Behavior and Ecology of Wild Slow Lorises (*Nycticebus coucang*): Social Organization, Infant Care System, and Diet

Dissertation
presented to the Faculty of Biology, Chemistry
and Geosciences of Bayreuth University in partial fulfillment of the
requirements for the degree of Doctor of Natural Sciences

by

Frank Wiens
from Frankfurt a.M.

February 2002
Bayreuth

This is a complete copy of the dissertation approved by the Faculty of Biology, Chemistry, and Geosciences of Bayreuth University in partial fulfillment of the requirements for the degree of Doctor of Natural Sciences.

The present dissertation was conducted at the Department of Animal Physiology, University of Bayreuth, between May 1995 and February 2002.

request for graduation submitted: 20.02.2002
date of the scientific presentation: 07.06.2002

1. referee: Prof. Dr. Dietrich von Holst
2. referee: PD Dr. Wolfgang Völkl

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Chapter 1

Allgemeine Einleitung

Auf der Welt leben etwa 200 Primatenarten. Die meisten von ihnen lassen sich einer von zwei klar abgegrenzten Gruppen zuordnen: Entweder den tagaktiven Primaten, die fast ausnahmslos gesellig lebend, oder den nachtaktiven Primaten, die alle solitär leben (*ca*. ein Achtel aller Arten). Während gesellige Primaten den größten Teil ihrer Aktivitätszeit in unmittelbarer Gegenwart von Artgenossen verbringen (Waser and Jones 1983), sind solitäre Primaten während ihrer Aktivitätsperiode meist allein unterwegs. Die Kenntnisse über das Verhalten der beiden Gruppen im Freiland, insbesondere über das Sozialverhalten, unterscheiden sich stark. Allgemein wissen wir nach etwa 70 Jahren systematischer Forschung von den geselligen tagaktiven Arten viel mehr als von den solitären nachtaktiven. Dafür gibt es offensichtlich methodische Gründe, denn die solitären nachtaktiven Primaten sind meist klein und verbringen fast ihre gesamte Zeit in Bäumen. Ein Einzelgänger von geringer Körpergröße, der sich im Dunkeln zwischen Blättern bewegt, kann ohne technische Hilfsmittel kaum beobachtet werden.

Die rezenten Primatenarten werden taxonomisch auf zwei Unterordnungen verteilt: die Anthropoidea (echte Affen) und die Prosimii (Halbaffen). Bis auf die Nachtaffen *Aotus* spp. gehören alle lebenden nachtaktiven Primaten zu den Prosimiern (tagaktive Prosimier sind unter den auf Madagaskar vorkommenden Lemuren zu finden). Die Prosimier ähneln den ausgestorbenen frühen Ahnenformen deutlich mehr als die anthropoiden Primaten. Die Nachtaktivität selbst gilt bei Säugern als ein ursprüngliches Merkmal, und vermutlich hat die überwiegende Zahl der nachtaktiven Prosimier im Laufe der Phylogenese seit dem ersten Säugerahnen nie ein tagaktives Stadium durchlaufen. Lediglich bei den lebenden Tarsiern *Tarsius* spp. deuten bestimmte Merkmale (z.B. das Fehlen einer lichtreflektierenden Schicht *Tapetum lucidum* im Augenhintergrund) auf tagaktive Formen in der Ahnenkette (Martin 1990).

Bis vor kurzem vermuteten die meisten Primatologen, dass die Evolution komplexerer Formen von Sozialität erst mit dem Übergang von der Nacht- zur Tagaktivität möglich

wurde, ja dass die soziale Evolution bei Primaten bzw. deren Säugerahnen überhaupt erst nach dem Übergang zur Tagaktivität begann (Charles-Dominique 1977; van Schaik und van Hooff 1983). Von den nachtaktiven Prosimiern nahm man folglich an, dass sie in bezug auf ihr Sozialverhalten keine oder zumindest keine wesentlichen evolutiven Änderungen gegenüber dem gemeinsamen Ahnen aller Säuger erfahren haben. Deshalb wurde ihnen bei der Entwicklung und dem Test von Hypothesen zu den ultimaten Ursachen der Sozialität bei Primaten meist nur wenig Aufmerksamkeit geschenkt. Diese Sicht der sozialen Evolution bei Primaten musste in den letzten Jahren jedoch korrigiert werden, nachdem neue Untersuchungen – teilweise mit Hilfe moderner Technologien wie Telemetriehalsbändern mit lange Strom gebenden Batterien (Gehrt und Fritzell 1998a, b), Nachtsicht- und Fernauslösekameras (Kruuk 1989) und hypervariablen, molekularen genetischen Markern (Waser *et al*. 1994; Gompper and Wayne 1996) – durchgeführt wurden. Die Unterschiede in der sozialen Organisation zwischen nachtaktiven solitären Prosimiern sind danach beträchtlich. Daraus muss man schließen, dass wichtige evolutive Veränderungen im Sozialverhalten unabhängig vom Übergang zur tagaktiven Lebensweise stattgefunden haben.

Die Primatologie steht damit vor zwei wichtigen, neuen Aufgaben. Erstens müssen die Kenntnisse vom natürlichen Verhalten nachtaktiver Primaten dringend vermehrt werden, denn es ist klar geworden, dass wir derzeit noch keinen vollständigen Überblick über das Spektrum der Verhaltensmuster von Prosimiern haben. Zweitens müssen für die evolutiven Veränderungen im Verhalten nachtaktiver Arten Erklärungen gefunden werden. Viele der derzeit diskutierten Hypothesen zur sozialen Evolution bei Säugern sind noch nie konsequent an nachtaktiven Primaten überprüft worden. Beiden Zielen, der Vermehrung des Wissens darüber, wie sich nachtaktive Primaten verhalten, und der Erklärung, warum sie sich so verhalten, ist die vorliegende Arbeit verpflichtet.

Die vorliegende Arbeit beschäftigt sich mit dem Verhalten und der Ökologie von freilebenden Plumploris *Nycticebus coucang*. Über den Plumplori und seine in der Unterfamilie Lorisinae (Loris und Pottos; Schwartz *et al*. 1998) zusammengefassten nächsten Verwandten gibt es besonders wenig Informationen aus dem Freiland. Lorisinen sind in mehreren Punkten außergewöhnlich: So scheinen direkte Kontakte zwischen Artgenossen extrem selten zu sein (Charles-Dominique 1977; Barrett 1984); die Reproduktionsraten wie die Stoffwechselraten sind sehr niedrig (Müller 1979; Müller *et al*. 1985; Rasmussen 1986);

und die Tiere bewegen sich nur relativ langsam mit eigentümlich fließenden Bewegungen - sie springen nie (Ishida *et al.* 1992).

Der Hauptteil der Arbeit gliedert sich in drei Kapitel. Diesen Kapiteln ist eine allgemeine Beschreibung des Plumploris (Kapitel 2), eine ausführliche Beschreibung des Untersuchungsgebietes (Kapitel 3) und eine Beschreibung der allgemeinen Methoden (Kapitel 4) vorangestellt. Kapitel 5 widmet sich der sozialen Organisation des Plumploris. Neben der Beschreibung der sozialen Beziehungen zwischen Artgenossen steht dabei die Frage nach den ultimaten Ursachen der gezeigten Sozialität im Mittelpunkt. In Kapitel 6 beschreibe ich erstens das Jungenaufzuchtsystem anhand der Beziehungen eines juvenilen Plumploris zu den älteren Artgenossen, mit denen er sein Wohngebiet teilt. Zweitens teste ich die Hypothese, dass Jungtiere beim Erwerb von Wissen oder Fähigkeiten, die im Zusammenhang mit der Ernährung stehen, auf ältere Artgenossen angewiesen sind. Kapitel 7 enthält eine Beschreibung der Nahrung des Plumploris und einen Test verschiedener Hypothesen, die den langsamen Lebensstil (charakterisiert durch langsame Bewegungen und niedrige Stoffwechsel- und Reproduktionsraten) in ursächlichen Zusammenhang mit der Nahrung bringen. Die Darstellung und Interpretation der Ergebnisse in den Kapiteln 4-7 ist so gehalten, dass jedes Kapitel für sich genommen verständlich ist. Alle dieser Einleitung folgenden Kapitel sind in englischer Sprache verfasst. Lediglich die abschließende Synopsis (Kapitel 8) ist wieder zweisprachig.

General Introduction

The primate order contains about 200 recognized living species. Most of these can be assigned to one of two separate groups: the diurnal primates, nearly all of which are gregarious, or the nocturnal primates which all live solitarily (*c*. one eighth of the species). While gregarious primates spend most of their active time in close proximity to conspecifics, solitary primates are mostly found alone during their active period (Waser and Jones 1983). A large difference exists in the level of our knowledge about the natural behavior, and in particular social behavior, of the two groups. Today, after 70 years of systematic primatological research, our knowledge about gregarious diurnal primates generally by far exceeds that about solitary nocturnal primates. There are obvious methodological reasons for this: solitary nocturnal primates are of small body size and are almost entirely arboreal. These features make observations without the use of technical tools nearly impossible.

The living primate species are taxonomically divided into two suborders, Anthropoidea ('higher primates') and Prosimii. With the exception of the night monkeys *Aotus* spp. all living nocturnal primates are prosimians (diurnal prosimians are some of the Malagasy lemurs). Prosimians are more similar to extinct ancestral forms than anthropoid primates. Nocturnality itself is assumed to be a primary mammalian feature. The majority of nocturnal prosimians probably never went through a nocturnal stage during the course of their phylogeny. Only the living tarsiers *Tarsius* spp. show features that hint towards diurnal ancestors (e.g. they lack a reflective layer *Tapetum lucidum* in their eyes; Martin 1990).

Until recently, most primatologists assumed that the evolution of more complex forms of sociality was only possible with the transition from the nocturnal to the diurnal lifestyle, and that social evolution in primates or their mammalian ancestors only started after the animals became diurnal (Charles-Dominique 1977; van Schaik und van Hooff 1983). Accordingly, it was assumed that the nocturnal prosimians have not undergone any, or at least not any substantial, evolutionary changes with respect to their social behavior compared to their common ancestor. Therefore, only little attention was paid to nocturnal prosimians in the development and the testing of hypotheses on the ultimate reasons for

primate sociality. However, in recent years this view on primate social evolution had to be corrected. New studies, some of which made use of advanced research tools, such as long-lasting radios (Gehrt and Fritzell 1998a, b), nightvision and remote cameras (Kruuk 1989), and hypervariable molecular genetic markers (Waser *et al*. 1994; Gompper and Wayne 1996), have revealed marked differences in social organization between nocturnal solitary prosimians. This suggests that important evolutionary changes in social behavior took place independently from any shift to a diurnal lifestyle.

Therefore, primatology finds itself confronted with two important new tasks. Firstly, the 'factual knowledge' about nocturnal species urgently needs to be widened because it has become clear that we still do not have a complete overview of the spectrum of behavioral patterns shown by prosimians. Secondly, explanations have to be found for the differences in the behavior between nocturnal species. Many of the currently discussed hypotheses on social evolution in mammals have never been consequently tested on nocturnal primates. The aims of the present study are both to discover new facts about how nocturnal primates behave and to find explanations for why they behave that way.

The present study is concerned with the behavior and ecology of wild slow lorises *Nycticebus coucang*. The slow loris and its closest relatives, grouped together in the sub-family lorisinae (lorises and pottos; Schwartz *et al*. 1998), are among the primates we know the least about. Lorisines are remarkable for several reasons. For example, direct contacts between conspecifics seem to be extremely rare (Charles-Dominique 1977; Barrett 1984); reproductive rates and metabolic rates are extremely low (Müller 1979; Müller *et al*. 1985; Rasmussen 1986); and animals move relatively slowly with peculiar floating movements - they never jump (Ishida *et al.* 1992).

The main part of the thesis is split into three chapters. These chapters are preceded by a general introduction (chapter 2), a detailed description of the study area (chapter 3), and a description of the general methods applied (chapter 4). In chapter 5 I detail the social organization of the slow loris. Besides a description of social relationships between conspecifics it centers around the possible ultimate reasons for the sociality shown. In chapter 6 I describe the infant care system, taking the relationships of one juvenile slow loris to the older conspecifics with whom it shares its home range as an example. Secondly, I test the hypothesis that diet learning by young depends on older conspecifics. Chapter 7 contains a description of slow loris diet, and a test of several hypotheses which assume a causal rela-

tionship between slow loris lifestyle (characterized by slow movements and low metabolic- and reproductive rates) and diet. The presentation and interpretation of results in chapters 4-7 is written in such a way, that each chapter taken alone is understandable. All chapters following this introduction are written in English. Only the concluding synopsis (chapter 8) is again bilingual.

