macaques *M. mulatta* (Melnick, 1981), stump-tailed macaques *M. arctoides* (Nieuwenhuijsen et al., 1985), baboons *Papio cynocephalus* (Lycett et al., 1998; Nicolson, 1982; Rhine et al., 1985), hamadryas *P. hamadryas* (Barrett et al., 2006; Garcia et al., 2006; Sigg et al., 1982) and patas monkeys *Erythrocebus patas pyrrhonotus* (Isbell et al., 2009). Although solid food began to be ingested at about 2 months in toque macaques (Figure 1d) and other cercopithecoids (Langer, 2003), the data imply that the early weaning, at approximately 7 months, marked a more substantial shift to a mixed milk-solid diet and that final weaning from milk occurs at a later age (12–20 months) (Dirks et al., 2010), as in the toque macaques. This early period also coincides with rapid infant growth in toque macaques (Cheverud et al., 1992) and other cercopithecoids (vervet: Lee, 1987; macaques: Saxton & Lotz, 1990; Tanaka, 1992).

4.4 | Weaning in other primates; early notice and shutting down

The bimodal schedule of weaning, with peaks at 7 months and 11–13 months (Figure 3) has not been well defined in most studies, partly because of the practical difficulties of determining the end of milk let-down especially in field studies (Borries et al., 2014). Our study has shown, however, that some amount of milk was available for some infants as old as 24 months in age (Figure 2). Nicolson (1982), too, was able to express milk from Kenyan wild baboons (*P. hamadryas*) as old as 15 months, and these baboons also had bimodal weaning peaks at 7.5 and 11–13 months, and one infant still nursed at 22.5 months. In baboons (*P. hamadryas anubis*) from Uganda, Dirks et al. (2010) identified accentuated lines of enamel in histological sections of teeth that were indicators of stress during weaning, the first at 6 months with an inferred reduction of suckling frequency and the second at 11 months at the cessation of suckling. Female howler monkeys (*Alouatta caraya*) also enhanced weaning at these times (Pavé et al., 2015). On a different timeframe, suited to apes (Langer, 2003), Eckardt et al. (2016) showed that in wild mountain gorillas (*Gorilla beringei beringei*) bimodal weaning peaks occurred at a relatively early age (35–40 months) and a relatively late age (45–50 months) in synchrony with the availability of solid weaning foods (tender bamboo) for infants composing these peaks. Given the long periods of offspring care typical of primate life histories it is understandable that the process of weaning would be timed to

promote the transition initially from milk to a mixed diet and finally off milk altogether but on schedules that vary among taxa in keeping with differences in digestive phenotypes (Langer, 2003), somatic maturation (Lee et al., 1991; Reitsema & Muir, 2015; Reitsema et al., 2016) as well as within species and population differences in environmental and social conditions (Barrett et al., 2006; Pavé et al., 2015) including the seasonal timing of births (Fürtbauer et al., 2010).

4.5 | Supplemental lactation supports the development of offspring foraging efficiency and survival in a competitive society under harsh ecological conditions

Weaned infants face challenges (Lee, 1996). Toque macaques forage on a variety of natural foods involving more than 120 different food items (Dittus, 1974). Juveniles are often supplanted from available food sources by older dominant group members with the effect that the youngest forage at food loci that are poorest in quality and quantity, at slower rates, and for longer periods than older group members in fulfilling their daily needs (Dittus, 1977a). Learning to forage efficiently among highly competitive macaque group members and being subject to the vagaries of a seasonally changing supply of water and food (Dittus, 1974; Hladik & Hladik, 1972) invites risks to infant survival: 40%–50% of infants may die in their first year of life (Dittus, 1975). In the present sample, 87% of the infants whose mothers had milk survived to the birth of the next infant or equivalent duration (18 months or more) in cases where the mother died. These observations suggest that the extended period of supplemental lactation is an adaptation of maternal investment to promote offspring growth and survival under an often-harsh seasonal natural environment in a competitive society where individual survivorship and population growth are capped by a limited supply of food and water (Dittus, 1977a; Dittus et al., 2019). The contrasting shorter periods of lactation, or early weaning, and lower infant mortality and superior body condition of females under food provisioned conditions (Dittus, 1980, 2013; Lee & Bowman, 1995; Reitsema et al., 2016) lends credence to this interpretation.

Looking beyond the Cercopithecidae, the prolonged lactation of 6–8 years among wild orangutans (*Pongo abelli* and *P. pygmaeus*) also has been attributed to environmental variability and uncertainty (Smith et al., 2017) and their long IBIs to high survival by nursing offspring (van Noordwijk et al., 2018). In humans, Barium analyses of a fossil tooth suggested that Neanderthal children were subject to primary weaning at 7 months followed by supplementary lactation for an additional 7 months (Austin et al., 2013) in a pattern reflecting that in wild toque macaques and other monkeys.

4.6 | Female reproductive costs and schedules

Pregnancy and especially early lactation are energetically costly in mammals (Clutton-Brock et al., 1989; Gittleman & Thompson, 1988;

Oftedal, 1984, 1991; Pond, 1977) including primates (Rosetta et al., 2011). Therefore, extended maternal investment would be expected to impact female reproduction. Female primates meet the high energy demands of reproduction by engaging diverse strategies (reviewed in Dufour & Sauther, 2002). These involved eating more and better-quality foods by wild baboons *P. cynocephalus* (Muruthi et al., 1991), macaques *M. assamensis* (Touitou et al., 2021) and *M. nigra* (Arismayanti et al., 2022) and/or minimizing energy expenditure as in free ranging hamadryas (Barrett et al., 2006), or a combination of both strategies as in chimpanzees *Pan troglodytes* (Murray et al., 2009), as well as using up body tissue stores in baboons *P. hamadryas anubis* (Bercovitch, 1987), and macaques *M. nemestrina* (Maninger et al., 2000).

Whether female toque macaques mitigate the costs of reproduction with diet adjustment was not considered. Notwithstanding, lactating females expended more time (or, energy) foraging than nonlactating parous females (Figure 8). Furthermore, an earlier investigation of body weight changes among 485 lactating nongravid parous females indicated that they met the cost of lactation also by using up stored bodily reserves, as is common among mammals (Rogowitz, 1996) and suggested for wild baboons (Altmann, 1980; Bercovitch, 1987); the effect of catabolism in toque macaques was evident in a progressive loss of body mass with lactation duration (tab. 3 in Dittus, 1998). Such maternal depletion of bodily resources is expected to exert an effect on birth spacing because ovarian cycling is sensitive to maternal energy balance, as laid out in the metabolic load hypothesis (Ellison, 2003; Lunn et al., 1984; Valeggia & Ellison, 2004, 2009). Consistent with this hypothesis, our results also indicated that conditions that are predicted to draw on the balance of maternal energy have the effect of extending the IBI. These conditions include lactation (Figure 6a), relatively poor or costly to attain natural food sources that are needed to replenish maternal reserves (Figure 6b), and the diversion of energy towards female growth among lactating primiparous mothers (Figure 6c).

