Development of locomotion and social behavior in infants of the fat-tailed dwarf lemur *(Cheirogaleus medius)*

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Abstract

The development of locomotor activity and social behavior was observed in four *Cheirogaleus medius* infants from their first day of life until all patterns were fully developed (40th day of life) and until they entered their winter lethargy. These data were compared to the locomotor development of other prosimian species. The occurrence, frequency, and distribution of behavior patterns are discussed in relation to the winter lethargy.

Introduction

Cheirogaleus medius (Cheirogaleidae; Petter and Petter-Rousseaux 1979) belongs to one of the most primitive prosimian families. Except for Varecia and the Galaginae, they are the only prosimians that are nest breeders and whose mothers carry their infants with their mouths. Cheirogaleidae are strictly nocturnal and in the wild, *Cheirogaleus medius* apparently hibernate seasonally (Petter-Rousseaux 1980; Martin 1972). In captivity, they show a seasonal lethargy during which their locomotor activity is reduced by half (Foerg and Hoffmann 1982). During this period of lethargy their food intake and weight decrease significantly (Russel 1975). Their active season starts in spring; it includes the breeding season (40–50 days), gestation period (61 days), parturition, and early infancy (Foerg 1982). Depending on their time of birth, infants enter the winter lethargy (Sept.–Oct.) between their 6th and 16th week of life. In their winter lethargy, during their normally active period of the night, the animals rest in large groups in their nestboxes. The majority of their non-sleeping time during resting is spent in grooming (75 %), greeting (12 %) and play (10 %), whereas agonistic and submissive behavior contributes to only 3 % of their activity. Marking occurs only sporadically and no sexual behavior was observed (Foerg, unpubl. ethogram 1980). Infants are sexually mature and usually breed after their first winter lethargy (Foerg 1982).

It has only been recently that the first studies on the development of locomotion and behavior in prosimians have been published (Galago, Doyle 1979; Galago and slow loris, Ehrlich 1974; *Microcebus murinus*, Glatston 1979; Summary on maternal behavior in prosimians, Klopfer and Boskoff 1979). There has been no descriptive and quantitative study describing the early development of social behavior in prosimians in the wild or in captivity. Furthermore, it is not yet understood if and how factors such as a winter lethargy or hibernation may influence the early development and structure of social behavior in infant primates. We therefore describe and compare the development of locomotion and social behavior in *Cheirogaleus medius* infants from their first week of life until the onset of winter lethargy (10th week).

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Methods

Ethogram

The ethogram was obtained from observations of two groups of *Cheirogaleus medius* from October 1980 until December 1980. Each of the 11 animals of one group (family group) was observed for 1483 minutes (total: 271.8 *Cheirogaleus* hours) and each of the 4 animals of the other group for 478 minutes (total: 31.86 *Cheirogaleus* hours). The observation times were evenly distributed in both groups, both over the observation period (10/17/80 to 12/15/80) and over the daily activity phase.

Housing

All observations were conducted on individuals born and raised in captivity at the Duke University Primate Center (DUPC), Durham, North Carolina, USA. Normally *Cheirogaleus medius* are housed in large family groups; pregnant females are separated from their family just prior to parturition and housed in a smaller subunit of the large family cage system, usually providing at least 1 m^3 of space for mother and newborn infants. Every cage has several climbing poles, water and food trays, and a nestbox (30 × 20 × 20 cm).

All observations were conducted in the room where the animals are housed. Data collection began as soon as the animals appeared not to be disturbed by the presence of the observer. Since all observations were conducted in dim red light, the use of one-way mirrors or other devices that would allow remote observation was not feasible.

All *Cheirogaleus* at the DUPC are provided with artificial daylight and dim red light. The duration of day-night lengths is controlled by timers which are adjusted frequently to match outside conditions (36° N, 80° W). Humidity (70–80 %) and temperature (22°–27°) are kept constant throughout the year.

Subjects

During the first 10 weeks of observation, every mother was housed together with her infants (Groups 1–4, see figure). Magdalene's and Eunice's infants were observed from their second week of life until the end of the observation period. Both groups were reunited with an adult male in the 11th (Magdalene) and 13th (Eunice) week. The observations on Diaz' infant (Group 4) and Dorcas' infants (Group 1) were cancelled three weeks after their birth due to their deteriorating health.