Chapter 2

The Slow Loris and Its Closest Relatives

The slow loris *Nycticebus coucang* is a 500 to 1,500 g prosimian primate with a wide distribution in South and Southeast Asia, inhabiting tropical forests from the Phillipine Islands, Borneo, Java, and Sumatra to Vietnam, South China, and Assam on the Asian mainland (Napier and Napier 1967; Groves 1971; Lekagul and McNeely 1977; Petter and Petter-Rousseaux 1979; Fooden 1991; Timm and Birney 1992). In Laos, Vietnam and South China the congeneric pygmy slow loris *Nycticebus pygmaeus* also occurs. The status of a third species from China, *Nycticebus intermedius,* is still debated (Zhang *et al*. 1994).

The genus *Nycticebus* has been placed in the family Lorisidae, the extant members of which are divided into two subfamilies, the Galaginae and the Lorisinae (Rasmussen and Nekaris 1998). All lorisids are strictly nocturnal and arboreal. Like all other nocturnal prosimians except the three species of tarsiers *Tarsius* spp., the retina contains an extra layer *tapetum lucidum* that enhances the ability to see at night by 'recycling' all incoming light (Fleagle 1988). The slow loris bright orange 'eye-shine', i.e. the reflection of incident light from a powerful light-source like a strong torchlight from the eyes, is visible over a distance of several hundred meters. In addition to sharp nightvision at night, lorisids are equipped with excellent olfaction (Schilling 1979). In lorisids, the two canines and four incisors of the lower jaw are pointed and almost horizontal. This dental structure, which is also found in all Malagasy lemurs, other than the aye-aye *Daubentonia madagascariensis*, has been termed 'toothcomb' or 'toothscraper'. The name toothcomb (Buettner-Janusch and Andrew 1962) refers to its frequent use in grooming. However, a number of species have been observed using it to scrape off gum (Martin 1979).

The subfamily Galaginae includes the African bushbabies or galagos, fast runners and agile leapers with long tails. Bushbabies communicate at night-time using loud cries resembling the cry of a newborn child, hence their name. In contrast, the members of the subfamily Lorisinae which includes the genus *Nycticebus*, the slender loris *Loris tardigradus* from India and Sri Lanka, and the potto *Perodicticus potto* and angwantibo *Arcto-*

cebus calabarensis from Africa (Schwartz *et al*. 1998) always move smoothly and deliberately. Most of the time substrate contact is maintained with at least three limbs. Even though they can develop considerable speed while walking or climbing, there is never a floating phase in the stride and they never jump (Ishida *et al*. 1992). Their hands and feet have reduced second digits and their limb arteries and veins form *retia mirabilia* (Osman-Hill 1953; Cartmill and Milton 1977; McArdle 1981). Both features allow them to keep a powerful grip on the substrate in all situations and for prolonged periods of time. They are probably part of an energy-saving strategy that also includes low metabolic rates (Hildwein 1972; Hildwein and Goffart 1975; Goffart 1978; Müller 1979; Müller *et al.* 1985). Unlike bushbabies, lorisines are remarkably silent (Petter and Charles-Dominique 1979). All lorisines have a short muzzle and small ears; the tail is short or absent. Various aspects of the biology of lorisines have been explored in some detail by observing captive animals, but information from the field is generally extremely scarce. They seem to be among the most solitary primates, i.e. conspecifics seem to congregate extremely rarely, even though the home ranges of neighboring animals may overlap considerably. Lorisines do not shelter in tree hollows or nests (Jewell and Oates 1969; Petter and Hladik 1970; Charles-Dominique 1977; Barrett 1984; Nekaris 2000). Furthermore, there is indication that the diets of all species include a relatively broad spectrum of different food types: arthropods, molluscs, small vertebrates, fruit, gum, and other plant exudates (Fooden 1967, 1976; Jones 1969; Lim *et al*. 1971; Charles-Dominique 1977; Barrett 1984). Compared with other mammals of similar size, members of the subfamily have low reproductive rates characterized by small litters (twins or singletons; slow lorises have young in singletons), long interbirth intervals, long gestation periods, extended periods of offspring dependency, and a late age at first reproduction (Rasmussen 1986).

Prior to the present study, only two quantitative field studies on the natural behavior of slow lorises have been conducted – both in Malaysia. This is probably due to the difficulties associated with following the nocturnal movements of slow lorises through the often dense rainforest. The first study, by Barrett (1984), compared gross features of slow loris ecology with those of sympatric flying squirrels, Petauristinae, and palm civets, Paradoxurinae. Barrett attempted to radio-tag slow lorises, but of the two transmitters he managed to attach to two different individuals, one was lost after two days, and the other ceased signaling after five nights. The second study, by myself (1995), was a radio-tracking case

study focusing on the movements and behavior of one female slow loris with the main intention of assessing the amount of locational data needed to adequately describe the home range.

Chapter 3

Study Area

I studied slow lorises between May 1995 and July 1999 within an 11-km^2 strip of coastal land in Manjung District, Perak, West-Malaysia (4° 18' N, 100° 34' E). The area included parts of the Segari Melintang, Tanjung Hantu and Batu Undan Forest Reserves as well as the village Labuan Bilek and surrounding land (Fig. 1). To the west the area is bordered by plantation land, to the south by river delta, to the east by sea, and to the north by forested area. Elevation reaches from sea level to 60 m above sea level. The mean annual rainfall over the years between 1951 to 1999 is 1,785 mm. There is a rainy season (north-east monsoon) typically lasting from October to December and a short dry season typically lasting from June to July (unpublished records of the Malaysian Meteorological Service for Sitiawan town, 4° 13' N 100° 42' E). Marked deviations from this pattern can occur during El Nino Southern-Oscillation (ENSO) events as happened in 1997 and 1998. Due to ENSO the study area experienced unusually long drought periods from January to June 1997 and February to April 1998, as well as much heavier rainfalls than usual in May and December 1998 (unpublished records of the Malaysian Meteorological Service for Sitiawan town).

Vegetation within the forest reserves is lowland dipterocarp forest and freshwater alluvial swamp forest (Whitmore 1984). One part of Segari Melintang Forest Reserve contains unlogged primary dipterocarp forest (Perak Virgin Jungle Reserve No 1, totalling 408 ha; Putz 1978), the remainder is logged-over forest. Labuan Bilek is small a small village with about 15 small houses that are sparsely distributed over an area of 18 ha. Vegetation in and around Labuan Bilek is more open secondary padang savanna (Whitmore 1984) intermixed with some crop trees like coconut palms *Cocos nucifera*, cashewnut trees *Anacardium occidentale*, and kapok tree *Ceiba petandra*.

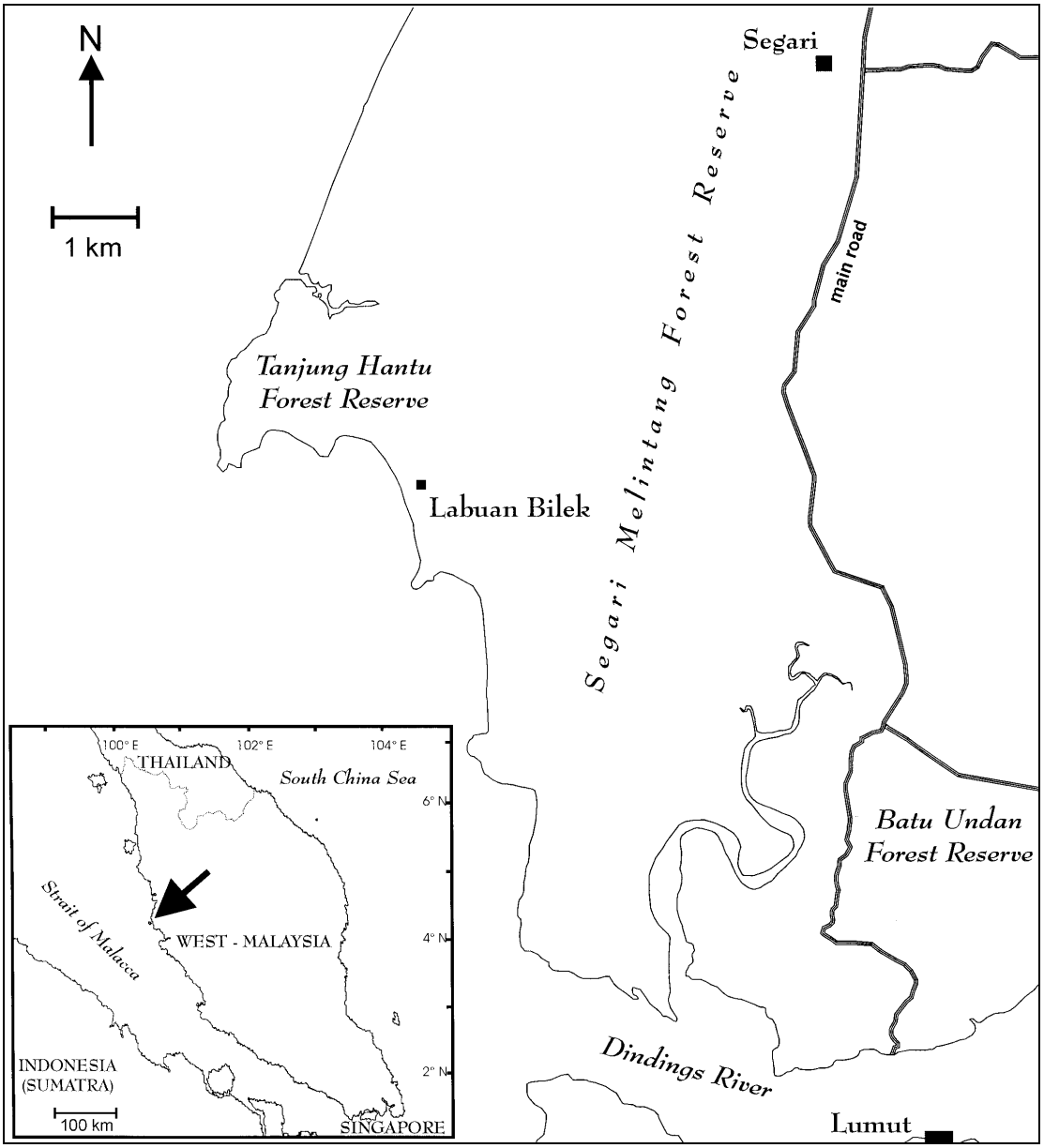

Fig. 1. Map of the strip of coastal land illustrating the location of the three forest reserves and the village Labuan Bilek where I conducted the study. The small map in the lower left corner shows Peninsular Malaysia and part of Sumatra with the study area indicated by the tip of the arrow.

At least with respect to arboreal species the mammalian community of the three forest reserves was largely intact, including top predators such as the clouded leopard *Neofelis nebulosa*. Density of slow lorises in one part of Segari Melintang Forest Reserve containing unlogged primary forest reached *c.* 80 individuals/km^2. In the other parts of the study area

densities seemed to be lower (pers. obs.), but they were probably everywhere higher than the maximum of 20 individuals/km^2 reported for the Malay Peninsular by Barrett (1981).

Sunrise in the area is between 0702 and 0733 hours. Sunset is between 1900 and 1934 hours.

Chapter 4

General Methods

CAPTURE

I caught 33 slow lorises in 84 total captures/recaptures (cap./recap.). I captured slow lorises by hand (42 cap./recap.), using wiremesh live traps baited with banana and hung in trees (37 cap./recap.), or specially designed traps that were mounted so as to cover the inflorescences of the bertam palm *Eugeissona tristis* (5 cap./recap.), where slow lorises often fed (chap. 7). Up to 200 wiremesh live traps were set simultaneously for a total of 800 nights (n = 40,000 trap nights). Trapping rate for slow lorises in these traps was 1 capture/1,081 trap nights. I tried to catch slow lorises by hand only if the circumstances seemed particularly well suited (when the animal was on the ground or on an isolated tree or branch). Of the special traps set up around bertam palm inflorescences there were a maximum of ten in use at any given time. They had to be triggered by hand and were mainly intended for recapturing radio-collared animals (see below).

I weighed newly caught slow lorises, sedated them with an injection of dissolved tiletamin and zolazepam (11-18 mg/kg body mass), and marked them individually with subcutaneously implanted transponders (Trovan, EURO I. D., Weilerswist, Germany). Age, gender and in females, reproductive state, were then recorded. I classified slow lorises as infants or subadults according to the following criteria: infant: Fur containing long hairs with white tips, body mass ≤ 350 g; subadult: body mass > 350 g, teeth white and unworn, no or little wear on inner surfaces and nails of hand and feet, fur containing long hairs with white tips, nipples short in females indicating a nulliparous animal. I found these physical differences correlated with marked shifts in the relationship between offspring and mother (chap. 6). Slow lorises with body mass > 500 g, stained and worn teeth, wear on hands and feet, short fur without white tips, elongated nipples or signs of pregnancy in females were classified as adults. When milk could be squeezed from the nipples I recorded females as lactating. I took a number of standard morphometric measurements, including head and body length

(in stretched position on a plane), and testis length and width. Data on testis length and width were used to calculate the volume of the spherical ellipsoid (Kappeler 1997)

$$\text{Volume} = \pi \times L \times W^2/6$$

where L = testis length and W = width of one testis. I averaged multiple morphometric measurements for each individual, excluding measurements of female body mass taken during periods of gestation, and compared adult males with females. I also examined each individual for injuries and ectoparasites.