The reduction of lactational amenorrhea and the IBI associated with the death of nursing infants (Figure 6a) was observed similarly among baboons (Altmann et al., 1978), bonnet macaques (Silk, 1990), and Japanese macaques (Scucchi, 1984; Takahata et al., 1998; Tanaka et al., 1970). Access to anthropogenic food in wild-living toque macaques underlay a reduction of the IBI by about 2 months from the 20 months IBI among natural diet feeders (Figure 6b); both of these distributions, however, were greater than the commonly observed IBI normatively of 10–14 months in provisioned primates, or in environments where food is abundant (Asquith, 1989; Williams, 1986; macaques: Burton & Sawchuk, 1982; Drickamer, 1974; Scucchi, 1984; Silk, 1990; Sugiyama & Ohsawa, 1982; vervets: Fairbanks & McGuire, 1984; Lee et al., 1986). A prolonged IBI, as in the toque macaques, agrees with that in other primates subject to restricted natural diets (baboons: Altmann et al., 1978; Gesquiere et al., 2018; Hill, 2000; Lycett et al., 1998; vervets: Hauser & Fairbanks, 1988; Whitten, 1983; macaques: Fürtbauer et al., 2010; Melnick & Pearl, 1987; Silk, 1990; Takahata et al., 1998). Relatively poor food input in toque macaques slows the rate of reproduction also in other ways: by retarding the female growth rate (Cheverud et al., 1992), raising

the age of menarche (Figure 7), and extending the weaning age (a secondary measure of lactation duration) (Figure 2). Other primate species subject to natural food restrictions, too, exhibit retardation of growth and delay of menarche (e.g., macaques: Koyama et al., 1992; Mori et al., 1997; baboons: Altmann & Alberts, 2003, 2005; Bercovitch & Strum, 1993).

In addition, young primate females often begin to reproduce when they are still growing and face tradeoffs in investing some of their bodily resources away from current reproduction towards their own continued growth (Clutton-Brock, 1991; Stearns, 1989). This has the consequence of compromised reproductive outcomes (Hinde et al., 2009) manifest, in part, by longer intervals between births among primiparas compared to multiparas in toque macaques (Figure 6c) and other primate species (baboons: Altmann et al., 1988; mandrills *M. sphinx*: Setchell et al., 2002; Setchell & Wickins, 2004; and macaques: Hinde, 2009; Koyama et al., 1992).

The distribution of reproductive phases in parous females indicated a full schedule whereby sexual cycling, pregnancy, or lactation occupied most females (Table 1) to the extent that lactation overlapped cycling and gestation (Figure 4). The combination of lactation with pregnancy is metabolically highly costly with elevated risks of infant mortality in humans (Molitoris, 2019; Wang et al., 2022). Of the 346 parous females 8% ($n = 29$) were pregnant but continued to provide milk for their older infants, albeit with decreasing numbers, up to a maximum of 84 days or about half-way into the duration of the next pregnancy (Figure 5). These observations point to a continuous lifelong cycle of costly reproductive engagement from menarche to menopause. It is also consistent with expectations of energy balance (Ellison, 2003; Lunn et al., 1984) that some females were quiescent to conserve or restore bodily reserves following weaning or the death of a new infant (Table 1).

4.7 | Maternal depletion, nutritional quality, and age-specific causes of infant mortality

Toque macaques feeding on a natural diet have approximately 2% body fat like most wild mammals (Pond & Mattacks, 1987) including wild-feeding baboons (Altmann et al., 1993), and this is significantly less than that among female primate counterparts on an enriched diet (see review Dittus, 2013). Toque macaque infants are born with virtually no body fat and mortality in the first year was 20%–50% (Dittus, 1975; and unpublished), a mortality rate that is equivalent to or somewhat greater than that observed in some other wild primates (Altmann et al., 1977; Bronikowski et al., 2011). The paucity of body fat in neonates points to little fallback resources for survival carried over from gestation and a heavy reliance on milk for life support. Lactating toque macaques that fed on a natural diet, too, had relatively low body fat, and lose body weight with the duration of lactation (Dittus, 1998). Persistent decreases in body fat over time indicate a consistent state of negative energy balance (Gesquiere et al., 2018). Under these nutritionally restrictive conditions among lactating mothers significantly shorter IBIs were associated with

females whose infants died before the birth of the next infant (Figure 11). Cause and effect are called into question, however; is the IBI short because infants died from care independent sources such as predation, disease, or infanticide (Kerhoas et al., 2014), or did infants die because maternal care was curtailed (short IBI) (Lycett et al., 1998). In this population, there is no evidence to suggest that extrinsic sources were a major contributor to death among dependent infants of engaged mothers (Dittus, unpublished). Instead, the observations suggest that maternal depletion played a causal role in the mortality of the youngest infants during primary lactation (Figure 9a). These infant survival outcomes were reminiscent of similar ones among humans (e.g., Wang et al., 2022) and rhesus macaques (Lee et al., 2019) with high birth rates, albeit under richer food supplies than available to wild toque macaques. Under natural conditions where survival and population growth are environmentally and socially constrained, we expect this pattern of maternal depletion and infant mortality to be exacerbated. Short periods between births reduce the time for lactating mothers to recover bodily resources from the environment in support of their body condition and that of their infants. We suggest that the high cost of lactation to maternal energy balance that resulted from rapid reproduction (Figure 11), a limiting food supply, especially a combination of both, depleted the maternal body reserves for a minority of parous females to the extent that they not only forfeited their ability to support infant survival during primary lactation (Figure 9a) but also drove a significantly higher proportion of mothers (57%) into quiescent recovery ($p < 0.001$) when compared to the 24% of lactating mothers whose infants survived (Table 1). This interpretation is consistent with the maternal depletion syndrome commonly reported in humans (e.g., Wang et al., 2022) and recently in rhesus macaques (Lee et al., 2019) and highlights the potentially multiple effects acting on maternal depletion (Winkvist et al., 1992). The corollary implies that engaged mothers of surviving toque macaque infants had sufficient bodily reserves to support lactation for infant survival with significantly fewer mothers (24%) in recovery. Access to superior nutrition (presumably a matching maternal energy balance) through high rank or rich food base has been linked to short IBIs in baboons (Barton & Whiten, 1993; Gesquiere et al., 2018; Smuts & Nicolson, 1989), macaques (van Noordwijk & van Schaik, 1999; Sugiyama & Ohsawa, 1982), chimpanzees *Pan troglodytes* (Pusey et al., 1997; Thompson et al., 2007), lemurs *Propithecus verreauxi* (Richard et al., 2000) and toque macaques (Figure 6b), and for some of these species also to increased infant survival in macaques *M. fascicularis*, (van Noordwijk & van Schaik 1999); *M. fuscata* (Sugiyama & Ohsawa, 1982); and chimpanzees (Pusey et al., 1997; Thompson et al., 2007). The toque macaques fit this pattern insofar as superior nutrition promoted maternal fatness (Figure 10) and infant survival, but the duration of the IBI had no effect on infant survival under food enrichment. It was only under the more restrictive natural diet that prolonged IBIs (high maternal investment) were associated with infant survival (Figure 11).

Although mortality during primary lactation among young nursing infants (<8 months old) (Figure 9b) was significantly less

than among their peers of dry mothers (Figure 9a), these survivors eventually faced elevated risk of mortality between 10 and 18 months (Figure 9b). The latter coincided with a final peak in behavioral weaning (Figure 1c) and the transition from supplemental lactation to solid food (Figure 1d) when the youngsters' handicap in resource competition with dominant group members (Dittus, 1977a) played a greater role in their nutrition and survival (Figure 9b) than nursing (Figures 1a and 2).