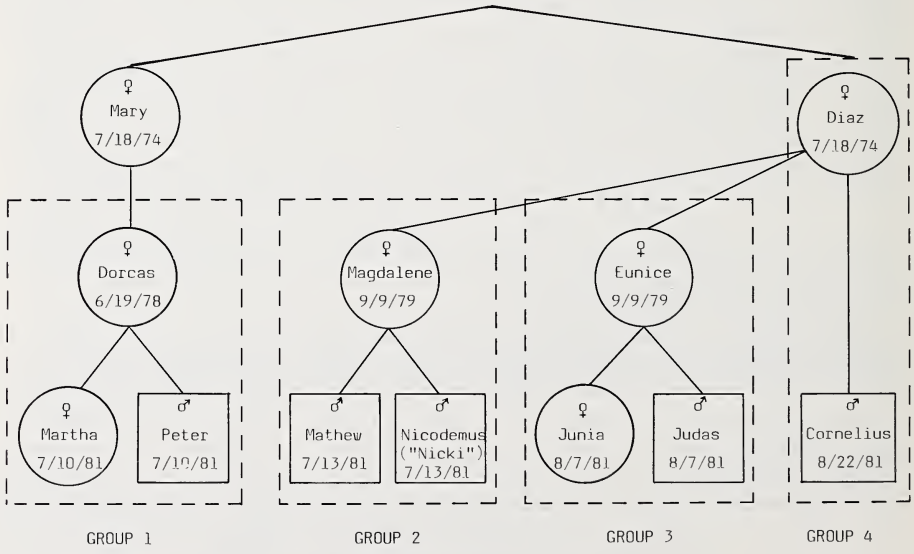

Fig. Group composition, sex, date of birth and origin of animals

Observations

The data to be discussed were derived from observations of: 1. Group 2: 2nd–11th week and 16th week of life of the infants, and 2. Group 3: 2nd–7th week and 13th week of life of the infants. During the last week of observation in both groups, the animals appeared to be well into their winterlethargy according to their overall activity and thus were not providing enough data for analyses of social interactions. Thereafter, observations were ended.

All animals were observed during their daily active period, usually during their second active phase when they were not eating. This phase occurs approx. 5–8 hours after the onset of darkness (Foerg and Hoffmann 1982). All activities and locations of animals were recorded for every animal in the group in 1 minute intervals over 10, 20, or 30 minute periods on checklists. Complex behavior patterns were dictated onto tape recorders and/or videotaped.

Group 3 was observed for a total of 2220 minutes (740 minutes/animal) and Group 2 for a total of 3600 minutes (1200 minutes/animal). The total observation time was evenly distributed over the study period for both groups. Locomotor activity of infants was recorded only over the first five weeks of development, i.e., until all patterns had developed.

Results

Early postnatal development

All infants (n = 7) were completely covered with fur when found a few hours after birth (2–6 hours) and had open eyes. Although newborns could not fully support their own body weight until their 6th day, they were able to crawl around in their nestbox. Several hours after birth, infants showed the ability to grasp and hold on to twigs and/or fingers, cage wire or poles, when put into their hand. They also were able to cling to the mother's fur. During the first week of life, the infants spent their entire time in the nestbox nursing and sleeping. Mothers left the nestbox only for food and water consumption. If disturbed by the observer, a mother would leave the nestbox carrying one of her infants with her in her mouth, holding the infant across its back close to the tail. This carrying behavior was observed to last up to 10 minutes, until the mother dropped the infant at a new place, usually a corner. Mothers initially remained with the dropped infant nursing it, and then returned to the other infant which had been left in the nestbox. The mother would sniff or shortly groom this infant and then return to the carried infant and become increasingly restless, running back and forth between both infants. At this point, observations were cancelled due to the mother's behavior. After the observer moved out of the mother's sight she would return the infant that had been removed back to the nestbox. While being carried, infants remained rigid, and after being dropped, would not leave that site. This behavior of mothers was observed only during the first four weeks of their infants' lives.

The first independent locomotor activity of the infants, not directed towards their mother, was crawling towards the nestbox exit and leaving the nestbox. This occured first on the 6th day in the female infant and on the 10th day in both infants of Magdalene. From this day on, infants increasingly left their nestbox, "explored" the environment, and returned to the nestbox. The infants started to chew on solid food between their 14th and 21st day, and lick on water bottles between the 27th and 39th day.

Until their 6th/7th week, the infants' defecation and urination was stimulated by their mother; she licked and groomed their ano-genital region until elimination occurred.