RADIO-TRACKING

I fitted 22 adult or subadult slow lorises (9 male, 13 female) as well as one male infant slow loris with collar-mounted transmitters (Biotrack Ltd., Wareham, UK) weighing about 12 g and 2 g respectively and tracked these animals on 451 days/nights for a total of *c.* 1,000 h (400 h at daytime and 600 h at night-time) during six tracking sessions (Table I).

Table I. Date range and duration of the six sessions during which radio-tracking of slow lorises was conducted at Manjung

Radio-tracking session No	Date range		Duration	
	Start	End		
1	11 May 1995	9 August 1995	3	months
2	7 January 1996	9 December 1996	11	months
3	8 July 1997	22 October 1997	3.5	months
4	11 March 1998	29 May 1998	2.5	months
5	10 August 1998	11 December 1998	4	months
6	4 March 1999	28 June 1999	3.5	months
		total	**27.5**	**months**

I conducted tracking by approaching on foot using a four-element Yagi antenna and a portable Yaesu FT-290 R II receiver until I observed the animal directly ('animal sighting') or until I identified the exact location of the animal. Usually this was the tree, palm, shrub,

or liana (hereafter 'trees') they were staying in. I obtained a total of 2265 locations, 1418 at night and 847 at daytime. I saw slow lorises during 52% of all nocturnal locational efforts; 17% of all daytime locations were sightings. I tagged locations, recorded them to the nearest meter (referring to the trunks of trees), and plotted them on a 1:1,000 map. In very rare cases (4% of all locations) when an animal was moving too fast to follow through rough terrain I approximated its location by triangulation and plotted the location onto the map. I collected data on two or more individuals suspected to share parts of their home ranges in the form of scans: individuals were located immediately after one another to obtain fixes with a minimum lag-time. I term two individuals with suspected home range overlap a dyad. Additionally, I located selected individuals outside normal scans (1) in order to follow movements of focus animals when they were outside their usual area; (2) to observe in more detail (with higher frequencies) what happened in certain situations, e.g. when animals entered or left sleeping sites; and (3) for long-lasting visual observations. All nocturnal locations of individuals with suspected home range overlap were usually recorded within a maximum time window of 30 min. Only when it became clear during a scan that an animal was very far away (> 2 x maximum home range diameter for a given habitat) from the other focus animals, was tracking of it abandoned, and the animal was recorded as absent. This happened exclusively in subadult animals with fixed home ranges (chap. 5, chap. 6) during occasional dispersal-related excursions out of the areas they resided in, and in one animal without a fixed home range that moved over a very large area. The exact location of animals recorded absent during a scan was determined after completion of the scan. During radio-tracking nights I usually collected an average of 2 fixes/individual. However, I conducted nine tracking sessions that covered the entire night from dusk until dawn. During those full night sessions I collected an average of 18 data points per individual (range: 12 - 25). Night-time scans were distributed evenly across all hours of the night. When two animals were in the same or in neighboring trees I estimated the distance between them to the nearest meter. I considered locations and absence records of different animals recorded within the same day, for diurnal data, and within a 30-min time interval, for nocturnal data, 'simultaneous'. I considered consecutive data points on any one animal 'independent' (*sensu* Lair 1987) when separated by > 2 h of the scotophase, 2 h being the time required by a slow loris to cross the length of an average home range. I considered consecutive scans 'independent' when consisting entirely of independent data points.

DIRECT OBSERVATIONS

During each animal sighting I scored the first behavior seen as an instantaneous observation (Altmann 1974). I also recorded whether any conspecifics were visible in the space surrounding a focus animal, and the behavior of such individuals as well as their distance from the focus animal. Radio-collared slow lorises that were regularly followed habituated quickly and could be observed at night without obvious disturbance even at distances < 5 m. During daytime lorises were more sensitive to my presence. Therefore, I approached animals very carefully and retreated as soon as possible after noting the location and behaviors of animals. I grouped behavioral records into four categories: resting, feeding, social interaction, or other. Behavior was scored as resting when an animal remained sitting for > 1 min. Feeding was defined as swallowing, chewing, or bringing animal prey or plant material to the mouth. In some cases where the behavior could not be seen clearly because of vegetation and foliage obstructing the view, feeding was scored because the pattern of movement in combination with falling fruit or flowers indicated that the animal was doing so. Whenever an animal was feeding, the particular food item was recorded. I considered a behavioral act shown by an individual as part of a social interaction with conspecifics if it was obviously caused by the presence or the behavior of one or several other slow lorises. I recorded sequences of behavior and observations not recorded as instantaneous observations *ad libitum*. I limited the duration of visual observations on each animal in a nocturnal scan to only a few minutes in order to be able to locate all focus group members within 30 min. If the animal did not disappear from sight sooner I terminated an observation opportunistically after a maximum of 12 min. Longer lasting observations were conducted outside scans. For quantitative analysis I used only instantaneous records. I conducted direct observations with the help of binoculars and a 4.5-V headlamp.

STATISTICAL ANALYSES

In general, parametric statistics were the preferred method for analyzing data sets. I tested data against a normal distribution using Kolmogorov-Smirnov tests. For data that were not normal, I used nonparametric statistics. I conducted most analyses with the SPSS program (SPSS Inc.). All probabilities reported here are two-tailed and statistical significance was

accepted at the $\alpha = 0.05$ level. Data are reported as means and standard deviations unless stated otherwise.

Chapter 5

Social Organization

Group-Living in the Slow Loris and the Routes towards Sociality Open to Solitary Mammals

INTRODUCTION

Solitary mammals spend most of their active time away from conspecifics (Waser and Jones 1983). The opposite of solitary is gregarious. Gregarious mammals are those that spend most of their active time with conspecifics (for other definitions of solitary and solitary *vs*. gregarious see e.g. Sandell 1989; Jarman and Kruuk 1996).

Similarly to their gregarious counterparts, many solitary mammals are known to maintain networks of social relationships, manifesting themselves in regular friendly interactions. Long-lasting social relationships organize populations of some of these solitary species into social systems that, at least on an abstract level, are very similar to the social groups found in gregarious mammals. Gregarious mammals live in social systems that differ widely in many aspects both within and between species, but all share the property that some form of co-operation occurs between co-members. Intrinsic factors, namely co-operative benefits from jointly defending food resources against conspecifics (Wrangham 1980), joint defense of mates (Packer and Pusey 1982), joint defense against predators (van Schaik and van Hooff 1983), increased vigilance (Rasa 1987), joint hunting (Bowen 1981), or alloparenting (Macdonald and Moehlman 1982) are thought to be responsible for an individual's decision to live together with conspecifics. In contrast, the social systems of solitary mammals have for a long time been regarded as being much more uniform and much less complex (Charles-Dominique and Martin 1970; Martin 1972; Alexander 1974; Eisenberg 1981; van Schaik and van Hooff 1983; Fleagle 1988). It has also been assumed that there is a large difference between solitary and gregarious mammals in the proportion of time that individuals spend with conspecifics; i.e. solitary mammals are thought to spend

much less than 50% of their active time together with conspecifics (Leyhausen 1965). In many solitary species there are either no obvious co-operative benefits from joint actions or inter-individual interactions, or the apparent benefits have been ruled out as being of importance for an individual's decision to share space with conspecifics (Carr and Macdonald 1986; Kruuk 1989; Woodroffe and Macdonald 1993; da Silva *et al*. 1994).

There is now good reason to believe that at least some of the purported basic differences between solitary and gregarious mammals are reflective of bias in the methods applied. Solitary mammals are generally difficult to observe without technical tools. They are mostly nocturnal, often small in size and in many cases arboreal. The collection of very detailed data on the social organization of solitary mammals has only become possible since the introduction of advanced research tools such as long-lasting radios (Gehrt and Fritzell 1998a, b), night vision and remote cameras (Kruuk 1989), and hypervariable molecular genetic markers (Waser *et al*. 1994; Gompper and Wayne 1996) over the last few years or decades. Since then we have been increasingly discovering a great diversity in sociality of solitary species within mammals as a whole and within mammalian orders. In various mammal species previously regarded as classic solitary species, higher rates of direct inter-individual encounters than expected have been found (Caro 1994; Waser *et al.* 1994; Sterling and Richard 1995; Gehrt and Fritzell 1998a; Kays and Gittleman 2001). This suggests a continuum between solitary and gregarious mammals with respect to time spent alone rather than a large difference. In slender mongooses *Herpestes sanguineus*, typically a species with very low association rates (Rood 1989), certain males associate frequently, probably to exclude other males from access to females within a common territory (Waser *et al.* 1994). Also in other solitary species 'gregarious tendencies' seem to be related to co-operative behaviors formerly believed to be exclusively found in 'truly gregarious' mammals (Gehrt and Fritzell 1998a; Kays and Gittleman 2001). This raises the possibility of similar 'routes' to sociality in both solitary and gregarious mammals, i.e. in both groups an individual's decision to live together with conspecifics may depend on co-operative benefits gained directly from the presence of conspecifics.

There may be other routes towards a social life. There remains a number of well-studied solitary species, such as the European badger *Meles meles*, where direct interactions between conspecifics sharing space or joint actions are extremely rare and co-operative benefits from such behaviors seem to be at best marginal (Woodroffe and Macdonald

2000). In the case of the European badger it has been suggested that not intrinsic factors but ecological constraints exerting selective pressures towards nondispersal of offspring are responsible for an individual's decision to share space (Woodroffe and Macdonald 1993; da Silva *et al.* 1994). Newly independent individuals are assumed to be forced to stay at home in order to gain access to a critical resource that is not a conspecific. In this scenario any benefits obtained directly from the presence of conspecifics have been considered a consequence rather than an evolutionary cause of space-sharing among conspecifics (Carr and Macdonald 1986; Kruuk 1989; da Silva *et al*. 1994; Woodroffe and Macdonald 1993, 2000). One resource that is often limited and the distribution of which seems to be the best predictor for the density and number of members of badger social units is suitable den sites for breeding and overwintering (Doncaster and Woodroffe 1993).

Here I report on the social organization of the slow loris *Nycticebus coucang*, a nocturnal prosimian primate. The only two previous systematic studies on slow loris behavior in the wild indicated extremely low rates of direct encounters between conspecifics despite them apparently sharing large parts of their home ranges, but provided no further details on slow loris sociality (Barrett 1984; Wiens 1995). However, in captivity slow lorises can be housed together in groups consisting of a male and several females and females seek friendly contact with each other (Ehrlich and Musicant 1977, Rasmussen 1986; Ehrlich and MacBride 1989). Wild slow lorises do not seem to use common shelters like nesthollows. The present study describes six critical elements of slow loris social organization: home range sizes, home range overlap, association rates, form of direct interactions, feeding behavior, and dispersal (all elements are described for adult and subadult individuals only; relationships between infants and older animals are described in chap. 6). The ultimate goal was to find clues as to why, under natural conditions, slow lorises, which seem neither to be able to derive substantial co-operative benefits from the presence of conspecifics nor to be 'forced' to share space with conspecifics by a limited availability of shelter sites, may decide to live a social life.

METHODS

Home Range Analyses

I used area-observation plots (Odum and Kuenzler 1955) to identify slow lorises with locations adequate to describe the full home range for any of the six tracking sessions (chap. 4): I calculated home range area using the minimum convex polygon (MCP) estimator (Mohr 1947 as reviewed by Worton 1987) for 3, 4, 5,..., *n*, where *n* is the number of independent locations for a slow loris. Prior to this, I removed unusual locations from movements that were obviously related to dispersal from the datasets of subadult individuals (dispersal-related movements showed a typical pattern that was easy to identify during radio-tracking, see RESULTS). Only if the resulting curve reached an asymptote did I include the data in further analysis of home ranges. Moreover, slow lorises for which I collected < 20 independent locations per tracking session were excluded from home-range analysis. For each of the remaining 13 adult or subadult slow lorises I calculated home range sizes with the MCP method using the Ranges V computer program (Kenward 1990). To exclude outlying points from a MCP and prevent a few extreme and atypical points from contributing a large additional area, I used a 95% MCP. This included using 95% of the independent data points lying closest to the arithmetic mean center of the range.

I conducted home range analyses separately for each tracking session. Home range overlaps were calculated for dyadic combinations of slow lorises that were tracked synchronously (during the same session) by overlaying the contours of two 95% MCPs. Overlap between home ranges of two different individuals, ranges A and B, is given two-directionally: as percentage overlap of range B on A, and of A on B.

For three slow lorises (two males and one female) I obtained data from more than one period, i.e. two periods. Two-directional overlap between the two home ranges of the same individual was averaged to obtain a measure of home range stability.

Average sample size used for analyzing single home ranges was 70 ± 28 (n = 18, range: 29-114) independent locations.

Time Budgets

I calculated the time spent for each nocturnal activity as proportion of all independent nocturnal instantaneous sightings. Slow lorises for which < 5 such observations were made were excluded from analyses. I pooled all observations for each of the remaining 15 individuals (total independent nocturnal sightings per individual 31 ± 22, range: 7-78) and calculated an average proportion of time spent for each activity per individual. I defined being alone as being further than 10 m away from any conspecific.