4.8 | Lactation duration in relation to reproductive seasons

In mammalian evolution, Dall and Boyd (2004) noted that lactation offers the female mammal to cope with unreliable food supplies. Potential maternal depletion suggests that nutritional support in a variable natural environment close to ecological carrying capacity for primates can, however, limit lactational support for infants and that the withdrawal from lactation that kills dependent infants safeguards maternal bodily resources for her own survival and prospects for future reproduction (Lee et al., 1991; Trivers, 1974; Williams, 1966). Empirical support for this phenomenon has been observed in a variety of other mammals (vervet monkeys: Fairbanks & McGuire, 1995; Lee, 1984; bighorn sheep: Berger, 1979; grizzly bears: Tait, 1980). The extended period of lactation, reflected in long IBIs would be expected to promote infant survival in harsh environments as shown for the mountain baboons of Drakensberg, South Africa (Lycett et al., 1998), and in the present study where 80.6% (279/346) of born infants did survive up to at least 1 year and 71.4% (247/346) lived to 2 years; the balance of 19.4% and 28.6% of infants died up to these ages, respectively.

The timing of conception is a female gamble on unreliable future food supplies for energy intake in support of reproductive costs, and along with other sources of infant mortality, risks reproductive failure. The observation of nonstop costly reproductive effort from menarche to menopause with little respite for recovery as manifest in toque macaques, or rapid reproductive rate with short IBIs in rhesus macaques and humans suggests that the risks of failure from initiating reproduction are less than slowing the rate of new reproductive attempts. The all-out reproductive effort appears as an adaptive strategy in contexts where it is difficult to predict postconception environments to support peak energy requirements for reproduction and suggests that natural selection would favor the timing of conception in accordance with environmental cues (daylength, seasonal weather) that predict future supplies of quality food and water that are best suited to support maternal condition during peak lactation and/or infant weaning foods, a topic that has received much attention in the literature (e.g. Barrett et al., 2006; Bercovitch & Harding, 1993; Foerster et al., 2012; Jönsson, 1997; van Schaik & Brockman, 2005). The fact that toque macaques exhibit a broad birth season suggests that females attempt adaptive timing of reproduction in relation to environmental cues and that this would contribute

to the onset of weaning or the observed variation in lactation duration after the first 7 months up to which infant age all mothers provided milk (Figure 2).

4.9 | Terminal investment

Female toque macaques accumulate injuries (Dittus & Ratnayeke, 1989) and lose body weight with age (Cheverud et al., 1992) that are indicative of declining body condition and social status as they approach menopause (Ratnayeke, 1994). Despite their infirmities, however, two old females past 27 years of age provided milk for their last offspring, before menopause and death, for the longest period of lactation (>24 months) in the sample. Their behavior is consistent under the hypothesis of terminal investment (Clutton-Brock et al., 1984; Gadgil & Bossert, 1970; Pianka & Parker, 1975; Trivers, 1972).

AUTHOR CONTRIBUTIONS

Wolfgang Dittus: Conceptualization (lead); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); validation (equal); visualization (lead); writing—original draft (lead); writing—review and editing (lead). **Anne Baker:** Conceptualization (supporting); data curation (supporting); formal analysis (equal); investigation (equal); methodology (equal); validation (supporting); writing—original draft (supporting); writing—review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw data variables, derived variables, tabulations, and analyses have been submitted for publication to a data repository under the following title and link: Dittus, Wolfgang (2023), The biology of prolonged lactation in wild *Macaca sinica*, Dryad Data set, <https://doi.org/10.5061/dryad.cc2fqz695>

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REFERENCES

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–266. <https://doi.org/10.1163/156853974x00534>
- Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press.
- Altmann, J., & Alberts, S. C. (1987). Body mass and growth rates in a wild primate population. *Oecologia*, 72, 15–20.
- Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, 15, 401–409. <https://doi.org/10.1002/ajhb.10157>
- Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: Ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, 57, 490–501. <https://doi.org/10.1007/s00265-004-0870-x>
- Altmann, J., Altmann, S. A., & Hausfater, G. (1978). Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In T. H. Clutton-Brock (Ed.), *Reproductive success* (pp. 403–418). University of Chicago Press.
- Altmann, J., Altmann, S. A., Hausfater, G., & McCuskey, S. A. (1977). Life-history of yellow baboons: Physical development, reproductive parameters, and infant mortality. *Primates*, 18, 315–330. <https://doi.org/10.1007/BF02383111>
- Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P., & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. *American Journal of Primatology*, 30, 149–161.
- Ardito, G. (1976). Check-list of the data on the gestation length of primates. *Journal of Human Evolution*, 5(2), 213–222. [https://doi.org/10.1016/0047-2484\(76\)90023-3](https://doi.org/10.1016/0047-2484(76)90023-3)
- Arismayanti, E., Waterman, J. O., Pasetha, A., Qomariah, I. N., Perwitasari-Farajallah, D., & Astuti, D. A. (2022). Pregnant and lactating *Macaca nigra*: Behavior and food selection. *BIOTROPICA*, 29(2), 150–160. <https://doi.org/10.11598/btb.2022.29.2.1687>
- Arlet, M. E., Isbell, L. A., Kaasik, A., Molleman, F., Chancellor, R. L., Chapman, C. A., Mänd, R., & Carey, J. R. (2015). Determinants of reproductive performance among female gray-cheeked mangabeys (*Lophocebus albigena*) in Kibale National Park, Uganda. *International Journal of Primatology*, 36, 55–73. <https://doi.org/10.1007/s10764-014-9810-4>
- Asquith, P. J. (1989). Provisioning and the study of free-ranging primates: History, effects, and prospects. *Yearbook of Physical Anthropology*, 32, 129–158. <https://doi.org/10.1002/ajpa.1330320507>
- Austin, C., Smith, T. M., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D., Hare, D. J., Doble, P., Eskenazi, B., & Arora, M. (2013). Barium distributions in teeth reveal early-life dietary transitions in primates. *Nature*, 498, 216–219. <https://doi.org/10.1038/nature12169>
- Austin, C., Smith, T. M., Farahani, R. M. Z., Hinde, K., Carter, E. A., Lee, J., Lay, P. A., Kennedy, B. J., Sarrafpour, B., Wright, R. J., Wright, R. O., & Arora, M. (2016). Uncovering system-specific stress signatures in primate teeth with multimodal imaging. *Scientific Reports*, 6, 18802. <https://doi.org/10.1038/srep18802>
- Baker-Dittus, A. M. (1985). *Infant and juvenile directed behaviors in adult toque macaques Macaca sinica* [Unpublished doctoral dissertation]. University of Maryland, College Park.
- Barrett, L., Halliday, J., & Henzi, S. P. (2006). The ecology of motherhood: The structuring of lactation costs by chacma baboons. *Journal of Animal Ecology*, 75, 875–886. <https://doi.org/10.1111/j.1365-2656.2006.01105.x>
- Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour*, 46, 777–789.
- Bayart, F., & Dittus, W. P. J. (1987). Vocal differences of infant and juvenile toque macaques (*Macaca sinica*) according to individuality and degree of social separation. *International Journal of Primatology*, 10(3), 415.
- Bercovitch, F. B. (1987). Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *American Journal of Primatology*, 12(2), 189–195. <https://doi.org/10.1002/ajp.1350120206>
- Bercovitch, F., & Strum, S. (1993). Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioral Ecology and Sociobiology*, 33, 313–318. <https://doi.org/10.1007/BF00172929>
- Bercovitch, F. B., & Berard, J. D. (1993). Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behavioral Ecology and Sociobiology*, 32, 103–109.
- Bercovitch, F. B., & Harding, R. S. O. (1993). Annual birth patterns of savanna baboons (*Papio cynocephalus anubis*) over a ten-year period at Gilgil, Kenya. *Folia Primatologica*, 61, 115–122.
- Berger, J. (1979). Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): An ecological interpretation. *Zeitschrift für Tierpsychologie*, 50, 188–200.
- Blass, E. M., & Teicher, M. H. (1980). Suckling. *Science*, 210(1980), 15–22. <https://doi.org/10.1126/science.6997992>
- Blomquist, G. E. (2009). Trade-off between age of first reproduction and survival in a female primate. *Biology Letters*, 5, 339–342. <https://doi.org/10.1098/rsbl.2009.0009>
- Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., & Koenig, A. (2014). The meaning of weaning in wild Phayre's leaf monkeys: Last nipple contact, survival, and independence. *American Journal of Physical Anthropology*, 154, 291–301. <https://doi.org/10.1002/ajpa.22511>
- Bronikowski, A. M., Altmann, J., Brockman, D. K., Cords, M., Fedigan, L. M., Pusey, A., Stoinski, T., Morris, W. F., Strier, K. B., & Alberts, S. C. (2011). Aging in the natural world: Comparative data reveal similar mortality patterns across primates. *Science*, 331, 1325–1328. <https://doi.org/10.1126/science.1201571>
- Burton, F. D., & Sawchuk, L. A. (1982). Birth intervals in *M. sylvanus* of Gibraltar. *Primates*, 23(1), 140–144. <https://doi.org/10.1007/BF02381446>
- Butte, N. F., & King, J. C. (2005). Energy requirements during pregnancy and lactation. *Public Health Nutrition*, 8(7A), 1010–1027.
- Bădescu, I., Katzenberg, M. A., Watts, D. P., & Sellen, D. W. (2016). A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. *American Journal of Physical Anthropology*, 162(2), 285–299. <https://doi.org/10.1002/ajpa.23116>
- Cameron, E. Z. (1998). Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour*, 56, 521–532. <https://doi.org/10.1006/anbe.1998.0793>
- Caro, T. (1999). The behaviour-conservation interface. *Trends in Ecology & Evolution*, 14(9), 366–369.
- Cerroni, A. M., Tomlinson, G. A., Turnquist, J. E., & Grynopas, M. D. (2003). Effect of parity on bone mineral density in female rhesus macaques