Development of locomotor behavior patterns

All active locomotor patterns used by adult *Cheirogaleus medius* were developed by the infants during the irst 40 days of their life. Crawling was observed first between the 6th and 16th day after birth, followed by climbing activity (13th–21st day), hopping (19th–39th day), more difficult climbing locomotion (20th–27th day), and at last, jumping

and running (27th–30th day). Except for "climbing pole", all locomotor activities occurred first in both infants in Eunice's group, Judas and Junia. They had shown all activity patterns within 21 days (6th–27th day), whereas Matthews and Nickis patterns not only appeared later but also their completion required 29 days.

Development of social behavior

The frequency of social activity/infant increased from 20 events/hour in the 3rd week to almost 35 events/hour in the 5th week, then decreased to an average of 28–30 events/hour from the 6th to the 9th week, and fell to an overall low of 10 events/hour in the 13th–16th weeks. The values for resting, evaluated as part of the total observed social behavior, indicate that resting in comparison to social behavior decreased from the 3rd to the 5th week, then increased again to an average level of 40 % of the total "activity" for the remainder of the observation period.

In two animals, every category of social behavior was observed during the observation period. The two other infants did not use agonistic behavior (Judas) or submissive behavior (Junia). Simple behavior patterns of marking, greeting, grooming, and play occured at least in two animals during the 3rd week of life, followed by agonistic and submissive behavior and eliminative rubbing. All categories, except eliminative rubbing and marking, appeared at least one week earlier in Eunice's group (Judas, Junia) than in Magdalene's group (see Table).

Table

First occurrence of social behavioral categories (weeks)

Category of behavior	First occurrence (week of life)			
	Judas ♂	Junia ♀	Matthew ♂	Nicki ♂
Marking	3	4	3	3
Greeting	3	3	4	4
Grooming (allomutual)	3	3	4	4
Play	3	3	4	5
Submission	5	–	6	6
Agonistic Beh.	–	5	9	7
Elim. Rubbing	13	7	6	6

Development of individual behavior patterns

Within 7 weeks (3rd to 10th week of life) most of the social behavior patterns of adult animals (n = 26) had appeared at least in some infants. Nursing as well as the various non-agonistic patterns of play behavior, grooming, and greeting together represented the majority of social interactions of infants during their first 10 weeks (91.3 %). Whereas nursing decreased steadily over time, the amount of play behavior rose during the first eight weeks to more than 50 % of the total social activity. Grooming and greeting, representing 15–20 % of the total social behavior over the first eight weeks, increased to 36 % in the 9th and 63 % in the 13th–16th weeks. The relative weekly frequency of submissive and agonistic behavior rose over the first 10 weeks, although constituting only 1.8 % of the total activity, and reached an average of 10.1 % in the 13th–16th weeks. Roughly two-thirds of the combined behavior had submissive character.

The relative frequency of marking behavior (licking, anogenital rubbing) in the first 10 weeks decreased in the 13th–16th weeks, whereas the relative frequency of adult elimination behavior with marking character (eliminative rubbing) increased over the last 5 weeks of the initial 10 week period ($\bar{x}$ = 3.5 %) to 10.6 % in the 16th week.

Play behavior

Play behavior represented the majority of all social activities from the 4th to the 10th week of life in *Cheirogaleus* infants. Wrestling, batting and biting behavior appeared in the 3rd week; all other patterns (jump, jump against, tail play, mount), except for chase, were observed at least once in the 4th week. The first three observed playing behaviors also represented the major part of the total play behavior over the observation period (together 73 %).

In Eunice's group, the infants developed all but one playing pattern (chase) within two weeks (3rd–4th), whereas the complete development of patterns in Magdalene's group took four weeks. 76.5 % of the infants' play in Magdalene's group was mutually directed and 23.5 % involved the mother. In Eunice's group only 12.3 % of the total play/week was directed towards the mother. Mounting, mounting-thrusting, and jumping against were used as single behavior patterns and used more often with the mother than with the sibbling. In later stages of development, the other playing patterns were used to form complex repetitive playing sequences such as: wrestling → beating → wrestling → biting → chasing → wrestling → chasing (Matthew-Nicki, 7th week). The sequences in Eunice's group were simpler, usually showing only 2 or 3 individual patterns. Both mothers never initiated any playing behavior or sequence.

Greeting behavior

Both forms of greeting behavior (nose-nose and nose-anal greeting) used by adult *Cheirogaleus medius* were observed in all three infant males during the first 10 weeks of life. Two of the three males used nose-nose greeting earlier (3rd and 4th weeks) than nose-anal greeting (5th week). The third male, Judas, showed nose-anal greeting only after his 7th week. We did not observe nose-anal greeting in the female at all. Except for two instances between brothers, all nose-anal greetings were directed towards the mother and, in the 16th week, towards the adult male. Nose-nose greetings were directed both against sibblings and mothers.