Dyadic Analyses of Association within Fixed Distances

Home range analyses showed home range overlap for eight dyads of adult and subadult slow lorises representing 11 different individuals. Where possible for these dyads I compared frequencies of association within certain fixed distances with expected values generated from null models of associations. I calculated observed frequencies of association as simple ratios (Cairns and Schwager 1987) of the number of occurrences of a given association in independent scans to total number of independent scans. I selected three critical distances: 50 m, 10 m, and 1 m. I selected a distance of 50 m because I assumed it to be the furthest at which two slow lorises can sense each other. 50 m has been suggested to be the furthest distance at which two pottos *Perodicticus potto* can smell each other in the forest environment (Charles-Dominique 1977). The potto is closely related to the slow loris and both species' olfactory senses can be expected to be similarly developed (Kollman and Papin 1925; Stephan 1966). The distance at which two slow lorises can see each other in the often dense vegetation is probably much shorter. I assumed it to be 10 m, which was the reason for selecting a critical distance of 10 m. Given the precision of the estimates of distances between individuals 1 m was the best value to indicate that two animals had physical contact. I calculated associations within critical distances for two different diel segments: daytime (within 1 m only) and central night-time (1 m, 10 m, and 50 m). I defined daytime as the period between sunrise and sunset and central nighttime as the period between 2 hours after sunset and 2 hours before sunrise. Proportions of central nocturnal time were calculated rather than proportions of the total nocturnal time between sunset and sunrise in order to avoid bias from movements to and from places where animals slept together during the day. The mean number of independent simultaneous pairs of locations per

dyad for both diel segments together was 65 ± 53 (*n* = 8, range: 31-192). I derived expected values from the distribution of the distances between all possible pairs of locations on the two animals in question with Doncaster's (1990) DYNAMIC software.

RESULTS

Morphometric Data

Adult males were significantly heavier than adult non-pregnant females (average male body mass: 737 ± 111 g, *n* = 8; average female body mass: 637 ± 61 g, *n* = 11; *t*-test: *df* = 17, *p* = 0.023).

Head and body length did not differ between male and female adults (average male head and body length: 292 ± 9 mm, *n = 8*; average female head and body length: 293 ± 5 mm, *n* = 11; *df* = 17, *p* = 0.896).

I compared testis volume and body mass of slow lorises with equivalent data from captive individuals of 18 species of prosimian primates (*Cheirogaleus medius, Microcebus murinus, Mirza coquereli, Hapalemur griseus, Lemur catta, Eulemur coronatus, Eulemur fulvus, Eulemur macaco, Eulemur mongoz, Eulemur rubriventer, Varecia variegata, Galago moholi, Otolemur garnettii, Otolemur crassicaudatus, Perodicticus potto, Loris tardigradus, Nycticebus coucang, Nycticebus pygmaeus*; Kappeler 1997). With Kappeler's data set, Fietz (1999a) calculated a regression line with body mass as the independent and testis volume as the dependent variable. The relationship of this model was significant and explained 51.9% of the variance (Fietz 1999a; Fig. 2). Adult male slow lorises at Manjung had a mean testis volume of 1,499 ± 285 mm^3 (*n* = 8). The regression gives an expected testis volume of 1,730 mm^3 for this species. Thus, testis volume of wild slow lorises is 13% below the value predicted for strepsirhine primates. Captive slow lorises had an average testis size of 1,434 mm^3 and an average body mass of 1,243 g (*n* = 8). Testis volume of captive animals is 45% below the predicted value (Fig. 2).

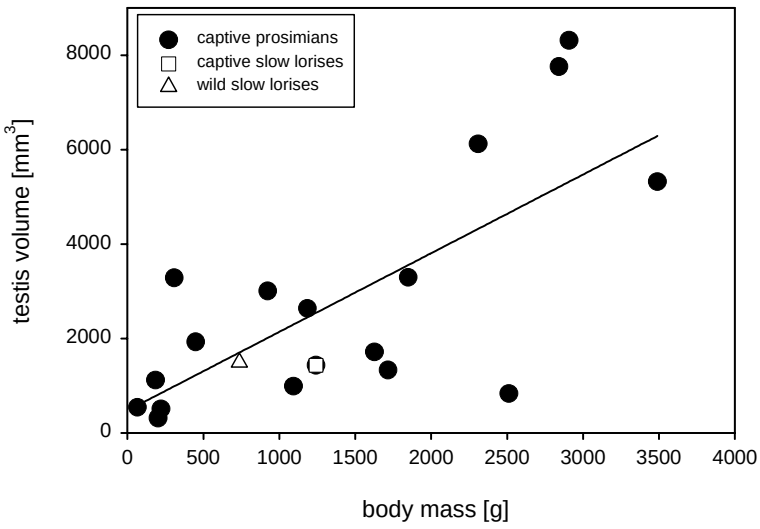

Fig. 2. Relationship between body mass and testis size in prosimian primate species. (equation $y = 1.7x + 477$). The relationship of this model is significant ($R^2 = 0.269$, $p < 0.001$). After Fietz (1999a); added are wild slow loris data from the present study.

Injuries and Ectoparasites

I found injuries of some form on the majority of slow lorises. Twenty-four percent of subadult and adult animals ($n = 29$) had one or several fingers or toes that were broken or stiff. These injuries seemed to be a result of 'accidents' without involvement of other animals. Injuries likely to be inflicted by bites from conspecifics were wounds on the head (around the snout, on the forehead and around the ears) and around the tail. Fifty percent of males had fresh or old wounds, while wounds were found on only 12% of females (difference was significant; Fisher exact test: $p = 0.033$; $n_{males} = 12$, $n_{females} = 17$)

Ectoparasites found on slow lorises were ticks (suborder Metastigmata; at various places on the body), mites (suborder Mesostigmata; in the ears) and lice (order Mallophaga; in the fur). I found small numbers of ticks on all captured slow lorises during rainy periods. I found mites on two individuals, one adult male and one adult female. Two other slow lorises had lice, one adult male (male CHR, the only identified individual that was not member of a social unit, see below) had large numbers (>50), and one infant had small numbers (<10) of lice.

Home Range Analyses

Of the 22 radio-tracked adult and subadult slow lorises, I removed nine from home range analysis because they either had < 20 independent fixes in all tracking sessions (three males, five females) or failed to exhibit an asymptotic component to their home range (one male). The sizes of the MCP home ranges of the remaining 13 slow lorises are shown in Table II. There was a great variability between individuals, with the smallest home range being only 1.6% of the largest (95% MCP of adult male ALI in Padang savanna: 25.0 ha; 95% MCP of adult female AHM in primary forest 0.4 ha; Table II).

Table II. Group composition, tracking periods, 95% minimum convex polygon (MCP) home range and home range overlap sizes for slow lorises at Manjung. Three letter codes represent individual slow lorises (see text and Fig. 4). Fixes are number of locations used to construct the MCP

	Tracking period		95% MCP Home	Per cent overlapped by:			
	Start date	End date	range ha (fixes)	Male	Female	Subadult1	Subadult2
group A primary forest							
Male UNM	seen 27/04/99, not caught		-	-	-	-	-
Female YVO	05/09/98	11/12/98	3.8 (109)	-	-	32.8	20.0
	04/03/99	25/06/99	3.0 (92)	-	-	40.2	47.0
Subadult1 female DEV	27/10/98	11/12/98	1.5 (114)	-	83.5	-	17.6
	04/03/99	25/06/99	1.4 (65)	-	84.6	-	50.5
Subadult2 female VRE	07/09/98	11/12/98	0.8 (102)	-	100.0	34.2	-
	04/03/99	25/06/99	1.4 (113)	-	100.0	50.9	-
Infant ERN	07/04/99	25/06/99		reported in chap. 6			
group B primary forest							
Male ULI	06/09/98	08/12/98	0.8 (60)	-	38.1	-	-
Female AHM	19/09/98	08/12/98	0.4 (54)	80.6	-	-	-
Subadult1	seen 16/10/98, not caught		-	-	-	-	-
group C logged over forest							
Male GER	02/03/96	09/12/96	5.6 (66)	-	83.8	-	-
	08/07/97	18/09/97	8.9 (53)	-	-	22.7	-
Female JAC	20/05/96	09/12/96	4.8 (50)	97.8	-	-	-
Subadult1 male PAU	15/08/97	22/09/97	2.8 (36)	70.6	-	-	-
Subadult2	seen 09/09/97, not caught		-	-	-	-	-
group D Padang savanna							
Male ALI	11/05/95	08/08/95	19.0 (56)	-	-	36.1	-
	07/01/96	26/05/96	25.0 (87)	-	39.4	-	-
Female DAI	05/02/96	26/05/96	10.4 (82)	94.6	-	-	-
Subadult1 male BOO	13/05/95	08/08/95	11.9 (29)	56.8	-	-	-
Subadult2 female FAT	caught 22/07/95, not radio-collared			-	-	-	-
Infant H	caught 14/03/96, not radio-collared			-	-	-	-
slow lorises not belonging to any of the above groups all from logged over forest							
Subadult female CON	19/05/95	09/08/95	7.6 (36)	-	-	-	-
Female INA	27/04/96	09/12/96	4.1 (47)	-	-	-	-

Home range sizes in group D from open habitat were biggest (mean: 14.8 ha), followed by group C from logged-over forest (mean: 5.0 ha), and groups A and B from unlogged primary forest ($mean_{group\ A}$: 2.0 ha; $mean_{group\ B}$: 0.6 ha; Fig. 3). This indicates that variation may be primarily due to habitat differences.

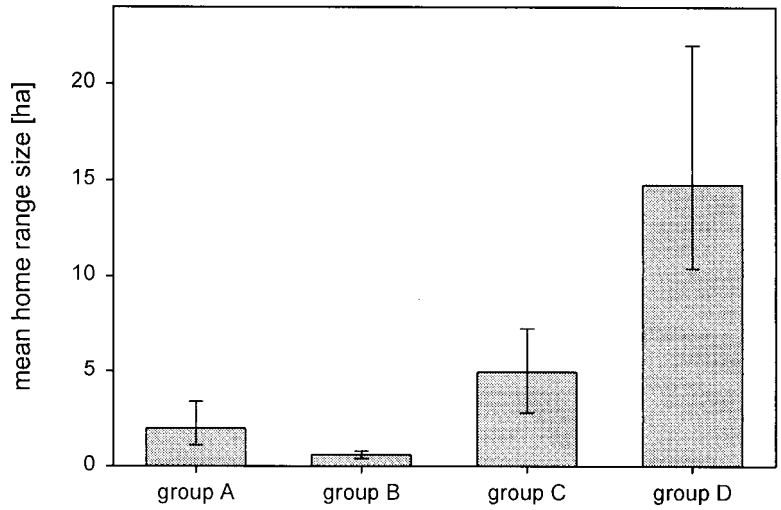

Fig. 3. Mean (minimum, maximum) size of adult and subadult slow loris home ranges for 4 different spatial groups. Group A (n = 3) and B (n = 2) lived in unlogged primary forest, group C (n = 3) in logged-over forest and group D (n = 3) in more open Padang savanna. Minimum and maximum values are shown in Table II.

Home range sizes and outlines of the same individual showed broad overlap between different tracking sessions for three adult slow lorises examined. Symmetrical home range overlap was 75.3% for the male ALI (duration of break between tracking sessions compared: 5 months), 77.9% for the male GER (duration of break between tracking sessions compared: 7 months), and 82.2% for the female YVO (duration of break between tracking sessions compared: 3 months; home range sizes, see Table II; home range outlines for the males ALI and GER, see Fig. 4).

Spatial Grouping Patterns

Even with so much effort spent on trapping the animals, I never managed to capture all slow lorises present in a given area at one time and fit them with radio-collars. Some slow

lorises seemed to have systematically avoided entering traps and capture by hand was a matter of pure chance. As a result simultaneous tracking of all individuals sharing a common area was not possible. Nonetheless, some consistent patterns emerged from the locational data obtained: None of the 13 radio-collared slow lorises with a fixed home range used its home range exclusively. This was suggested by data on radio-collared slow lorises as well as by chance visual observations of uncollared slow lorises made during tracking of focal animals. However, I never positively identified same-sexed adult slow lorises sharing their home range with another. Also, I never positively identified adults sharing their home range with more than one adult of the opposite sex.

Patterns of home range sharing showed consistencies in four designated spatial groups living in three different habitats. A total of 11 of the 13 individuals with fixed home ranges could be assigned to one of these groups. Each spatial group consisted of one adult male, one adult female, and up to three younger individuals (two subadults and one infant). Home ranges overlapped extensively among all dyadic combinations of individuals from the same spatial group for which data allowed such analysis (Table II, Fig. 4). The home ranges determined for the only two neighboring groups monitored (group A and group B) showed virtually no overlap (Fig. 4a). In group A the female, but not the male, was radio-tracked. However, an adult male and an adult female were tracked synchronously in the other groups (groups B, C, D). In all three cases the males' home ranges were larger than the females' and the females' home ranges laid almost entirely within the males' (Table II, Fig. 4a,b,c).

