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NEWS AND PERSPECTIVES

Paternal behavior in captive fat-tailed dwarf lemurs (*Cheirogaleus medius*) is preserved under socially relevant conditions

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Abstract

Fat-tailed dwarf lemurs (*Cheirogaleus medius*), primates endemic to Madagascar, are obligate hibernators that form stable, lifelong pairs in the wild. Given the temporal constraints imposed by seasonal hibernation, infant dwarf lemurs must grow, develop, and wean within the first two months of life. Maternal as well as paternal infant care, observed in the wild, has been deemed critical for infant survival. Given the importance of fathers' involvement in early infant care, we expect this behavior to persist even under captive conditions. At the Duke Lemur Center, in Durham NC, we observed two families of fat-tailed dwarf lemurs and focused on the behavior of adult males within the first two months of the infants' lives. We report evidence of paternal involvement, including babysitting, co-feeding, grooming, accompanying, and leading infants, consistent with observations from the wild. As expected, paternal babysitting decreased as infants gained independence, while co-feeding increased. Supplemental anecdotes, video recorded by observers, also highlight clear cases of involvement by both parents, and even older siblings, in safeguarding and socializing new infants. We argue that maintaining captive fat-tailed dwarf lemur populations under socially and ecologically relevant conditions facilitates the full expression of physiological and behavioral repertoires. Most importantly, it also allows dwarf lemurs to realize their species' potential and become robust proxies of their wild kin.

Keywords Duke Lemur Center · Hibernation · Pair-living · Primate

Introduction

Fat-tailed dwarf lemurs (*Cheirogaleus medius*) are unusual not only among primates but also among lemurs: They are small-sized, nocturnal, long-lived obligate hibernators (Dausmann et al. 2009; Fietz and Dausmann 2006). In the dry deciduous forests of western Madagascar, fat-tailed dwarf lemurs can hibernate for up to 7 months a year, which has consequences for life history traits (Lahann and Dausmann 2011). Indeed, because of hibernation, dwarf lemurs combine traits characteristic of species living in the "slow" and "fast" lanes (Blanco and Godfrey 2013). For instance, dwarf lemur females mate soon after emergence from hibernation, and experience short gestations and lactation periods (~2 months each) allowing time for fattening prior to the following hibernation season (Fietz and Dausmann 2006). Infants, generally twins or triplets, experience fast growth and dental development early in life (Blanco and Godfrey 2013), and by ~2 months of age, are fully weaned and begin to fatten in anticipation of their first hibernation (Fietz and Dausmann 2006). Unlike species on a fast track, however, young dwarf lemurs do not achieve adult size until they are ~2 years of age, and reproductive maturation may be delayed until after their second hibernation season, because growth and development are halted during hibernation (Blanco and Godfrey 2013; Müller 1999a). Adult dwarf lemurs can breed yearly, though they can skip reproduction in resource-challenging years (Lahann and Dausmann 2011). They also generally live long lives for animals of their size, with maximum recorded longevity extending to nearly 30 years in captivity (Blanco and Zehr 2015).

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Dwarf lemurs, like all primates, are social. Unfortunately, given their elusive nocturnal lifestyle, and the fact that they are often observed foraging alone, their sociality has generally been ignored (Müller 1999b; Petter et al. 1977). As far as social organization is concerned (sensu Kappeler 2019), fat-tailed dwarf lemurs form lifelong male–female pairs that defend a shared territory (Fietz 1999a; Müller 1999b). Their social groups may include subadult offspring from a previous year (Fietz 1999a; Müller 1999b).

For a hibernating species like dwarf lemurs, female-male pairs that jointly defend territories can better secure critical food resources at either end of the hibernation season: prior to hibernation when they must deposit enough fat stores to survive months-long periods without food or water, and after emergence from hibernation which coincides with the onset of the reproductive season. Hence, under hibernation constraints, involvement by both parents may be necessary for females to successfully reproduce and fatten and to ensure successful infant growth and development. In fact, field data support the infant care hypothesis (as described in Fernandez-Duque et al. 2020), and paternal care has been suggested as a driving factor in the evolution of pair-living in fat-tailed dwarf lemurs rather than a consequence of it (Muller 1999b; Fietz 1999a,b).