Grooming behavior

From the 3rd to the 5th week, autogrooming was the dominant form of grooming in all four infants. During the 6th and 7th week, autogrooming decreased, and after the 8th week, only allo/mutual grooming was observed. During the 6th and 7th week, both infants in Eunice's group showed no autogrooming, and switched earlier to allomutual grooming than Magdalene's infants did.

Marking and eliminative behavior

Although simple elimination without rubbing was almost never observed in adults, two infants (Matthew and Nicki) urinated and defecated during their 9th and 10th week.

All forms of eliminative rubbing and marking behavior (urinating-rubbing, defecating-rubbing, and urinating-defecating-rubbing) were primarily executed on the ground and on horizontal cage poles. There appeared to be no visual or social stimuli for the initiation of either behavior in an animal, nor did a marking or rubbing infant seem to elicit any immediate reaction in any other animal. There also seemed to be no preferred spot on the ground for marking or rubbing; all areas were marked or rubbed with the same frequency.

Agonistic and submissive behavior

A total of four agonistic behavior patterns (adult *Cheirogaleus*: 5) and five submissive behavior patterns occurred during the observation period. Biting (agonistic) and flight

behavior (submissive), both the most intense patterns of agonistic and submissive behavior, were not observed in infants. 75 % of all recorded events in these categories had submissive character.

The earliest developed submissive behavior pattern was squeaking (5th week), followed by leaving and openmouth behavior (6th week), teeth blecking (8th week), and finally chatter (16th week).

During the first two weeks of it's occurrence, squeaking was directed entirely against the mother, usually when she approached the infant suddenly or accidentally bit it while trying to carry it. Later squeaking as well as leaving and teeth blecking was directed against the sibbling. Most of the chatter occurred while being attacked by the group male in the 16th week.

Discussion

Contrary to *Cheirogaleus medius* infants other Cheirogaleid infants (*C. major:* Petter-Rousseaux 1964; *Microcebus murinus:* Glatston 1979) are born with their eyes closed. Whereas *Lepilemur mustelinus* (Petter-Rousseaux 1964; Petter 1965; Jolly 1966) and *Lemur catta* (Petter-Rousseaux 1964; Petter 1965) infants are very active at their 3rd and 4th days, *C. medius* infants showed no activity other than sleeping and nursing until their 6th day (earliest observation of active crawling). Infant transport by the mother (mouth transport) was observed until the 30th day, *Galago senegalensis* infants are carried up to their 56th day (Doyle et al. 1969). Interestingly, in *C. medius* one particular infant was always carried first. Whether the preference of the female infant to be carried first was incidental or strategical is yet unanswered due to the small number of observed infants.

The first occurrence of eating solid foods and drinking water appeared to be within the range of Galago infants (Ehrlich 1974; Doyle 1979), but much earlier than in Lorisinae and Lemuridae (Doyle 1979).

The development of locomotor activities in *Cheirogaleus medius* showed the same sequence of development as *Microcebus murinus* (Glatston 1979), with arboreal locomotion (climbing) being "exercised" first, followed by hanging, hopping, running, and jumping. Most interestingly *Cheirogaleus medius* infants, who reach their adult weight in their 10th week of life (Foerg 1982), also developed almost all social behavior patterns within their first 10 weeks of life.

So far there seems to be no other prosimian species being able to almost completely develop their set of social behavior patterns so early in life (3rd–13th week) and within such a short time span. We furthermore assume that the beginning of winter lethargy, if indicated by decreasing activity and increasing rest, in Eunice's group may have resulted in a shorter time period available for the infants, both daily and over the weeks. We suppose that two reactions to this rather limited time span were apparent in Eunice's infants: They a. not only developed almost all behavior patterns earlier in life, but b. also over a shorter period. Behavior patterns that represented only a minor fraction of the time budget in adult *Cheirogaleus medius* during their winter lethargy (marking, agonistic, and submissive behavior), did either not occur in early infancy or were hardly used in Eunice's infants in comparison to Magdalene's infants. We therefore suggest that *Cherogaleus medius* infants may be able to strategically "budget" their social development: if they are born late seasonally, they use most social and locomotor behavior patterns relatively earlier in life than infants born early and they develop the same number of social, nonagonistic patterns in a shorter time period, before entering winter lethargy.