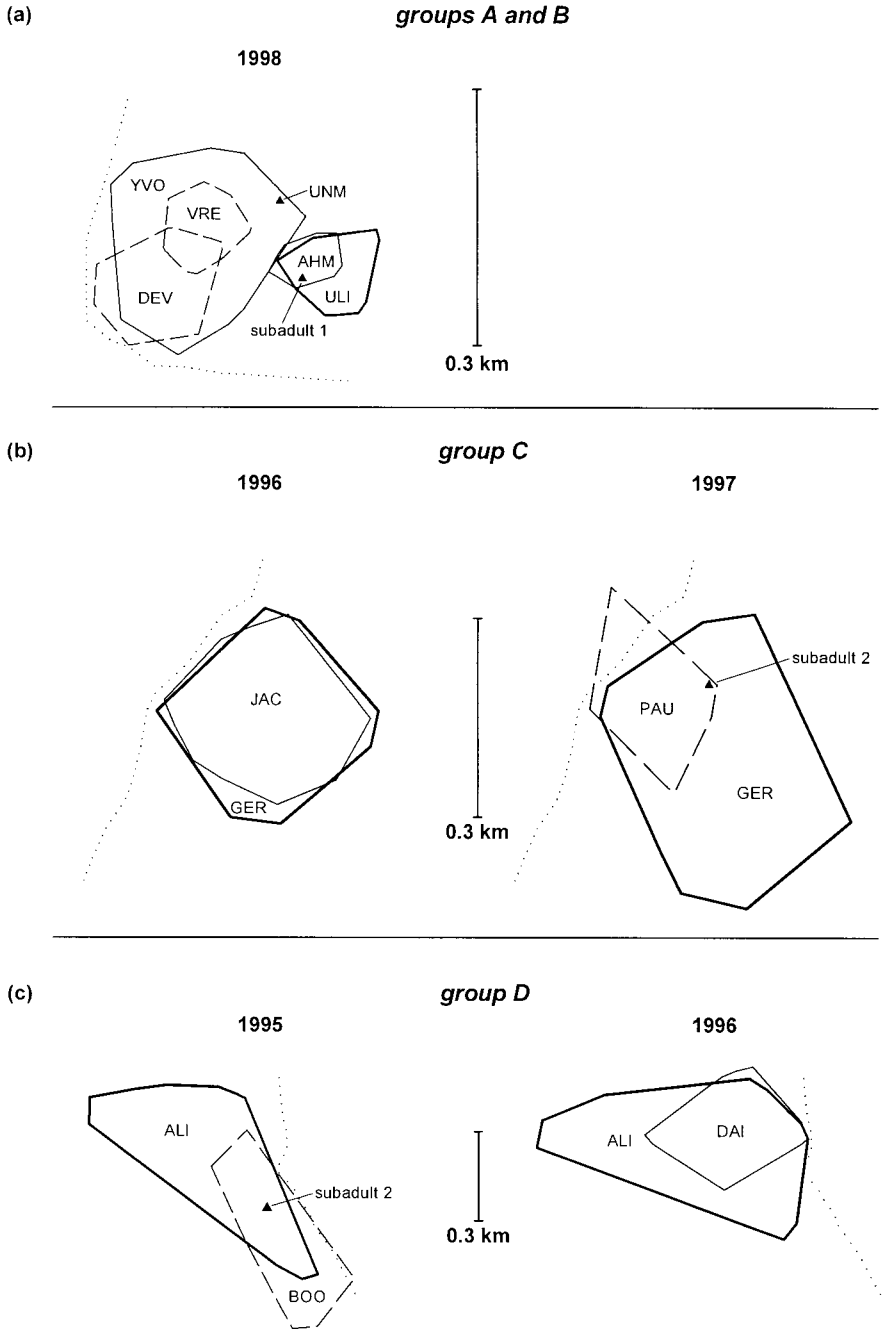

Fig. 4. Home range outlines (95% MCP) and points of capture (indicated by triangles) or chance observations for synchronously tracked slow lorises in three different subplots: (a) individuals from groups A and B during the later 1998 tracking session; (b) individuals from group C during the 1996 and 1997 tracking sessions; (c) individuals from group D during the 1995 and 1996 tracking sessions. Three-letter codes represent individual slow lorises (see text). Thick lines represent home range outlines for adult males. Thin lines represent home range outlines for adult females. Home range outlines for subadults are drawn in dashed lines. The irregular dotted line through the plots is an old logging road.

However, not all individuals were members of a spatial group. One young adult male (male CHR), for which 58 and 12 independent locations were recorded during two tracking sessions, occasionally used the same area as group A without showing signs of a special attachment to this or any other area; i.e. area-observation curves showed no asymptotic component.

In group A some of the geneological relationships between individuals were known: at least the younger of the two subadult females (subadult VRE) as well as the infant (infant ERN) were offspring of the adult female (female YVO; see also chap. 6).

Activity Patterns

Slow lorises were exclusively nocturnal and became active soon after sunset. The earliest time I ever recorded an active slow loris was 2 min before sunset. The latest time I observed an active slow loris was 14 min before sunrise. Slow lorises were active for most of the time between sunset and sunrise (hereafter 'active time'). Resting only made up an average of 5.4 ± 1.6% (n = 15) of active time. Time spent resting did not differ significantly between the sexes (Mann-Whitney U test: z = -0.818, p = 0.413; n_{males} = 7, $n_{females}$ = 8), or between adults and subadults (z = 0.124, p = 0.901; n_{adults} = 10, $n_{subadults}$ = 5).

Slow lorises spent an average of 93.3 ± 5.4% (n = 15) of their active time alone. Time spent alone did not differ significantly between the sexes (z = -0.350, p = 0.726; n_{males} = 7, $n_{females}$ = 8), or between adults and subadults (z = 0.987, p = 0.329; n_{adults} = 10, $n_{subadults}$ = 5).

Slow lorises spent an average of 20.5 ± 12.1% (n = 15) of their active time feeding. There was no significant difference in the time spent feeding between the sexes (z = -0.347, p = 0.728; n_{males} = 7, $n_{females}$ = 8), or between adults and subadults (z = 0.858, p = 0.391; n_{adults} = 10, $n_{subadults}$ = 5).

Daytime Sleeping

During the daytime slow lorises slept exclusively in trees above ground. I identified 426 different sleeping sites (trees: 73.7%; palms: 19.2%; shrubs: 5.9%; lianas: 1.2%) on 768 different occasions. The height above ground of sleeping lorises ranged from 1.8 m to 35.0 m. In ten days animals used an average of 7.4 different sleeping sites (±1.8, n = 16 slow lorises of which >10 independent daytime fixes were collected). There was no signifi-

cant difference in the average number of different sleeping sites used in ten days between the sexes (two-way ANOVA: $F_{(1,12)} = 0.466$, $p = 0.508$), or between adults and subadults ($F_{(1,12)} = 0.142$, $p = 0.713$). The maximum number of successive days a tree was used for sleeping was 2. The number of available sleeping sites for any slow loris was probably large; i.e. can be expected to be >60. This is indicated by the logistic regression describing the number of independent daytime fixes by the number of different sleeping sites (trees) used (Fig. 5).

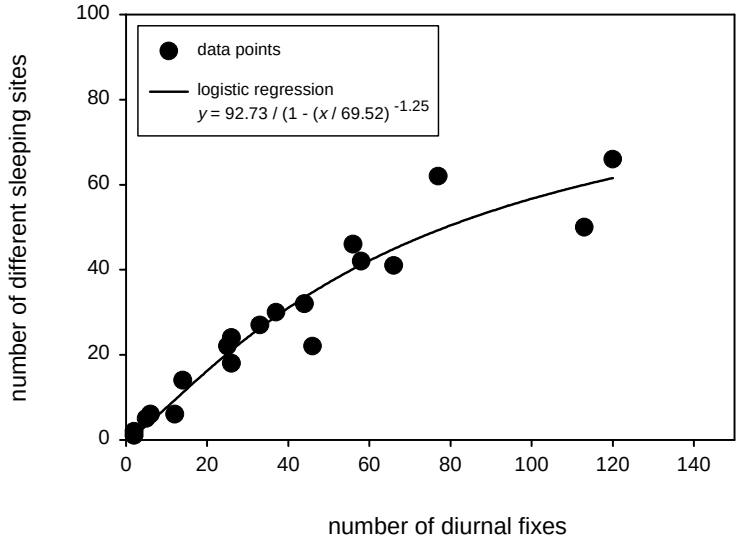

Fig. 5. The relationship between the number of independent daytime fixes and the number of different sleeping sites (trees) used by slow lorises ($n = 19$), modeled by a logistic regression ($R^2 = 0.923$, $p < 0.001$). Each point represents one individual.

I obtained 126 independent sightings of adult or subadult day sleeping slow lorises. The animals exclusively slept on branches, twigs, palmfronds, or on lianas at places where they were hidden from view by foliage. They never used any other shelter, like treehollows, for example.

Slow lorises were seen to sleep alone, in duos, and in trios (radio-locations also never revealed any sleeping associations larger than a trio). On average, adult or subadult slow lorises slept alone (associations with infants excluded) on 73.9 ± 24.5% of the days and on

the remainder (26.1 ± 24.5%) in direct physical contact with other adult or subadult slow lorises (difference significant; Fig. 6). Duos consisted of an adult female and another individual of any sex and age class or two subadult females. I never observed a trio that consisted exclusively of adult or subadult animals; all trios observed included one infant.

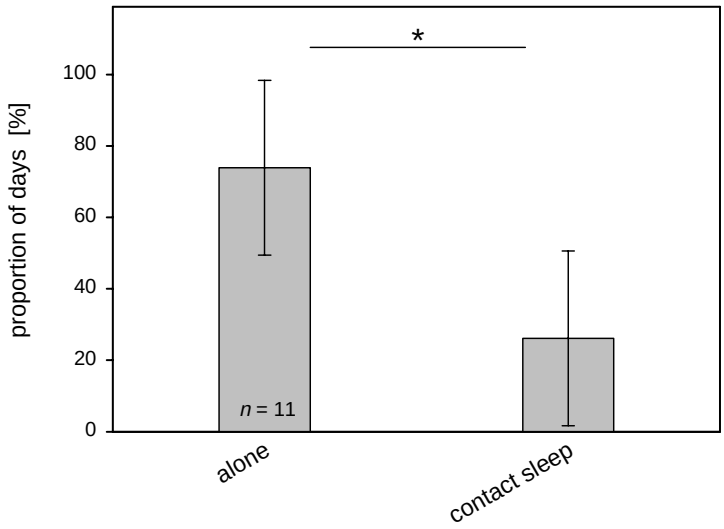

Fig. 6. Comparison of mean (± SD) proportions of days slow lorises slept alone and with contact to at least one other adult or subadult conspecific (Wilcoxon test: $z = -2.344$, $p = 0.019$).

Direct Nocturnal Interactions

I witnessed four different forms of obvious nocturnal direct interactions between adult or subadult slow lorises during the study: allogroom, alternate click calls, follow, and pant-growl (Table III). Alternate click-call was observed between individuals moving towards each other before assembling at a sleeping site shortly before dawn. While allogroom, alternate click call and follow were friendly behaviors, pant-growl was utilized in agonistic encounters. All interactions occurred between individuals sharing large parts of their home ranges with each other. I never witnessed any direct interaction between individuals whose home ranges were adjacent to each other, such as territorial fights. Nor did I observe any direct interaction between the male CHR, who was not a member of any spatial group, but shared space with group A, and a conspecific.

Table III. Forms of obvious direct interactions between adult or subadult slow lorises during the night

Direct interaction	Description
Allogroom	Application of the tongue or toothcomb to parts of another individual's body in repetitive, frictional movements (cf. Rasmussen 1986)
Alternate click calls	Sharp clicks emitted singly or in short series in turns by at least two conspecifics with all callers within hearing range of the human observer
Follow	Quadrupedal locomotion by at least two individuals occurring within 5 m behind one another with all of them moving in the same direction using the same substratum and matching in pace
Pant-growl	Highly variable vocalization including atonal growling or gasping inspirations and expirations (cf. Rasmussen 1986)

Even all forms of interaction taken together made up only a small proportion, i.e. on average 3.1% (range: 0.0 - 7.7%; interactions with infants excluded), of the individuals' total active time. I witnessed only six incidents of follow, three incidents of pant-growl, one incident of allogroom and one incident of alternate click calls. I observed follow between adult males and females (male following) and between an adult female and a subadult female (subadult following). I observed pant-growl between an adult male and a subadult male, between an adult female and a subadult female, and between two subadult females. I observed allogroom (mutual) between an adult female and a subadult male. Alternate click calling took place between two subadult females.