- from Cayo Santiago. *American Journal of Physical Anthropology*, 121, 252–269. <https://doi.org/10.1002/ajpa.10238>
- Charnov, E. L. (1991). Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences United States of America*, 88, 1134–1137. <https://doi.org/10.1073/pnas.88.4.1134>
- Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews*, 1, 191–194.
- Cheney, D. L., Seyfarth, R. M., Andelman, S. J., & Lee, P. C. (1988). Reproductive success in vervet monkeys. In T. H. Clutton-Brock (Ed.), *Reproductive success: Studies of individual variation in contrasting breeding systems* (pp. 384–402). University of Chicago Press.
- Cheverud, J. M., Wilson, P., & Dittus, W. P. J. (1992). Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of toque macaques (*Macaca sinica*). *Journal of Human Evolution* 23, 51–77. [https://doi.org/10.1016/0047-2484\(92\)90043-9](https://doi.org/10.1016/0047-2484(92)90043-9)
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press.
- Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1984). Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*, 308, 358–360. <https://doi.org/10.1038/308358a0>
- Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, 337, 260–262. <https://doi.org/10.1038/337260a0>
- Coelho, A. M., & Watts, E. S. (Eds.). (1985). Baboon dimorphism: Growth in weight, length and adiposity from birth to 8 years of age, *Nonhuman primate models for human growth and development* (pp. 125–159). Alan R. Liss, Inc.
- Crockett, C. M., & Sekulic, R. (1984). Infanticide in red howler monkeys (*Alouatta seniculus*). In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 173–191). Aldine Publishing Co.
- Dall, S. R. X., & Boyd, I. L. (2004). Evolution of mammals: Lactation helps mothers to cope with unreliable food supplies. *Proceedings of the Royal Society B: Biological Sciences*, 271, 2049–2057. <https://doi.org/10.1098/rspb.2004.2830>
- Dewey, K. G., & Cohen, R. J. (2007). Does birth spacing affect maternal or child nutritional status? A systematic literature review. *Maternal & Child Nutrition*, 3(3), 151–173. Portico. <https://doi.org/10.1111/j.1740-8709.2007.00092.x>
- Dirks, W., Humphrey, L. T., Dean, M. C., & Jeffries, T. E. (2010). The relationship of accentuated lines in enamel to weaning stress in juvenile baboons (*Papio hamadryas anubis*). *Folia Primatologica*, 81, 207–223. <https://doi.org/10.1159/000321707>
- Dittus, W. (2012). An online forum for exchanging ideas for dealing with issues of pest monkeys. *Journal of Primatology*, 01(2), 1000e1107. <https://doi.org/10.4172/jpmt.1000e107>
- Dittus, W. P. J. (1974). *The ecology and behavior of the toque monkey, Macaca sinica* [Unpublished doctoral dissertation]. University of Maryland, College Park.
- Dittus, W. P. J. (1975). Population dynamics of the toque monkey, *Macaca sinica*. In R. H. Tuttle (Ed.), *Socioecology and psychology of primates* (pp. 125–151). Mouton Publishers.
- Dittus, W. P. J. (1977a). The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour*, 63(3/4), 281–322. <https://doi.org/10.1163/156853977X000450>
- Dittus, W. P. J. (1977b). The ecology of a semi-evergreen forest community in Sri Lanka, *Biotropica*, 9(4), 268–286. <https://doi.org/10.2307/2388145>
- Dittus, W. P. J. (1977c). The socioecological basis for the conservation of the toque monkey (*Macaca sinica*) of Sri Lanka (Ceylon). In P. H. S. H. Rainier & G. H. Bourne (Eds.), *Primate conservation* (pp. 237–265). Academic Press.
- Dittus, W. P. J. (1980). The social regulation of primate populations: A synthesis. In D. G. Lindburg (Ed.), *The macaques: Studies in ecology, behavior and evolution* (pp. 263–286). Van Nostrand Reinhold.
- Dittus, W. P. J. (1988a). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, 36, 1626–1645. [https://doi.org/10.1016/S0003-3472\(88\)80104-0](https://doi.org/10.1016/S0003-3472(88)80104-0)
- Dittus, W. P. J. (1988b). An analysis of toque macaque cohesion calls from an ecological perspective. In D. Todt, & D. Symmes (Eds.), *Primate vocal communication* (pp. 31–50). Springer-Verlag.
- Dittus, W. P. J. (1990). *Manual for the identification of individual toque macaques (Macaca sinica)*. Smithsonian Primate Research Station.
- Dittus, W. P. J. (1998). Birth sex ratios in toque macaques and other mammals: Integrating the effects of maternal condition and competition. *Behavioral Ecology and Sociobiology*, 44, 149–160. <https://doi.org/10.1007/s002650050527>
- Dittus, W. P. J. (2004). Demography: A window to social evolution. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 87–112). Cambridge University Press.
- Dittus, W. P. J. (2013). Arboreal adaptations of body fat in wild toque macaques (*Macaca sinica*) and the evolution of adiposity in primates. *American Journal of Physical Anthropology*, 152, 333–344. <https://doi.org/10.1002/ajpa.22351>
- Dittus, W. P. J. (2023). *The biology of prolonged lactation in wild Macaca sinica*. Dryad Dataset. <https://doi.org/10.5061/dryad.cc2fqz695>
- Dittus, W. P. J., & Gunathilake, K. A. S. (2015). Validating skinfold thickness as a proxy to estimate total body fat in wild toque macaques (*Macaca sinica*) using the mass of dissected adipose tissue. *American Journal of Primatology*, 77, 618–632. <https://doi.org/10.1002/ajp.22385>
- Dittus, W. P. J., Gunathilake, S., & Felder, M. (2019). Assessing public perceptions and solutions to human-monkey conflict from 50 years in Sri Lanka. *Folia Primatologica*, 90(2), 89–108. <https://doi.org/10.1159/000496025>
- Dittus, W. P. J., & Ratnayeke, S. M. (1989). Individual and social behavioral responses to injury in wild toque macaques (*Macaca sinica*). *International Journal of Primatology*, 10(3), 215–234. <https://doi.org/10.1007/BF02735201>
- Dixon, A. F. (1983). Observations on the evolution and behavioral significance of sexual skin in female primates. *Advances in the Study of Behavior*, 13, 63–106. [https://doi.org/10.1016/S0065-3454\(08\)60286-7](https://doi.org/10.1016/S0065-3454(08)60286-7)
- Drickamer, L. C. (1974). A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatologica*, 21, 61–80. <https://doi.org/10.1159/000155596>
- Dufour, D. L., & Sauther, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, 14, 584–602. <https://doi.org/10.1002/ajhb.10071>
- Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, 36, 970–980.
- Dunbar, R. I. M., Hannah-Stewart, L., & Dunbar, P. (2002). Forage quality and the costs of lactation for female gelada baboons. *Animal Behaviour*, 64, 801–805. <https://doi.org/10.1006/anbe.2002.1972>
- Durnin, J. V. G. A., & Rahaman, M. M. (1967). The assessment of the amount of fat in the human body from measurements of skinfold thickness. *British Journal of Nutrition*, 21(03), 681–689. <https://doi.org/10.1079/BJN19670070>
- Eckardt, W., Fawcett, K., & Fletcher, A. W. (2016). Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): Influential factors. *Behavioral Ecology and Sociobiology*, 70, 493–507. <https://doi.org/10.1007/s00265-016-2066-6>
- Ellison, P. T. (2003). Energetics and reproductive effort. *American Journal of Human Biology*, 15, 342–351. <https://doi.org/10.1002/ajhb.10152>