Unfortunately, most results were obtained from only four infants due to the high mortality rate in captivity. We realize that these results must be regarded tentatively and strongly urge that more research be done on the behavior and ecology of Cheirogaleids.

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Zusammenfassung

Entwicklung lokomotorischer und sozialer Verhaltensweisen bei juvenilen Fettschwanzmakis (Cheirogaleus medius)

Bei vier Kindern des mittleren Katzenmakis *(Cheirogaleus medius)* traten innerhalb der ersten 10 Lebenswochen alle bei erwachsenen Tieren beobachteten lokomotorischen und fast alle sozialen Verhaltensweisen auf. Die Verhaltenskategorien Markieren, Kontaktaufnahme, soziale Körperpflege und Spielverhalten wurden zum erstenmal zwischen der dritten und vierten, agonistisches und Unterlegenheitsverhalten zwischen der fünften und neunten Woche beobachtet. Über den Beobachtungszeitraum hinweg nahm Spielverhalten den größten Teil des Gesamtverhaltens ein, agonistisches und Unterlegenheitsverhalten trat am wenigsten häufig auf. Die verschiedenen Verhaltensweisen einer Verhaltenskategorie, die bei erwachsenen Tieren zur gleichen Zeit beobachtet werden können, wurden bei Jungtieren mit unterschiedlicher Häufigkeit und sukzessiv auftretend zu verschiedenen Zeiten der Entwicklung beobachtet.

Gegen Ende September, 10 Wochen nach der Geburt der Kinder in Gruppe 2 und 7 Wochen nach der Geburt der Kinder in Gruppe 3, nahm die Gesamtaktivität bei allen Tieren ab und das Ruhen zu; dies zeigte den Beginn der Winterruhe an. Bei den Kindern der Gruppe 3 traten während der Entwicklungszeit fünf der insgesamt sieben Verhaltenskategorien mindestens eine Woche eher auf als in Gruppe 2, und die Ausübung einer bestimmten Verhaltensweise beschränkte sich auf einen kürzeren Zeitraum. Wir schließen daraus, daß Jungtiere von *Cheirogaleus medius* eventuell in der Lage sind, die Entwicklung ihrer Verhaltensweisen dem von der Geburt bis zum Eintritt in die Winterruhe zur Verfügung stehenden Zeitraum, unabhängig vom Zeitpunkt ihrer Geburt, anzupassen.

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Parturition and related behavior in wild American beavers *(Castor canadensis)*

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Abstract

Parturition in a family of wild American beavers *(Castor canadensis)* was observed in their natural lodge in two consecutive years. Behavioral and/or morphological characteristics of eight neonates, five yearlings and an adult pair before and during parturition are described and compared with analogous data gathered by other authors on captive beavers. It is shown that while beavers, with respect to parturition, definitely have many traits that are typical of precociality, they also possess a number of characteristics akin to altriciality, both in behavior and morphology.

Introduction

Speaking about Eutherians in her Ethology of Mammals, R. F. Ewer (1968) stated: "In general, if the adult normally occupies a protected lair or burrow, the young are altricial; if there is no such home and the limbs are not adapted to constructing one to cope with the special needs of the young, then they must needs be precocial. This correlation is shown very clearly in the rodents" (p. 245). Beavers, both the American *(Castor canadensis)* and the European *(C. fiber)* species are noticeable exceptions to that rule. According to all accounts found in the literature (references in Djoshkin and Safonow 1972; Jenkins and Busher 1979), beaver kits are born hairy and toothed, and their eyes open at most a few hours after birth: in these respects, they are precocial animals. However, they are born in their parents' protected home (e.g., the beaver lodge), in which they normally remain absolutely confined for 4–5 weeks: in this respect, they are literally "nidicolous" animals, in spite of their precociality. Exceptions are often very useful for understanding general rules. Considering the various correlates of altriciality and precociality (Dieterlen 1963; Ewer 1968), the behavioral study of parturition and ontogeny in beavers might contribute to a better characterization of these strategies in mammals.

The present paper deals with parturition. Incidental indications on behavior related to parturition in beavers are found in Grey Owl (1935), Wilsson (1971), Hirai (1975), Richards (1977), Doboszynska and Zurowski (1982). Shadle (1930) and Hediger (1970) have produced more substantial accounts on the topic. All these papers deal with captive or semi-captive individuals, and the question arises of possible "forcing" effects of keeping conditions on behavior (e.g., nest building or fitting, presence or absence of conspecifics with the mother and her kits, movements of neonates, etc.). The objectives of this paper are to present the results of observations made on parturition in wild American

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