Dyadic Analyses of Association within Fixed Distances

Of the eight dyads included in the association analyses, none showed repulsion, i.e. less frequent association than expected, for any of the distances und diel segments tested. Four out of seven dyads tested (all male-female dyads and one female-subadult dyad) showed attraction during daytime (distance: within 1 m of each other; Table IV). Since suitable

sleeping sites did not seem to be a limited resource (see above), and individuals co-ordinated their approaching a sleeping site by alternate click-calls (see above), there can be little doubt that this attraction reflected mutual attraction of two slow lorises towards each other ('social attraction'; Mitani *et al.* 1991). During the night one male-female dyad (distances: within 1 m, 10 m, and 50 m of each other) and one female-subadult dyad showed greater than expected frequencies of association (for 1 m and 10 m; Table IV). My data did not allow me to test whether this attraction was social or due to the animals being independently attracted towards food sources. Moreover, small sample sizes may have prohibited the detection of non-random patterns in some dyads.

Table IV. Frequencies of association of slow loris dyads within certain fixed distances. Differences between observed and expected frequencies of associations were compared using binomial analyses. Non-random patterns are all significant. Expected values were derived from the distribution of the distances between all possible pairs of locations on two animals (Doncaster 1990)

	Dyad class			
	male - female	male - subad. male	female - subad. fem.	subad. fem. - subad. fem.
Diurnal time	*n* = 3	*n* = 1	*n* = 2	*n* = 1
within 1 m:				
mean	14.3%	0.0%	7.9%	0.0%
(min-max)	(8.3% - 20.9%)		(0.0% - 15.9%)	
Differ. obs. – exp. frequency	all attraction	random	1 attraction 1 random	random
Nocturnal time (central)	*n* = 3	*n* = 2	*n* = 2	*n* = 1
within 1 m:				
mean	3.4%	0.0%	3.6%	0.0%
(min-max)	(0.0% - 6.3%)	(0.0% - 0.0%)	(2.4% - 4.8%)	
Differ. obs. – exp. frequency	2 random 1 attraction	all random	1 attraction 1 random	random
within 10 m:				
mean	9.7%	2.4%	6.5%	0.0%
(min-max)]	(8.0% -12.5 %)	(0.0% - 4.8%)	(3.5% - 9.5%)	
Differ. obs. – exp. frequency	2 random 1 attraction	all random	1 attraction 1 random	random
within 50 m:				
mean	28.3%	6.4%	16.6%	21.1%
(min-max)	(12.0% - 47.8%)	(3.2% - 9.5%)	(14.3% - 18.8%)	
Differ. obs. – exp. frequency	2 random 1 attraction	all random	all random	random

Associations and Interactions within Food Patches

Slow lorises shared a large proportion of the food resources with co-members of their group or floating individuals. Of all food trees (*n* = 88) used by adult or subadult members of the four spatial groups (see above), I positively identified 49% to be also used by other conspecifics. Since I undertook no specific effort to monitor visitation patterns in food trees

the real value can be expected to be much higher. However, I never observed individuals from two different groups using the same food tree.

During an average of only 19.4 ± 17.0% of all independent instances when I saw a particular slow loris (n = 12) staying in a food tree, did I record another slow loris in the same or an adjacent tree of the same species (difference between sexes not significant; Mann-Whitney U test: z = -0.808, p = 0.412; n_{males} = 6, $n_{females}$ = 6; difference between adults and subadults not significant; z = 0.093, p = 0.925; n_{adults} = 10, $n_{subadults}$ = 5; only slow lorises of which I recorded >5 independent visits to food trees were included in the analysis). This value may underrate the actual occurrence of more than one slow loris being in the same food patch simultaneously because not all slow lorises visiting such trees may have carried radio-collars and slow lorises without radio-collars may have passed my notice due to poor visibility. Yet, there were extremely few cases, when after long lasting continuous observation of a particular tree, it turned out that there were more animals in a tree than I had initially noted. Therefore, I suggest that in the majority of cases of a slow loris visiting a food patch, the animal was alone.

Seven of the direct nocturnal interactions described above happened in food trees: two occurrences of pant-growl, one occurrence of allogroom, two occurrences of follow. In one instance pant-growl seemed to have no consequences and both animals continued feeding, in the other instance one slow loris left the food tree.

Dispersal

I determined two possibly completed dispersal events and observed two more while they were still going on. The first concerned a female (NEU). NEU was first captured as a juvenile when her estimated age was 4 months (body mass: 325 g). Exactly one year later she was captured a second time and fitted with a radio-collar. At her second capture NEU was subadult (body mass: 603 g). Four locational records of her were obtained before she disappeared (according to local people she had been caught and sold as a pet). The positions indicated a dispersal distance from the natal area of about 3,000 m. The second dispersal event concerned a male (PAU). PAU was a radio-collared subadult (body mass: 670 g) residing in the same area as his mother JAC and the adult male GER (group C; see Table II). At an estimated age of 21 months he suddenly started making peculiar excursions from the

area that he had formerly used: he moved fast following a straight line, something I had never observed before. They lasted up to 2 days and nights and took him up to 500 m away from his home range. Inbetween these excursions he returned to his natal area. When I resumed radio-tracking after a five month break, PAU stayed within an area directly adjacent to his natal home range, but never intruded into GER's home range again (13 fixes). Forays into areas previously never visited similar to the ones by PAU, but even further away from the former home range (up to 1,000 m) were observed in two more radio-tracked subadults with similar body masses, BOO, a male (body mass: 705 - 746 g; age unknown; member of group D; see Table II) and a female (DEV; body mass: 545 g; estimated age 19 - 27 months; maximum observed time period away from the home range: 5 days/nights; group A; see Table II), but never in any other slow loris, adult or subadult. However, both BOO and DEV had returned to their former home range at the time their last fixes were taken (I recaptured both to remove their radio-collars; I never saw them again after that).

My limited data suggest that dispersal from the natal area occurs in both sexes at an age of between about 16 and 27 months. It remains to be seen whether an obligate longer lasting 'floating stage' (Fietz 1999b) exists or whether some slow lorises disperse directly from their natal area to an area where they stay permanently and breed.

DISCUSSION

Solitariness and its inversion, gregariousness, are quantifiable in terms of the proportion of time that animals are alone and together with conspecifics, respectively. Therefore, it is possible to speak of species/populations/individuals being more solitary, or less gregarious, than others. However, in practice few studies on primates and mammals in general have measured exactly the proportion of time individuals spend alone. For a long time this was deemed unimportant, because mammals were thought to fall into two classes so distinct from each other that species could be assigned to either the one or the other at first look: a 'solitary class' consisting of species (or populations) where individuals spend close to 100% of their time alone and a 'gregarious class' consisting of species where individuals spend close to 0% of their time alone (Leyhausen 1965). Other widely made assumptions were that the social organizations of solitary mammals are more homogeneous and gener-

ally much less complex than those of gregarious mammals (Charles-Dominique and Martin 1970; Martin 1972; Alexander 1974; Eisenberg 1981; van Schaik and van Hooff 1983; Fleagle 1988). However, recent field studies have revealed a great diversity in the social organization of solitary mammals both between as well as within orders. Unexpected frequent associations and a surprising level of social complexity have been found in various solitary nocturnal mammal species (Caro 1994; Waser *et al*. 1994; Kays and Gittleman 2001). As more and more data become available, a continuum between solitary and gregarious species is predicted with respect to time spent with conspecifics as well as to social complexity (Caro 1994; Waser *et al*. 1994; Sterling and Richard 1995; Gehrt and Fritzell 1998a; Bearder 1999). Throughout this chapter I have given the label 'solitary' to populations or species where individuals spend more than 50% of their active time alone; 'gregarious species' refer to species where individuals spend less than 50% of their active time alone. For my purpose these are useful definitions. But obviously, if indeed future research finds a continuum between the solitary and the gregarious life-style, continuing to divide the social organizations of mammals in this manner would make little sense.

In this study adult and subadult slow lorises spent on average only 6.7 % of their active time within a 10 m distance from a conspecific and slept in direct contact with conspecifics on only 3 out of 10 days. These figures suggest that slow lorises are among the most solitary mammal species.

Slow Lorises and Solitary Group-Living

In solitary mammals, just like in their gregarious relatives, individuals are often organized into groups larger than a male-female pair that are spatially separated from other groups. The only difference is that in gregarious species all members of the same group have identical home ranges in most cases (home range overlap in all possible combinations of two co-members is 100%), while in solitary species home range overlap between two members of the same group can vary over a broad range. Many, probably even most solitary mammals also maintain networks of long-term social relationships manifesting themselves in friendly interactions and the sharing of a sleeping site between co-members of a group (Richard 1985). Friendly interactions observed in solitary mammals include allogrooming, play, contact calling, huddling and alloparental care (e.g. Clark 1985; da Silva *et al*. 1994;

Sterling and Richard 1995); the latter meaning behaviors directed towards other individual's young that deviate from normal patterns. Some authors have designated social systems of a group of conspecifics that share space and maintain networks of friendly relationships amongst each other but not with neighboring conspecifics 'social groups' (e.g. Wilson 1975; Slobodchikoff and Shields 1988). Most slow lorises at Manjung seem to live in social systems that fulfill these criteria for a social group despite individuals spending very little time within close proximity to each other: All except one of the 14 intensively tracked slow lorises had fixed home-ranges of which they shared large parts with conspecifics. Groups of individuals sharing home ranges amongst each other were spatially separate from other such groups. Some sort of direct friendly interaction (allogroom, alternate click-call, follow, contact sleep) was observed between most slow loris dyads with overlapping home ranges, but never between members of different groups. Social cohesion between slow lorises sharing home ranges was further indicated because at least some of them slept close to each other more often than expected. Therefore, slow lorises can be termed both 'solitary' and 'group-living' (to call certain populations 'solitary group-living' is common practice, for example, in the carnivore literature). Not all slow lorises were members of a social group, however. One young adult male (male CHR) had no fixed home-range and never interacted with any other slow loris, even though part of the area he used was occupied by a social group (group A). My data do not allow me to answer whether such floaters (Fietz 1999b) are in a transient or permanent stage or whether they have any chance to obtain matings with females while in that stage.

Composition of Social Groups and Mating System

My data suggest that slow lorises at Manjung live in extended family groups consisting of an adult pair and its own offspring. It is therefore likely that the mating system is monogamy. This finding is inconsistent with anecdotal evidence from Elliot and Elliot (1967) of a mating aggregation involving six animals, one female slow loris and at least two males in pursuit of her. The latter observation hints more towards a promiscuous mating system in which females are able to mate with a number of males.

I never observed any copulations and apparently never tracked a female during her receptive period. This is not surprising given that each receptive period probably only lasts

for very few days and that, if gestation occurs, it takes 6 months for a female to become receptive again (Izard *et al.* 1988). Yet, from my data it seems unlikely that females at Manjung are usually able to mate with a number of different males: home range overlap patterns indicate that males are able to monopolize access to females. Wounds and scars found on many adult males may be due to territorial fights with other males. Support for monogamy as the more likely mating system comes from data on testis volume and dispersal. Monogamy leads to scramble competition being absent or much reduced compared to mating systems where each female mates with several males. Therefore, sexual selection theory predicts small testes in monogamous species (Harcourt *et al.* 1981; Kappeler 1997). Consistent with this prediction testis volume of captive slow lorises is small compared with equivalent data from other prosimian species (Kappeler 1997). Wild slow lorises still have smaller testes than expected from comparative analysis of captive data, but the difference is less pronounced (13% below expected against 45% below expected for captive animals). Relative testis size in other prosimian species show similar relationships between captive and wild animals (Fietz 1999a), presumably due to captive animals being overfed (pers. obs.). I did not find another often quoted correlate of monogamy, a weak sexual size dimorphism due to reduced intrasexual selection. Males had substantially larger body masses than females. This indicates that contest competition may not be altogether absent in slow lorises. In accordance with the suggestion that slow lorises are monogamous, dispersal occurs in both sexes. Age of dispersing young was about 16 - 27 months. Female slow lorises copulate for the first time between 18 and 24 months of age; the period to sexual maturity for male slow lorises has been reported to be 17 months (data from captive animals; Izard *et al.* 1988). Hence, natal dispersal probably takes place around the time when sexual maturity is reached and long after weaning (lactation period in slow lorises ranges from 5 to 7 months (Izard *et al.* 1988; Zimmermann 1989; chap. 6). Slow loris groups apparently form through delayed dispersal of young and are not related to individuals achieving better mating opportunities.

Why Be Solitary?