- Ellison, P. T. (2008). Energetics, reproductive ecology, and human evolution. *PaleoAnthropology*, 2008, 172–200.
- Fairbanks, L. A., & McGuire, M. T. (1984). Determinants of fecundity and reproductive success in captive vervet monkeys. *American Journal of Primatology*, 7, 27–38. <https://doi.org/10.1002/ajp.1350070106>
- Fairbanks, L. A., & McGuire, M. T. (1995). Maternal condition and the quality of maternal care in vervet monkeys. *Behaviour*, 132(9/10), 733–754.
- Foerster, S., Cords, M., & Monfort, S. L. (2012). Seasonal energetic stress in a tropical forest primate: Proximate causes and evolutionary implications. *PlosOne*, 7(11), e50108. <https://doi.org/10.1371/journal.pone.0050108>
- Fürtbauer, I., Schülke, O., Heistermann, M., & Ostner, J. (2010). Reproductive and life history parameters of wild female *Macaca assamensis*. *International Journal of Primatology*, 31, 501–517. <https://doi.org/10.1007/s10764-010-9409-3>
- Gadgil, M., & Bossert, W. H. (1970). Life historical consequences of natural selection. *The American Naturalist*, 104(935), 1–24. <https://doi.org/10.1086/282637>
- Garcia, C., Lee, P. C., & Rosetta, L. (2006). Dominance and reproductive rates in captive female olive baboons, *Papio anubis*. *American Journal of Physical Anthropology*, 131, 64–72. <https://doi.org/10.1002/ajpa.20405>
- Garcia, C., Lee, P. C., & Rosetta, L. (2008). Impact of social environment on variation in menstrual cycle length in captive female olive baboons (*Papio anubis*). *Reproduction*, 135, 89–97. <https://doi.org/10.1530/REP-06-0320>
- Gesquiere, L. R., Altmann, J., Archie, E. A., & Alberts, S. C. (2018). Interbirth intervals in wild baboons: Environmental predictors and hormonal correlates. *American Journal of Physical Anthropology*, 166(1), 107–126. <https://doi.org/10.1002/ajpa.23407>
- Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, 28, 863–875. <https://doi.org/10.1093/icb/28.3.863>
- Goto, K., Fukuda, K., Senda, A., Saito, T., Kimura, K., Glander, K. E., Hinde, K., Dittus, W., Milligan, L. A., Power, M. L., Oftedal, O. T., & Urashima, T. (2010). Chemical characterization of oligosaccharides in the milk of six species of New and Old World monkeys. *Glycoconjugate Journal*, 27, 703–715. <https://doi.org/10.1007/s10719-010-9315-0>
- Hauser, M. D., & Fairbanks, L. A. (1988). Mother-offspring conflict in vervet monkeys: Variation in response to ecological conditions. *Animal Behaviour*, 36, 802–813.
- Hill, O. W. C. (1939). The menstrual cycle of the toque macaque (*Macaca sinica* Linn.), with observations on its uterine structure, compared with that of other macaques. *Ceylon Journal of Science (D)*, 5(2), 21–36.
- Hill, R. A. (2000). Ecological and social determinants of birth intervals in baboons. *Behavioral Ecology*, 11(5), 560–564. <https://doi.org/10.1093/beheco/11.5.560>
- Hinde, K. (2009). Richer milk for sons but more milk for daughters: Sex-biased investment during lactation varies with maternal life history in rhesus macaques. *American Journal of Human Biology*, 21, 512–519. <https://doi.org/10.1002/ajhb.20917>
- Hinde, K., & Milligan, L. A. (2011). Primate milk: Proximate mechanisms and ultimate perspectives. *Evolutionary Anthropology: Issues, News, and Reviews*, 20(1), 9–23. Portico. <https://doi.org/10.1002/evan.20289>
- Hinde, K., Power, M. L., & Oftedal, O. T. (2009). Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology*, 138, 148–157. <https://doi.org/10.1002/ajpa.20911>
- Hladik, C. M., & Hladik, A. (1972). Disponibilités alimentaires et domaines vitaux des Primates à Ceylan. *La Terre et La Vie, Revue d'Histoire Naturelle*, 26, 149–215. <https://doi.org/10.3406/rev.1972.4665>
- Hoelzer, G. A., Dittus, W. P. J., Ashley, M. V., & Melnick, D. J. (1994). The local distribution of highly divergent mitochondrial DNA haplotypes in toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka. *Molecular Ecology*, 3, 451–458. <https://doi.org/10.1111/j.1365-294X.1994.tb00123.x>
- Isbell, L. A., Young, T. P., Jaffe, K. E., Carlson, A. A., & Chancellor, R. L. (2009). Demography and life histories of sympatric patas monkeys, *Erythrocebus patas*, and vervets, *Cercopithecus aethiops*, in Laikipia, Kenya. *International Journal of Primatology*, 30, 103–124. <https://doi.org/10.1007/s10764-009-9332-7>
- Engelen, T., & Wolf, A. P. (2011). Maternal depletion and infant mortality. In T. Engelen, J. R. Shapard & Y. Wenshan (Eds.), *Death at the opposite ends of the Eurasian continent: Mortality trends in Taiwan and the Netherlands 1850–1945* (pp. 275–288). Amsterdam University Press.
- Jay, P. (1965). Mother-infant relations in langurs. In H. L. Rheingold (Ed.), *Maternal behavior in mammals* (pp. 282–304). John Wiley & Sons.
- Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78, 57–66.
- Kerhoas, D., Perwitasari-Farajallah, D., Agil, M., Widdig, A., & Engelhardt, A. (2014). Social and ecological factors influencing offspring survival in wild macaques. *Behavioral Ecology*, 25, 1164–1172. <https://doi.org/10.1093/beheco/aru099>
- Kiltie, R. A. (1982). Intraspecific variation in the mammalian gestation period. *Journal of Mammalogy*, 63(4), 646–652. <https://doi.org/10.2307/1380270>
- Koenig, A., Borries, C., Chalise, M. K., & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology*, 243, 215–235. <https://doi.org/10.1111/j.1469-7998.1997.tb02778.x>
- Koyama, N., Takahata, Y., Huffman, M. A., Norikoshi, K., & Suzuki, H. (1992). Reproductive parameters of female Japanese macaques: Thirty years data from the Arashiyama troops, Japan. *Primates*, 33(1), 33–47. <https://doi.org/10.1007/BF02382761>
- Kozuki, N., & Walker, N. (2013). Exploring the association between shot/long preceding birth intervals and child mortality: Using reference birth interval children of the same mother as comparison. *BMC Public Health*, 13, 56. <http://www.biomedcentral.com/1471-2458/13/S3/S6>
- Langer, P. (2003). Lactation, weaning period, food quality, and digestive tract differentiations in eutheria. *Evolution; International Journal of Organic Evolution*, 57(5), 1196–1215. <https://doi.org/10.1111/j.0014-3820.2003.tb00328.x>
- Lee, P. C. (1984). Ecological constraints on the social development of vervet monkeys. *Behaviour*, 91(4), 245–262. <https://doi.org/10.1163/156853984X00092>
- Lee, P. C. (1987). Nutrition, fertility, and maternal investment in primates. *Journal of Zoology*, 213, 409–422. <https://doi.org/10.1111/j.1469-7998.1987.tb03717.x>
- Lee, P. C. (1996). The meanings of weaning: Growth, lactation, and life history. *Evolutionary Anthropology: Issues, News, and Reviews*, 5(3), 87–98. [https://doi.org/10.1002/\(SICI\)1520-6505\(1996\)5:3<87::AID-EVAN4>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T)
- Lee, P. C., & Bowman, J. E. (1995). Influence of ecology and energetics on primate mothers and infants. In C. R. Pryce, R. D. Martin, & D. Skuse (Eds.), *Motherhood in human and nonhuman primates* (pp. 47–58). Basel Karger.
- Lee, P. C., Brennam, E. J., Else, J. G., & Altmann, J. (1986). Ecology and behaviour of vervet monkeys in a tourist lodge habitat. In P. C. Lee (Ed.), *Primate ecology and conservation* (pp. 229–235). Cambridge University Press.

- Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology*, 225, 99–114. <https://doi.org/10.1111/j.1469-7998.1991.tb03804.x>
- Lee, S. D., Ruiz-Lambrides, A. V., & Higham, J. P. (2019). Higher offspring mortality with short interbirth intervals in free-ranging rhesus macaques. *Proceedings National Academy of Science United States of America*, 116(13), 6057–6062. <https://doi.org/10.1073/pnas.1817148116>
- Lipkin, E. W., Aumann, C. A., & Newell-Morris, L. L. (2001). Evidence for common controls over inheritance of bone quantity and body size from segregation analysis in a pedigreed colony of nonhuman primates (*Macaca nemestrina*). *Bone*, 29, 249–257. [https://doi.org/10.1016/S8756-3282\(01\)00508-7](https://doi.org/10.1016/S8756-3282(01)00508-7)
- Lunn, P. G., Austin, S., Prentice, A. M., & Whitehead, R. G. (1984). The effect of improved nutrition on plasma prolactin concentrations and postpartum infertility in lactating Gambian women. *The American Journal of Clinical Nutrition*, 39, 227–235. <https://doi.org/10.1093/ajcn/39.2.227>
- Lycett, J. E., Henzi, S. P., & Barrett, L. (1998). Maternal investment in mountain baboons and the hypothesis of reduced care. *Behavioral Ecology and Sociobiology*, 42, 49–56. <https://doi.org/10.1007/s002650050410>
- Maestripietri, D. (2002). Parent-offspring conflict in primates. *International Journal of Primatology*, 23(4), 923–951. <https://doi.org/10.1023/A:1015537201184>
- Maninger, N., Sackett, G. P., & Ruppenthal, G. C. (2000). Weaning, body weight, and postpartum amenorrhea duration in pigtailed macaques (*Macaca nemestrina*). *American Journal of Primatology*, 52, 81–91. [https://doi.org/10.1002/1098-2345\(200010\)52:2<81::AID-AJP2>3.0.CO;2-L](https://doi.org/10.1002/1098-2345(200010)52:2<81::AID-AJP2>3.0.CO;2-L)
- Martin, P. (1984). The meaning of weaning. *Animal Behaviour*, 32(4), 1257–1259. [https://doi.org/10.1016/S0003-3472\(84\)80245-6](https://doi.org/10.1016/S0003-3472(84)80245-6)
- Melnick, D. J. (1981). *Microevolution in a population of Himalayan rhesus monkeys (Macaca mulatta)* [Unpublished doctoral dissertation]. Yale University.
- Melnick, D. J., & Pearl, M. C. (1987). Cercopithecines in multimale groups: Genetic diversity and population structure. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 121–134). University of Chicago Press.
- Milligan, L. A., Rapoport, S. I., Cranfield, M. R., Dittus, W., Glander, K. E., Oftedal, O. T., Power, M. L., Whittier, C. A., & Bazinet, R. P. (2008). Fatty acid composition of wild anthropoid primate milks. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 149, 74–82. <https://doi.org/10.1016/j.cbpb.2007.08.006>
- Molitoris, J. (2019). Breast-feeding during pregnancy and the risk of miscarriage. *Perspectives on Sexual and Reproductive Health*, 51(3), 153–163. <https://doi.org/10.1363/psrh.12120>
- Mori, A., Yamaguchi, N., Watanabe, K., & Shimizu, K. (1997). Sexual maturation of female Japanese macaques under poor nutritional conditions and food-enhanced perineal swelling in the Koshima troop. *International Journal of Primatology*, 18(4), 553–579.
- Murray, C. M., Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2009). Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology*, 20(6), 1211–1216. <https://doi.org/10.1093/beheco/arp114>
- Muruthi, P., Altmann, J., & Altmann, S. (1991). Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia*, 87(4), 467–472. <https://doi.org/10.1007/BF00320408>
- National Research Council. (1981). Techniques for sexing and aging primates. In *Techniques for the study of primate population ecology* (pp. 81–127). The National Academy Press. <https://doi.org/10.17226/18649>
- Nicolson, N. A. (1982). *Weaning and the development of independence in olive baboons* [Unpublished doctoral dissertation]. Harvard.
- Nieuwenhuijsen, K., Lammers, A. J. J. C., de Neef, K. J., & Slob, A. K. (1985). Reproduction and social rank in female stump-tail macaques (*Macaca arctoides*). *International Journal of Primatology*, 6(1), 77–99. <https://doi.org/10.1007/BF02693697>
- van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, 128(1), 137–142. <https://doi.org/10.1086/284547>
- van Noordwijk, M. A., & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, 40(1), 105–130. <https://doi.org/10.1007/BF02557705>
- van Noordwijk, M. A., Utami Atmoko, S. S., Knott, C. D., Kuze, N., Morrogh-Bernard, H. C., Oram, F., Schuppli, C., van Schaik, C. P., & Willems, E. P. (2018). The slow ape: High infant survival and long inter birth intervals in wild orangutans. *Journal of Human Evolution*, 125, 38–49. <https://doi.org/10.1016/j.jhevol.2018.09.004>
- Oftedal, O. T. (1984). Milk composition, milk yield and energy output at peak lactation: A comparative review. *Symposium Zoological Society of London*, 51, 33–85.
- Oftedal, O. T. (1991). The nutritional consequences of foraging in primates: The relationship of nutrient intakes to nutrient requirements. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 334, 161–170. <https://doi.org/10.1098/rstb.1991.0105>
- Oftedal, O. T., Jayawickrama, L., & Dittus, W. P. J. (unpublished). Is extended lactation nutritionally important for the weaning of toque macaques, *Macaca sinica* Manuscript? Evidence from milk composition.
- Pagel, M. D., & Harvey, P. H. (2002). Evolution of the juvenile period in mammals. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates* (pp. 28–37). University of Chicago Press.
- Paule, M. G., Li, M., Allen, R. R., Liu, F., Zou, X., Hotchkiss, C., Hanig, J. P., Patterson, T. A., Slikker, W., & Wang, C. (2011). Ketamine anesthesia during the first week of life can cause long-lasting cognitive deficits in rhesus monkeys. *Neurotoxicology and Teratology*, 33(2), 220–230. <https://doi.org/10.1016/j.ntt.2011.01.001>
- Pavé, R., Kowalewski, M. M., Zunino, G. E., & Giraudo, A. R. (2015). How do demographic and social factors influence parent-offspring conflict? The case of wild black and gold howler monkeys (*Alouatta caraya*). *American Journal of Primatology*, 77, 911–923. <https://doi.org/10.1002/ajp.22420>
- Phillips-Conroy, J. E., & Jolly, C. J. (1988). Dental eruption schedules of wild and captive baboons. *American Journal of Primatology*, 15, 17–29.
- Pianka, E. R., & Parker, W. S. (1975). Age-specific reproductive tactics. *The American Naturalist*, 109(968), 453–464. <https://doi.org/10.1086/283013>
- Pond, C. M. (1977). The significance of lactation in the evolution of mammals. *Evolution*, 31(1), 177–199. <https://doi.org/10.2307/2407556>
- Pond, C. M., & Mattacks, C. A. (1987). The anatomy of adipose tissue in captive Macaca monkeys and its implications for human biology. *Folia Primatologica*, 48, 164–185.
- Pontzer, H., Raichlen, D. A., Gordon, A. D., Schroepfer-Walker, K. K., Hare, B., O'Neill, M. C., & Ross, S. R. (2014). Primate energy expenditure and life history. *Proceedings National Academy of Science United States of America*, 111(4), 1433–1437. <https://doi.org/10.1073/pnas.1316940111>
- Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277, 828–831.