When new offspring are born, and for the first weeks of life, adult males (social fathers) are actively involved in infant care. At this time, infants are primarily "parked" inside tree holes and slowly begin exploring their surroundings. For the first two weeks after birth, "babysitting" duties are key: Babysitting allows lactating mothers to forage while males stay with the infants and vice versa. Moreover, while staying inside tree holes, males may keep the infants warm during cold nights (Fietz and Dausmann 2003). They can also defend infants from predators, as adults have been observed fighting and sometimes fending off snake attacks (Fietz and Dausmann 2003). Once infants begin exploring their environment outside of their tree holes, parents take turns accompanying and leading infants around and back to their nests. It has been proposed that the presence of fathers is not only beneficial but necessary for infant survival, as single mothers may be unable to keep young offspring alive (Fietz 1999a; Fietz and Dausmann 2003). As Fietz and Dausmann (2003, p251) stated "In *C. medius*, both sexes were observed to take care of their offspring: babysitting, playing and travelling with them, defending them and sleeping with them within nest holes during the day and responding to their calls". In contrast, older siblings were not observed to contribute to infant care (Fietz and Dausmann 2003).

Paternal involvement even extends to infants that may not be a genetic match to the social father (Fietz et al. 2000), highlighting the strong selection to preserve stable, territory-holding, female-male pairs (Fietz 1999a). Given the advantage of fathers' involvement in infant care, we expect this behavior to be inherent to the dwarf lemur repertoire, regardless of habitat conditions, including in captivity. The Duke Lemur Center (DLC), in Durham, North Carolina, currently maintains the only reproductive population of dwarf lemurs outside of Madagascar. We took advantage of a recently successful reproductive season at the DLC, with two family groups giving birth to triplets and twins respectively. We collected behavioral observations focused on the adult male of each family group. We predict that dwarf lemur fathers will show paternal behavior consistent with that of their wild kin in western Madagascar, including babysitting parked infants, co-feeding with foraging offspring, and showing various prosocial behaviors such as grooming and leading.

Methods

Subjects and housing

We observed two dwarf lemur families. Group 1 comprised 6 individuals: A male and female breeding pair, their subadult daughter from the previous year, and triplet offspring (3F) born on June 18th, 2021. Group 2 comprised a male and female breeding pair and their twin offspring (1 M, 1F) born on June 23rd, 2021. At the DLC, pregnant females are separated from their social groups into "baby cages" where they are provided with nest boxes and nesting materials in preparation for birth. Group members, including fathers, remain in visual and olfactory contact of the baby cage, and are slowly introduced to new infants at around two weeks of life. We began observations once family units were permanently re-established at 22 days of life for Group 1 and 16 days of life for Group 2.

Both groups were maintained in indoor, hexagonal observational rooms with a total volume of approximately 83 m^2 and a height of 5 m (Klopfer and Klopfer 1970). The rooms were furnished with wooden posts that held feed stations, natural branching and bamboo, nest boxes and various hanging sleeping sites. Because DLC dwarf lemurs do not have access to naturalistic "tree holes", we refer to sites with parked infants as "sleeping sites". Both rooms were maintained on a reverse and alternating "North-Carolina" like photoperiod, with white lights turning off at 11:30 each day. DLC husbandry policies require dwarf lemurs to be fed the first half of their daily diet within 30 min of "lights out". The second half of daily diets are typically provided around 4 pm. Fresh water was always freely available and changed daily.

Behavioral observations

We conducted continuous, focal observations of dwarf lemur fathers (Fig. 1) between July 9th and August 11th, 2021, when infants were between 16 and 54 days of life. We conducted 50 observation sessions split between groups that averaged 1.63 h in duration (range of 0.63–2.95 h). Observation duration varied, in large part, with observer availability and because we sometimes terminated sessions after prolonged periods of inactivity (i.e., when all family members were inside sleeping sites). All but two observation sessions began between 11:30 and 13:00 to capture the peak of activity. We did conduct two observation sessions in the afternoon hours and quickly learned that families were almost exclusively inside sleeping sites.