Once detected, solitary individuals have a higher risk of falling victim to a predator than individuals that are close to conspecifics. The presence of conspecifics can reduce preda-

tion risk by the dilution effect, increased vigilance, and by a better chance to fight off predators. Solitary mammals may not rely on any of these gregarious anti-predator tactics but on crypsis, i.e. on evading being detected by a predator. Slow lorises have a peculiar slow mode of locomotion; they never jump and rarely make any noise when moving (Ishida *et al*. 1992; pers. obs.). The combination of a high degree of solitariness, nocturnality, arboreality, and slow locomotion appears effective in avoiding regular predation (Clutton-Brock and Harvey 1977; Schaik and van Hooff 1983; Isbell 1994; Hill and Dunbar 1998). The only known non-human predators of slow lorises are reticulated python *Python reticulatus* (Wiens and Zitzmann 1999) and orang utan *Pongo pygmaeus* (Utami and van Hooff 1997). Orang utans (long extinct on mainland Asia) have been reported to kill and eat Borneon slow lorises sometimes when they come across one sleeping during daytime. Orang utans only occasionally eat any meat, however. At Manjung slow lorises most often slept in places that were inaccessible for larger mammalian predators, because the substrate would not support their weight (pers. obs.). During the present study only one focus animal was known to be killed by predation. I located its radio-collar inside a 3.5 m reticulated python. The attack happened in Padang savanna, possibly when the slow loris was forced to walk on the ground in order to cross open space between two forested patches (Wiens and Zitzmann 1999). There seems to be no regular predation on slow lorises in closed forest, its assumed natural habitat. Indeed, the finding of a high predation rate on slow lorises would have come as a surprise, given their extremely low reproductive rates (see Hill and Dunbar 1998).

Why Live Together with Conspecifics?

Gregarious group-living, as shown by many diurnal mammals, is not the only alternative to solitary group-living of slow lorises. There are two other major alternatives for an individual: it can decide not to share space with any conspecific and try to evict all other conspecifics from its home range, or it can tolerate conspecifics in its home range, but ignore them (I shall not consider floating as another alternative here). The second alternative, termed an intersexual territorial system (Balharry 1993), is exemplified by European badgers *Meles meles* in Central Italy (Pigozzi 1987). The third alternative is exemplified by the European hedgehog *Erinaceus europaeus*. Hedgehogs remain in the same general locality

from year to year without being territorial. Ranges overlap considerably and often completely in both sexes, adults and subadults. Nonetheless, hedgehogs are nearly always found alone. This holds true not only for the active period at night but also for inactive periods when they are in a nest (during the day and while hibernating). Adult males and females associate for a few days only for the purpose of mating. Affiliative behaviors outside mating and maternal care of the young have not been observed and lasting social relationships between adult animals are seemingly non-existent under natural conditions (Lindemann 1951; Dimelow 1963; Campbell 1973; Grzimek 1975; Reeve 1982; Boitani and Reggiani 1984). The question 'why live together with conspecifics?', therefore, is in fact two questions: (1) why share space with conspecifics?; and (2) why maintain friendly relationships with conspecifics? Clearly, the problems are interrelated: question 2 is always a subproblem of question 1. However, as the hedgehog proves, question 1 is not always related to question 2: some aspects of the problem of space-sharing among conspecifics (or living together) are independent of inter-individual interactions.

In many gregarious mammals and in some solitary mammals the answers to both questions (1 and 2) may be identical: individuals may share space with same-sexed conspecifics and maintain lasting relationships because this enables them to accrue substantial co-operative benefits. It has been suggested that this is generally so in social systems where individuals show joint defense against predators or increased vigilance (Rasa 1987), joint defense of food resources against other groups of conspecifics (Wrangham 1980), communal hunting (Bowen 1981), or some form of alloparenting (Macdonald and Moehlmann 1982).

However, not all group-living mammals display such behavior. For example, none of this behavior has been observed in the particularly well-studied European badger (Woodroffe and Macdonald 1993) and in this study in the slow loris. As just outlined, slow lorises rely on crypsis not on joint active defense to escape predation. Vigilance is also unlikely to be increased: slow lorises do not use alarm calls; neither have alarm calls been reported from captive animals (Rasmussen 1986), nor did I ever hear any such call in the field. Even during instances when a civet or a large owl, which have been mentioned as potential predators for some of slow loris' closest relatives, the African potto *Perodicticus potto* and angwantibo *Arctocebus calabarensis* (Charles-Dominique 1977), were within viewing distance of a slow loris, the latter remained silent (Wiens and Zitzmann 1999). Any calls may attract the attention of predators and enhance predation risk considerably for

species that are relatively slow and do not flee into shelters like slow lorises. There is also no evidence suggesting that slow lorises gregariously defend single food patches or home range boundaries. Animals only rarely associate at food resources and boundaries of home ranges of co-members of a social group are often incongruent. Furthermore, I found no form of alloparenting during my study (chap. 6).

Yet, slow lorises and many other solitary group-living mammals do show at least one behavior qualifying as co-operation: allogrooming. Slow lorises spent only a minute proportion of their active time (maximum value observed for an individual: 6.7%) on allogrooming. However, allogrooming may be regularly exchanged between two slow lorises sleeping in contact with each other shortly after sunrise and shortly before sunset when twilight makes visual observations difficult. Extensive allogrooming bouts during these periods have been reported in captive colonies (Rasmussen 1986). Allogrooming probably reduces parasite load of the groomee. In this respect it may be more effective than self-grooming, because places are groomed that an animal cannot reach itself. It is interesting to note that the only slow loris determined in this study not to be a member of any social group and not to be involved in any interaction with conspecifics (male CHR) had an unusually high ectoparasite load (lice). While a positive effect of allogrooming is widely acknowledged (to my knowledge the exact benefits of allogrooming have never been measured; however, a parasite-reducing effect of selfgrooming has been determined in mammals as well as birds; Clayton 1991; Mooring *et al*. 1996; Hart 1997), most authors have categorically denied that allogrooming could be a cause for the formation or maintenance of social groups (or the sharing of space) and, thus, have not considered it ‘notable’. The reason given is that allogrooming can at best merely reduce specific costs that only occur from group-living, namely a higher risk of contraction of diseases through ectoparasites (Carr and Macdonald 1986; Kruuk 1989; Woodroffe and Macdonald 1993; da Silva *et al*. 1994). In contrast, it is assumed that the joint co-operative behavior characteristic of gregarious mammals (joint defense, joint hunt, *etc*.) often lead to a net benefit, i.e. that benefits from such behavior outweigh any costs of group-living.

Another form of co-operative behavior shown by some solitary group-living mammals is huddling. In cold environments huddling can reduce thermoregulatory costs (e.g. Bazin and MacArthur 1992). However, this positive effect has also been dismissed as being too small to be of importance in explaining group-formation in most species (Gittleman 1989; but see

Ligon *et al.* 1988 for a discussion of the importance of thermal benefits for the evolution of co-operative breeding in birds). For slow lorises living in tropical forest, contact sleep between adult and subadult individuals is indeed unlikely to have any positive thermal effect.

In some solitary mammals such as the European badger individuals seem to be unable to accrue benefits from co-operative behaviors that outweigh the costs of group-living. It has therefore been assumed that the decision to share space with conspecifics in these species depends entirely on environmental factors. Firstly, environmental factors influence the cost side of sharing space. Generally, apart from a higher risk of contraction of diseases, costs arise from an enhanced predation risk and increased food competition. The former two are thought to be neglectable in solitary mammals. Costs from ectoparasite-borne diseases are reduced by regular grooming (e.g. Clark 1985) and predation risk is not or only minimally enhanced (see above). An elaborate discussion on the third factor that makes space-sharing costly, food competition, is contained in the carnivore literature. Specifically, many researchers interested in carnivore sociality have looked for environmental conditions under which food competition and thus the costs of tolerating conspecific foragers are low. One model, the Prey Renewal Hypothesis, predicts such costs as a function of harvesting rate and food renewal rate (Waser 1981). Waser concluded that, if food resources renew rapidly, conspecifics may have little competitive impact upon each other. He used this model to explain group-living in the nocturnal white-tailed mongoose *Ichneumia albicauda* feeding on large insects active on the surface of the ground, a prey which he showed to have rapid renewal rates (70% renewal after total depletion within 24 hours). Slow lorises feed to a large extent on shared resources that can be expected to have similar rapid renewal rates like floral nectar, and plant sap (chap. 7). The predictions of the Prey Renewal Model, therefore, may hold true for slow lorises. Another family of models, the Resource Dispersion Hypotheses (Macdonald 1983, Macdonald and Carr 1989), demonstrates that the rule applied by a primary occupant of an area in defending borders in conjunction with a patchy distribution of food in space and time may lead to more food being available within a territory than is actually needed. As a consequence, accepting additional conspecifics into the territory during certain periods incurs no negative effect on foraging efficiency of the primary holder (Carr and Macdonald 1986). It assumes that the primary territory holders decide upon the position of the borders that they defend mainly based on the availability of

food resources; and secondly that they adjust borders not in short (days or nights) but relatively long intervals (months to years), or even keep them constant for the entire lifespan of the holders (von Schantz 1984). A territory contains more food than is needed by its primary holders if they decide to include extra space as an insurance policy for 'bad times' or if increases in food availability are not immediately followed by an adjustment of territory borders. A number of predictions follow from the Resource Dispersion Hypotheses: food should be patchily distributed, territory borders should be actively defended, borders should remain constant for longer periods, and group size as well as food availability should be variable. In the slow loris the distribution of food resources is certainly patchy, both temporally as well as spatially. Flowers or floral nectar, sap, fruit and gum of trees constitute major parts of the slow loris diet (chap. 7). Only the parts of certain tree species are consumed and these often grow widely separated from one another. Some of the parts consumed are seasonal (some flowers, fruit; pers. obs.). Active defense of borders is suggested by bite wounds found on many slow lorises. However, territorial fights or any other form of overt aggression was never directly observed. Home range borders were fairly stable. Whether changes in home range borders determined reflected changes in defended borders remains unanswered. Group size, at least in one group (group A), of which I obtained detailed locational data from two tracking sessions, was stable over a period of one year. In this study, I did not measure food availability directly. However, for slow lorises from primary forest (groups A and B) I tested, whether use of food types differed between the rainy- and dry seasons. I found no significant difference (chap. 7). The predictions of the Resource Dispersion Hypotheses, therefore, seem to only partly hold true.

Assuming that the costs of sharing space for slow lorises are indeed relatively low, because of food resources renewing rapidly, individuals may decide to tolerate conspecifics simply because the effort it would take to drive them away would be greater. This scenario has been considered for kinkajous *Potos flavus* (Kays and Gittleman 2001); it seems more likely for the European hedgehog. However, for most solitary group-living carnivore species it is assumed that in addition to the short-term benefits already discussed, there is a mid-term and indirect benefit from the presence of conspecifics. In most cases it is not just any conspecifics that share space, but always a primary pair and its own offspring. Indeed group-formation through natal philopatry (delayed dispersal or non-dispersal of independent offspring from the natal area) is a pattern found in most solitary mammalian species

(Greenwood 1980; Waser and Jones 1983). The slow loris fits this standard pattern. Net benefits through natal philopatry for both the parent primary territory holder and the offspring can result if the chances for survival or future reproductive success for philopatric offspring are higher than for dispersers. Such conditions are especially likely to exist in saturated environments when resources are limited and usually monopolized by conspecifics (Emlen 1982). Constraints on dispersal are a second way in which environmental factors influence the pay-offs from sharing space. Resources likely to be monopolized in saturated environments are food and/or shelter. In the European badger both seem to be important. Regions of apparently good feeding habitat may be unoccupied by badgers if suitable den sites are not available (Neal 1986). At Manjung the area seemed saturated with slow lorises; I made chance spot observations of slow lorises in every part of the general study area including rural human settlements, mixed-crop plantations, bushland and closed forest. Therefore, external constraints on dispersal are likely to exist for slow lorises. However, unlike in many other mammal species they are not related to shelter sites, but entirely to food. Shelter sites is not a limited resource as is indicated by the great number of different trees each individual used during daytime. I suggest that the low ecological costs of group-living, combined with the high costs of dispersing in a saturated habitat, are important extrinsic factors determining social life in slow lorises as probably in many other solitary mammals.

However, the finding that extrinsic factors are important, or even causal factors for the formation of social groups does not say anything about the importance of intrinsic factors. Intrinsic factors (inter-individual interactions or joint actions) may still be critical (the same is true *vice versa*). In the field of behavioral ecology it is common practice to assume that out of several alternatives open to it, an individual will choose the one that, statistically, yields the highest fitness relative to the other options. Implicit in most approaches on the evolution of group-living in solitary carnivores (e.g. European badgers) is the assumption that in the long-term the fitness of non-dispersing offspring minus the fitness of early dispersing offspring, that is, the fitness differential between the two strategies, is positive even without any positive contribution from intrinsic factors (intrinsic costs, however, are usually included). The same assumption is made for the fitness differential between the parents of nondispersers and early dispersers. This route to sociality would fundamentally differ from that alleged for gregarious mammals, in that it would be completely independent from

any co-operative benefits gained directly from the presence of conspecifics. Such benefits, made possible by the maintenance of friendly relationships, only contribute to further improving the pay-offs. Maybe this is the scenario under which slow loris groups form or are maintained, maybe it is not. A straightforward test of the hypothesis that extrinsic factors alone are responsible for the decision to stay or disperse in a population of facultative dispersers would be to remove the suspected constraints on early dispersal, e.g. by offering breeding space (a territory or a shelter site). Newly independent young should then disperse. If they do not, intrinsic benefits exceed the fitness loss due to nondispersal (Koenig *et al*. 1992). Such experiments have been conducted on birds (Rabenold 1990). I am not aware of any such attempts on mammals, however.