- Rajpurohit, L. S., & Mohnot, S. M. (1991). The process of weaning in Hanuman langurs *Presbytis entellus entellus*. *Primates*, 32, 213–218. <https://doi.org/10.1007/BF02381178>
- Rao, A. J., Ramesh, V., Ramachandra, S. G., Krishnamurthy, H. N., Ravindranath, N., & Moudgal, N. R. (1998). Growth and reproductive parameters of bonnet monkey (*Macaca radiata*). *Primates*, 39(1), 97–107. <https://doi.org/10.1007/BF02557748>
- Ratnayeke, S. (1994). The behavior of postreproductive females in a wild population of toque macaques (*Macaca sinica*) in Sri Lanka. *International Journal of Primatology*, 15(3), 445–469. <https://doi.org/10.1007/BF02696103>
- Rawlins, R. G., & Kessler, M. J. (1986). Demography of the free-ranging Cayo Santiago macaques (1976–1983). In R. G. Rawlins & M. J. Kessler (Eds.), *The Cayo Santiago macaques: History, behavior and biology* (pp. 47–72). State University of New York.
- Reitsem, L. J. (2012). Introducing fecal stable isotope analysis in primate weaning studies. *American Journal of Primatology*, 74, 926–939. <https://doi.org/10.1002/ajp.22045>
- Reitsem, L. J., & Muir, A. B. (2015). Growth velocity and weaning $\delta^{15}\text{N}$ “Dips” during ontogeny in *Macaca mulatta*. *American Journal of Physical Anthropology*, 157(2), 347–357. <https://doi.org/10.1002/ajpa.22713>
- Reitsem, L. J., Partrick, K. A., & Muir, A. B. (2016). Inter-individual variation in weaning among rhesus macaques (*Macaca mulatta*): Serum stable isotope indicators of suckling duration and lactation. *American Journal of Primatology*, 78(10), 1113–1134. <https://doi.org/10.1002/ajp.22456>
- Rhine, R. J., Norton, G. W., Wynn, G. M., & Wynn, R. D. (1985). Weaning of free-ranging infant baboons (*Papio cynocephalus*) as indicated by one-zero and instantaneous sampling of feeding. *International Journal of Primatology*, 6, 491–499. <https://doi.org/10.1007/BF02735572>
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirason, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381–391.
- Robinson, J. J. (1986). Changes in body composition during pregnancy and lactation. *Proceedings of the Nutrition Society*, 45, 71–80.
- Rogowitz, G. L. (1996). Trade-offs in energy allocation during lactation. *American Zoologist*, 36, 197–204. <https://www.jstor.org/stable/3884195>
- Rosetta, L., Lee, P. C., & Garcia, C. (2011). Energetics during reproduction: A doubly labeled water study of lactating baboons. *American Journal of Physical Anthropology*, 144, 661–668. <https://doi.org/10.1002/ajpa.21475>
- Rutenberg, G. W., Coelho, Jr., A. M., Lewis, D. S., Carey, K. D., & McGill, Jr., H. C. (1987). Body composition in baboons: Evaluating a morphometric method. *American Journal of Primatology*, 12, 275–285.
- Saxton, J. L., & Lotz, W. G. (1990). Growth of rhesus monkeys during the first 54 months of life. *Journal of Medical Primatology*, 19, 119–136.
- van Schaik, C. P., & Brockman, D. K. (2005). Seasonality in primate ecology, reproduction, and life history: An overview. In D. K. Brockman & C. P. Van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 3–19). Cambridge University Press.
- Scucchi, S. (1984). Interbirth intervals in a captive group of Japanese macaques. *Folia Primatologica*, 42, 203–208. <https://doi.org/10.1159/000156163>
- Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixon, A. F. (2002). Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, 23(1), 51–68. <https://doi.org/10.1023/A:1013245707228>
- Setchell, J. M., & Wickings, E. J. (2004). Social and seasonal influences on the reproductive cycle in female mandrills (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 125(1), 73–84. <https://doi.org/10.1002/ajpa.10375>
- Sigg, H., Stolba, A., Abegglen, J.-J., & Dasser, V. (1982). Life history of hamadryas baboons: Physical development, infant mortality, reproductive parameters, and family relationships. *Primates*, 23(4), 473–487. <https://doi.org/10.1007/BF02373959>
- Silk, J., Short, J., Roberts, J., & Kusnitz, J. (1993). Gestation length in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 14(1), 95–104. <https://doi.org/10.1007/BF02196505>
- Silk, J. B. (1990). Sources of variation in interbirth intervals among captive bonnet macaques (*Macaca radiata*). *American Journal of Physical Anthropology*, 82(2), 213–230. <https://doi.org/10.1002/ajpa.1330820210>
- Smith, T. M., Austin, C., Hinde, K., Vogel, E. R., & Arora, M. (2017). Cyclical nursing patterns in wild orangutans. *Science Advances*, 3:e1601517. <https://doi.org/10.1126/sciadv.1601517>
- Smuts, B., & Nicolson, N. (1989). Reproduction in wild female olive baboons. *American Journal of Primatology*, 19, 229–246.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268. <https://doi.org/10.2307/2389364>
- Stephansson, O., Dickman, P. W., & Cnattingius, S. (2003). The influence of interpregnancy interval on the subsequent risk of stillbirth and early neonatal death. *Obstetrics & Gynecology*, 102(1), 101–108. [https://doi.org/10.1016/s0029-7844\(03\)00366-1](https://doi.org/10.1016/s0029-7844(03)00366-1)
- Sugiyama, Y., & Ohsawa, H. (1982). Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatologica*, 39, 238–263. <https://doi.org/10.1159/000156080>
- Tait, D. E. N. (1980). Abandonment as a reproductive tactic—The example of grizzly bears. *The American Naturalist*, 115(6), 800–808.
- Takahashi, H. (2002). Female reproductive parameters and fruit availability: Factors determining onset of estrus in Japanese macaques. *American Journal of Primatology*, 57(3), 141–153. <https://doi.org/10.1002/ajp.10041>
- Takahata, Y., Suzuki, S., Agetsuma, N., Okayasu, N., Sugiura, H., Takahashi, H., Yamagiwa, J., Izawa, K., Furuichi, T., Hill, D. A., Maruhashi, T., Saito, C., Saito, S., & Sprague, D. S. (1998). Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: A preliminary report. *Primates*, 39(3), 339–349. <https://doi.org/10.1007/BF02573082>
- Tanaka, I. (1992). Three phases of lactation in free-ranging Japanese macaques. *Animal Behaviour*, 44, 129–139. [https://doi.org/10.1016/S0003-3472\(05\)80762-6](https://doi.org/10.1016/S0003-3472(05)80762-6)
- Tanaka, T., Tokuda, K., & Kotera, S. (1970). Effects of infant loss on the interbirth interval of Japanese monkeys. *Primates*, 11(2), 113–117. <https://doi.org/10.1007/BF01731136>
- Thompson, M. E., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73, 501–512. <https://doi.org/10.1016/j.anbehav.2006.09.007>
- Touitou, S., Heistermann, M., Schülke, O., & Ostner, J. (2021). The effect of reproductive state on activity budget, feeding behavior, and urinary C-peptide levels in wild female Assamese macaques. *Behavioral Ecology and Sociobiology*, 75, 128. <https://doi.org/10.1007/s00265-021-03058-5>
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. C. Campbell (Ed.), *Sexual selection and the ascent of man* (pp. 139–179). Aldine.
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249–264. <https://doi.org/10.1093/icb/14.1.249>
- Turnquist, J. E., & Kessler, M. J. (1989). Free-ranging Cayo Santiago rhesus monkeys (*Macaca mulatta*): I. Body size, proportion, and allometry. *American Journal of Primatology*, 19(1), 1–13. <https://doi.org/10.1002/ajp.1350190102>