Our team of eight observers comprised two DLC research scientists (MBB and LKG) and 6 experienced volunteers. The two research scientists conducted nearly half of the observations ($n = 24$) and were responsible for training the volunteers to accurately score behavioral data. We tested a simple ethogram to record paternal behavior, partially adopted from Fietz and Dausmann (2003) (See Table 1). Indeed, given the sheer number of observers, we customized our ethogram specifically for the purpose of clarity. Both state behaviors, i.e., babysitting and co-feeding, were easily scored with certainty to the nearest minute. All other behaviors, clustered as "prosocial" were scored as events when the interactions between infants and the adult male were clear. Observers were trained to not score behaviors unless they were confident about the interaction.

At the DLC, all dwarf lemurs are habituated to human presence and are exposed to different staff and volunteers who feed, clean, and monitor individuals multiple times per day. All the observers were familiar with practices and protocols and had been working at the DLC for multiple years. In addition, DLC dwarf lemurs are easily identifiable by unique tail shaves (e.g., tip shave) or markings (e.g., white-tipped tail).

Each observation session was conducted by a single observer and individual observers conducted between 2–12 sessions each. At the start of each session, the observer turned on low, overhead red lights and wore a red-light headlamp. We recorded fathers as "out-of-view" when behavior could not be reliably assessed. We recorded additional anecdotes ad libitum of any other behaviors of potential interest for descriptions.

We first determined the duration of state behaviors and total occurrences of event behaviors per observation session. To account for differences in observation time, we divided these by total observation time corrected for any time the father was out-of-view. We thus report data as

Fig. 1 dwarf lemur "fathers" in **A** Group 1 and **B** Group 2 with one of the twins

Table 1 Ethogram of recorded paternal behaviors

Behavior	State or event	Definition
Babysit	State	Father is in sleeping site with minimally 1 infant.
Co-feed	State	Father feeds from same bowl with minimally 1 infant.
Approach	Event	Father moves towards infant in a purposeful manner.
Sniff	Event	Father touches infant with nose.
Groom	Event	Father runs toothcomb through the fur of an infant.
Lead	Event	Father encourages infant to follow him.

rates in minutes/observation hour or occurrences/observation hour. Given the small size of our dataset, we use simple descriptive statistics to compare paternal behaviors against infant age, as captured by continuous days and by binning observations into under 1 month of age (16–30 days) and over 1 month of age (31–54 days). For continuous age data, we performed linear regressions in GraphPad Prism for both males combined.

Ethical note

Our research protocols complied with the Duke Institutional Animal Care and Use Committee (IACUC) under protocol A213-20–11.

Results

Main findings

We observed clear evidence of paternal behavior exhibited by both dwarf lemur fathers. As expected, babysitting was the most observed and consistent paternal behavior. Infants under 30 days of age were babysat by fathers, either alone or with other group members present, on average for 29.1 and 31.7 min/h. Of this time, fathers babysat their offspring alone, on average, for 12.9 and 20.0 min/h (range 1.8–44.1 min/h). We recorded only one observation of infants under 30 days where fathers did not babysit alone at all. As expected, babysitting became less common as infants got older and became more independent ($F_{1,48} = 18.55$, $R^2 = 0.28$, $p < 0.001$; Fig. 2).

We observed fathers co-feeding with their offspring, a behavior that increased as infants got older and became more independent ($F_{1,48} = 11.04$, $R^2 = 0.19$, $p = 0.002$; Fig. 3). The first observation of infant-father co-feeding in our study was at 36 days for Group 1 and 28 days for Group 2. Infants over 30 days of age co-fed with their fathers, either alone or with other group members present, for 1.5 and 2.5 min/h on average. Fathers co-fed with their offspring alone, on average, for 1.0 and 1.7 min/h (range 0.0–6.1 min/h).

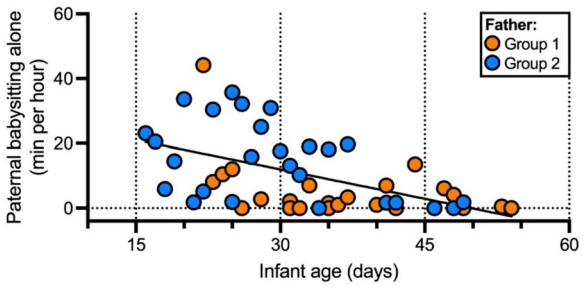

Fig. 2 Time spent babysitting alone by fathers (minutes per observation hour) relative to infant age (in days), for the fathers in Group 1 (orange) and Group 2 (blue). The solid line depicts the regression line

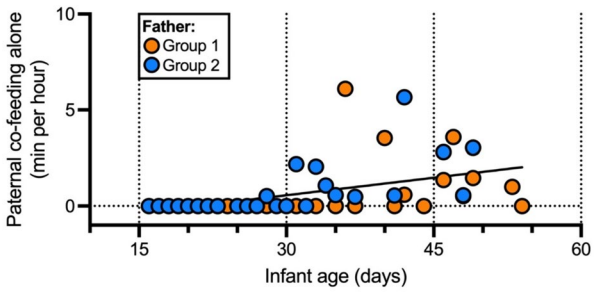

Fig. 3 Time spent co-feeding with infant/s alone by fathers (minutes per observation hour) relative to infant age (in days), for the fathers in Group 1 (orange) and Group 2 (blue). The solid line depicts the regression line

We observed fathers performing all the various prosocial behaviors in our ethogram across the study period, including approaching, sniffing, grooming, and leading their offspring. We recorded minimally one prosocial behavior by fathers in 36 out of our 50 observation sessions, with a range of 0.0–12.0 behaviors per hour. The father from Group 1 performed, on average 2.9 prosocial behaviors towards offspring per hour, whereas the father from Group 2 only performed 1.3 prosocial behaviors towards offspring per hour, perhaps reflecting a difference in the number of offspring per family (triplets versus twins).

Noteworthy anecdotes

Outside of our ethogram, we documented three particularly interesting anecdotes of paternal care, cooperative group care, and subadult play with infants. We describe these here and provide video clips of each anecdote in the supplementary material.

Anecdote 1 (52 s): Returning to the nest (link to Suppl. Mat. Video1). On July 10th, 2021, one of us (LKG) was observing Group 2. The infants were 17 days of age. One infant (presumably the female based on personality) was exploring the room and took a mild tumble down a few feet. The infant got up quickly, seemed a little unsure of her surroundings but did not audibly vocalize. The mother approached the infant, groomed her briefly, and left. At this point, the observer began video recording. Both parents approached the infant and guided her back to the sleeping site. The father is seen sniffing and grooming the infant while the mother leads. The father then used his snout to nudge the infant up a branch and steadied the infant on a vertical substrate using his hands. The infant followed the mother up the vertical substrate with the father following the infant. At one point, the infant paused along the way, and the father can be seen continuing to groom, sniff, and checking on the infant. The father then jumped ahead of the infant

and the infant followed him from the vertical to horizontal substrate near the nest. Both parents accompanied/guided the infant all the way back to the sleeping site. The second infant remained in the sleeping site the entire time. After this event, the father stayed in the sleeping site with both offspring minimally until the observation session ended.

Anecdote 2 (45 s): It takes a village (link to Suppl. Mat. Video 2). On July 16th, 2021, one of us (MBB) was observing Group 1. The infant triplets were 28 days of age, and already exploring their environment outside of their sleeping site. During one of the exploration trips, one of the infants found herself inside a horizontal bamboo branch positioned ~ 3 m high. This bamboo was placed as part of the structural branching of the room. The infant immediately appeared hesitant to exit the hole and other group members came to assist. The mother first appeared (seen on top of the branch, close to the hole) and then the infant's older sister (seen vertical on branch perpendicular to the bamboo). Seconds later the father came from behind the adult female. The mother and father moved away from the bamboo hole while the older sister approached the infant still inside. Once the infant began to exit the hole, the mother assisted her with her snout and father approached as well. Once the infant was out and moving around, all individuals dispersed.