- Valeggia, C., & Ellison, P. T. (2004). Lactational amenorrhoea in well-nourished toba women of Formosa, Argentina. *Journal of Biosocial Science*, 36, 573–595. <https://doi.org/10.1017/s0021932003006382>
- Valeggia, C., & Ellison, P. T. (2009). Interactions between metabolic and reproductive functions in the resumption of postpartum fecundity. *American Journal of Human Biology*, 21(4), 559–566. <https://doi.org/10.1002/ajhb.20907>
- Valeggia, C. R., & Ellison, P. T. (2001). Lactation, energetics, and postpartum fecundity. In P. T. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 85–106). Aldine de Gruyter.
- Wang, Y., Zeng, C., Chen, Y., Yang, L., Tian, D., Liu, X., & Lin, Y. (2022). Short interpregnancy interval can lead to adverse pregnancy outcomes: A meta-analysis. *Frontiers in Medicine*, 9, 922053. <https://doi.org/10.3389/fmed.2022.922053>
- Whitten, P. L. (1983). Diet and dominance among female vervet monkeys. *American Journal of Primatology*, 5, 139–159. <https://doi.org/10.1002/ajp.1350050205>
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, 100(916), 687–690.
- Williams, R. F. (1986). The interbirth interval in primates: Effects of pregnancy and nursing. In K. Benirschke (Ed.), *Primates, the road to self-sustaining populations* (pp. 375–386). Springer-Verlag.
- Winkvist, A., Rasmussen, K. M., & Habicht, J.-P. (1992). A new definition of maternal depletion syndrome. *American Journal of Public Health*, 82, 691–694.
- Womersley, J., & Durnin, J. V. G. A. (1977). A comparison of the skinfold method with extent of 'overweight' and various weight-height relationships in the assessment of obesity. *British Journal of Nutrition*, 38, 271–284.
- Zou, X., Patterson, T. A., Divine, R. L., Sadovova, N., Zhang, X., Hanig, J. P., Paule, M. G., Slikker, W., & Wang, C. (2009). Prolonged exposure to ketamine increases neurodegeneration in the developing monkey brain. *International Journal of Developmental Neuroscience*, 27(7), 727–731. <https://doi.org/10.1016/j.ijdevneu.2009.06.010>

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