Anecdote 3 (43 s): Older sister playing with two of the younger infants (link to Suppl. Mat. Video 3). On the same day as Anecdote 2, two of the triplets were playing in the corner of the "baby cage" (with door open to the larger room), hanging from a small horizontal branch. The older sister joined the playing session, and alternated between playing and grooming the infants, with particular emphasis on one of the triplets. This scene continued after the observer stopped video recording.

Discussion

By observing families of dwarf lemurs in captivity with new infants, we demonstrate clear involvement by fathers during the first two months of offspring life. During the first month, fathers spent considerable time babysitting offspring at their sleeping sites, providing lactating females opportunity to forage or engage in other behaviors unrelated to infant care. As offspring gained independence, fathers co-fed with their offspring while accompanying and leading them around their environment. The difference in the timing of co-feeding by the infants, about a week later for triplets in Group 1 compared to twins in Group 2, was likely due to the faster pace in growth and development in the smaller litter. By day 35, the twins had already fully erupted their first molar and weighed ~ 100 g each; in contrast, at the same age, two of the triplets were still erupting their first molar, and weighed, on average, 20 g less (Blanco, unpublished data).

Results from this study echo paternal behavior documented in the wild (Fietz 1999a,b), highlighting that under socially relevant conditions of stable family units with social contact among members soon after infants are born, captive dwarf lemurs can display "wild" behavior. We also documented involvement by subadult siblings in playing and grooming with new offspring. That the subadult sibling contributed to infant socialization in our study is noteworthy, as this behavior has not been reported in the wild (Fietz and Dausmann 2003). Given the challenges of observing dwarf lemurs in Madagascar, perhaps this behavior does occur but has yet to be documented. Alternatively, perhaps the greater food availability and environmental stability of captivity allowed the subadult to engage in social interactions.

That said, our study was limited by ongoing husbandry constraints that isolate mothers with new offspring from the rest of the family for the first weeks of life in small "baby cages". These practices are intended to promote maternal-infant bonding and ensure infant safety; however, they inhibited study fathers and older siblings from bonding with new infants and prevented fathers from participating in infant care during early life. We argue that paternal and sibling behaviors are necessary for bonding, socializing, and safeguarding infants during developmentally critical timeframes from birth onward. Follow-up studies could beneficially observe both parents and older siblings concurrently across infant development, to document family dynamics and discern the roles of each individual in rearing offspring.

We previously demonstrated that under ecologically relevant conditions of seasonal diets, food availability, and changes in ambient temperature-modeled after field observations- captive dwarf lemurs can achieve appropriate seasonal fattening, fat depletion, and express hibernation for more than 4 months a year (Blanco et al. 2021, 2022a, 2022b). DLC dwarf lemurs can thus respond to a variety of environmental perturbations in a predictable manner. This is somewhat remarkable, given that today's captive colony stems from only three original founders that arrived from Madagascar more than 50 years ago (Blanco et al. 2021).

For captive fat-tailed dwarf lemurs, facilitating the formation of lifelong pairs and associated behaviors including infant care by both parents may be as important as facilitating appropriate fattening and depletion and hibernation itself, with implications for individuals' wellbeing. Dwarf lemurs evolved to experience cycles of feast and fast, metabolic depression and seasonal reproductive schedules, solitary foraging and social learning. Taken together, our results call for greater consideration of species' ecological, social, and behavioral data from the wild, to inform species-specific husbandry practices. While recognizing the value of husbandry procedures in zoological institutions that focus on environmental stability and safety to avoid injury, we also acknowledge the importance of maintaining captive animals

under more "naturalistic" conditions to promote the full range of behavioral, social, and physiological repertoires. Balancing the risk of less human intervention while facilitating social learning, safely challenging physiological capacity, and perhaps tolerating some level of injury or short-term stress can, in turn, strengthen an often-neglected component of animal welfare: to allow individuals to experience their "ecological" potential and, in the process, become robust proxies of their wild counterparts.

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Author contributions MBB, LKG designed study; MBB, RB, LMD, LH, MM, JS, LW, LKG collected observational data; MBB, LKG analyzed data; MBB, LKG wrote the paper.

Data Availability Raw behavioral data used in this study can be provided by corresponding author on reasonable request.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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