Even if known, the absolute size of any positive effect from intrinsic factors alone would not be sufficient to determine whether their contribution was critical or not. Since we are dealing with fitness differentials, even a small contribution can be decisive (and if so should be regarded as causal and certainly as 'notable'). Even when benefits from direct interactions are only marginal and only reduce costs, they can still tip the balance towards delayed dispersal and group-living (Macdonald 1983; Macdonald and Carr 1989). For the slow loris this means that even a marginal positive effect from behavior such as allogrooming might be a decisive factor in an individual's decision to live together with conspecifics. If true, this means the route leading to the formation or maintenance of groups is similar to that supposed for gregarious mammals in that there is a critical dependence on co-operative benefits from the presence of conspecifics.

Moreover, there is a possibility that 'hidden' co-operative benefits from solitary group-living exist that have been overlooked so far. Mammals are able to communicate using the visual, tactile, vocal and chemical channels. Communication taking place via the visual, tactile or the vocal channel are relatively easy to study because they depend on two animals being near to each other. However, for many mammals including the slow loris the chemical sense is the most important sense (Seitz 1969; Schilling 1979). Information contained in chemical clues can be readable for a long time, sometimes for months. This property has two important consequences. Firstly, chemical communication can also be indirect, that is, temporally dispatched, and does not depend on the provider and receiver of the information ever being close to one another. Secondly, information contained in urine, feces, other scent marks or just the scent of an animal's trail is public and can be read by all animals present

in an area. Given the high cognitive abilities of solitary mammals such as the slow loris, I think it likely that a such information is incorporated into decisions where to stay or where to go, if the individuals profit from doing so. In the laboratory, information concerning a vast array of different resources have been demonstrated to be transmitted by indirect chemical communication between mammals. Information contained in scent marks may concern, for example, the harvest state of food resources (Devenport *et al*. 1999). Captive slow lorises commonly urine mark the substrate during locomotion (Rasmussen 1986). In the wild, this behavior is difficult to discern, but does occur (pers. obs.). By sharing knowledge about food resources animals may be able to accrue mutual benefits through an enhanced foraging efficiency. Slow lorises use food resources that occur in widely separated clumps so that travel to one is costly. Clumps are large enough (fruiting, sap-producing and flowering large trees) or renew rapidly enough (floral nectar of some plants) to be shared. Mutual benefits would result, e.g. if information provided by conspecifics that a certain clump has been emptied saves an animal the effort of traveling to that clump. The consequences of public knowledge about important resources used by solitary group-living mammals is a complicated subject that certainly deserves special attention in future studies. It holds the potential to illuminate some of the many enigmas of mammalian social evolution still left.

In summary, extrinsic factors are likely to be important for the formation or maintenance of slow loris groups in that they lead to foraging costs from tolerating conspecifics as well as chances for successful dispersal being low. Whether for the slow loris in addition intrinsic benefits are critical for an individual's decision to live together with conspecifics is still an open question. It is possible that the route to sociality for the slow loris and other solitary mammals differs fundamentally from that for gregarious mammals. It is also possible, however, that the two routes are very alike; i.e. that both depend on co-operative benefits gained directly from the presence of conspecifics.

SUMMARY

I describe the social organization of the slow loris *Nycticebus coucang* from locational and observational data on wild animals collected during 1,000 h of radio-tracking. On average

individuals were alone for 91.3 % of their active time at night and slept alone on 7 out of 10 days. Despite extremely low frequencies of direct encounters with one another, slow lorises formed stable social groups characterized by the occurrence of home range overlap and friendly interactions between members that were separated from other social groups. I observed four such groups, each consisting of a single adult female, a single adult male and a varying number of non-adult individuals. Group composition together with dispersal patterns and data on testis size hints towards a monogamous mating system. Indeed, in one case I could ascertain that extended family groups formed by delayed dispersal of a primary pairs offspring. I discuss two major evolutionary 'routes' by which slow lorises may reach or maintain social group-living. The first depends on co-operative benefits gained directly from the presence of conspecifics, the other is independent of such intrinsic benefits. I argue that current knowledge does not allow us to rule out either of the two routes for any solitary group-living mammal.

Chapter 6

Infant Care System

Social Dependence of Infant Slow Lorises to Learn Diet

INTRODUCTION

It has been suggested for many gregarious animals that individuals are capable of acquiring new or improve existing skills or knowledge through visual observation of or direct interaction with conspecifics and profit from doing so (Galef 1988; Whiten and Ham 1992). Immature individuals in particular may depend on some form of socially mediated learning for their survival. Skills and knowledge learned from older individuals may concern food and foraging (Galef 1977), the social environment (de Waal 1996), or predator avoidance (Curio 1988; Mineka and Cook 1988). Evidence that social interaction may be crucial for infant diet learning comes e.g. from a number of field studies on diurnal primates (Kawamura 1959; Silk 1978; Watts 1985; Whitehead 1986; Hauser 1988).

In contrast to their diurnal relatives, most nocturnal primates including the slow loris *Nycticebus coucang* lead a life characterized by low frequencies of direct interactions between individuals (Bearder 1987; chap. 5). This often also holds for contacts between dependent offspring and older conspecifics. During the early phases of infant development the mothers in many species either place the infants in a nest while they forage or leave them clinging to branches for considerable periods of time. This latter pattern of maternal care, called 'parking' of infants, is used by all members of the subfamily Lorisinae (Schwartz *et al.* 1998) studied so far: slow loris, slender loris *Loris tardigradus,* angwantibo *Arctocebus calabarensis*, and potto *Perodicticus potto* (Ehrlich 1974; Charles-Dominique 1977; Rasmussen 1986; Zimmermann 1989; Nekaris 2000). Neither of these species build nests. Intuitively, such 'absentee care systems' (Martin 1968) appear unlikely contexts in which to find older individuals to play an important role for improving skills and knowledge of young. However, it has been observed, both under captive conditions (slow lorises, slender

lorises, pottos, and angwantibos) and in the wild (slender lorises, pottos, and angwantibos), that during the weaning period young lorisines followed their mother virtually everywhere, either riding on her back or walking just behind. Further, young of these species obtained their first solid foods through scrounging from their mother under captive conditions. That is, the young managed to grab parts of insects and fruit from their mother's mouth or hand (Charles-Dominique 1977; Rasmussen 1986; Zimmermann 1989; Nekaris 2000). Lorises and pottos are omnivorous, feeding on a broad range of plant and animal foods (Charles-Dominique 1977; Nekaris 2000; chap. 7). Based on his observations, but without presenting quantitative data, Charles-Dominique (1977) suggested, that in the two lorisine species he studied, i.e. potto and angwantibo, food preferences are learned from the mother through direct interaction over food and that this learning process commences at the age at which weaning from maternal milk begins. So far, explicit tests of that hypothesis have been conducted with gregarious diurnal primates (Whitehead 1986; Rapaport 1999), but never with any nocturnal primate.

The main objective of this study was to test the diet-learning-hypothesis for the slow loris in the light of five predictions derived from it: (1) an infant will not eat items outside its social group's diet; (2) an infant will show concordance in frequency of use of feeding sites with other members of his social group; (3) an infant will watch conspecifics feeding; (4) an infant will stay within a distance to older conspecifics where it can see the other feeding more often than expected if it was moving independently; and (5) an infant's feeding will be restricted to periods when a visible nearby conspecific feeds (predictions 1 and 3-5 are taken from Whitehead 1986; prediction 2 is my own).

In addition to learning through direct observation several other mechanisms of learning from contemporaries have been discovered in mammals (Galef 1990). The first two predictions are independent of the mechanism involved; they should turn out true if young slow lorises indeed depend on older conspecifics for diet learning as opposed to independent learning by trial and error. However, test results cannot yield any clues towards the specific mechanisms of socially dependent learning working. If, as suggested, young slow lorises learn from older conspecifics about diet through direct interaction or observation the first two and the other three predictions should turn out true. The opportunity for such investigations was provided during this project when one infant slow loris and four older con-

specifics living in the same area (hereafter 'focus group') could be fitted with radio-collars and tracked simultaneously.

Detailed descriptions of slow loris social structure and infant care system exist from captive studies (Rasmussen 1986; Ehrlich and MacBride 1989), but the patterns observed may in fact be artifacts resulting from social or physical constraints. Lorisines generally have been rarely studied in the wild and quantitative data on infant-adult and infant-subadult relationships from the field are altogether lacking. Therefore, the second aim of this chapter was to give a detailed description of the social relationships between the infant and the older slow lorises of the focus group. I do this in terms of content of direct interactions and quantity of associations. Such data are needed to identify other possible forms of care received by immature slow lorises from conspecifics. I supplement focus group data with observations of slow lorises from neighboring areas to evaluate the likelihood that results are representative for the local slow loris population.

METHODS

Study Population

Among the slow lorises captured were six infants four of which had a mother that was known to me. Four of the adult animals fitted with radio-collars were females, that during some time of the total radio-tracking periods lactated.

The bulk of data was collected on the aforementioned focus group consisting of five individuals with overlapping activity areas between 7.4.1999 and 25.6.1999, the period when all of them carried functioning radio-collars (hereafter 'focus period'). The focus group lived in a section of Segari Melintang Forest Reserve containing unlogged primary forest (Perak Virgin Jungle Reserve No 1). In addition, I report here all relevant data on other individuals seen in the study area (infants, mothers, and other members of social groups with infants, whether individuals were ever captured or not) and on focus group members collected before the focus period.

Animals from primary forest spend most of their feeding time on floral nectar and nectar-producing parts (65.0%), followed by phloem sap (20.5%), fruit (17.4%), arthropods

(0.7%), and gum (0.4%; values are medians and therefore do not sum up to 100%). For the procurement of sap slow lorises gouge holes in the bark of trees (chap. 7).

Adult and subadult slow lorises in the study area usually began their locomotive activities within a few minutes after sunset and terminated them shortly before sunrise (chap. 5).

History of the Focus Group

The infant of the focus group, ERN, was the only infant ever fitted with a radio. ERN was male. At his first capture on the 7.4.1999, when he was radio-collared, he weighed 191 g (collar mass: 2 g). I estimated his age at approximately 8 weeks. This estimate is based on own observations and neonatal body mass and growth data from the literature (Acharjyo and Misra 1973; Rasmussen 1986; Zimmermann 1989). At the end of the focus period, 80 days later, ERN's body mass was 346 g. The collar was then removed (it had been changed once in between). The rest of the focus group was comprised by one adult female, two subadult females and one adult male. These individuals had been captured for the first time at places within 30 m of each other and were observed for considerable periods of time before ERN's birth (chap 5). The adult female, YVO (first captured and radio-collared on the 25.5.1998) was the only one in the focus group lactating during the focus period. Therefore, I assume that she was ERN's mother. Of the two subadult females one, VRE, was known since very early age. She was first captured on the 6.5.1998 (body mass: 181 g), but was radio-collared only much later on the 7.9.1998 at a body mass of 407 g. Because VRE too at an early age was observed being suckled by YVO, I assume she was also one of YVO's offspring. At their first captures ERN and VRE had nearly identical body masses. I assume therefore, that their ages at the respective dates were also nearly identical (± 1 week). Following this logic, VRE was 11 months older than ERN and since gestation length in slow lorises is around 6 months (Manley 1966; Zimmermann 1989; Izard *et al.* 1988; Weisenseel *et al.* 1998) she must have been ERN's next-eldest full- or half-sister. The interbirth interval of 11 months is – at least to my knowledge – the first such record for wild slow lorises. The second subadult female in the focus group, DEV, was older than VRE and already subadult when captured for the first time (on the 27.10.1998, then also radio-collared) and may have been another daughter of YVO. The male CHR was captured and radio-collared for the first time on the 17.10.1998. That time he had already been adult.

Intensive tracking of radio-collared older focus group members (49-109 independent locations per individual) was conducted before the focus period between 5.9.1998 and 11.12.1998. Area (minimum convex polygon)-observation plots (Odum and Kuenzler 1955) calculated yielded asymptotes between 30 and 40 independent locations for the three females suggesting that they had fixed home ranges during this period. The area enclosed in the minimum convex polygon around their combined locations from that period prior to the focus period hereafter is called 'focus site' (size: 4.4 ha). In contrast, area-observation plots for the male CHR (n = 55 independent locations) yielded no asymptote suggesting he did not have a fixed home range (chap. 5). CHR also used a large area outside the focus site. On a single occasion (on the 27.04.1999) an additional slow loris, an adult male, UNM, was observed within the focus site, but could not be captured. He was seen soon after sunset coming from a place where YVO and ERN had been recorded sleeping a few hours earlier. He was following YVO with ERN being only 5 m away. However, given the time that I spent on observations, I am sure that UNM did not come close to ERN often. I assume the five members of the focus group plus the additional unmarked male were all slow lorises present within the focus site during the focus period (the focus group is not exactly identical with a social group; the focus group contained all of the members of group A mentioned in chap. 5 except the male UNM; it also included the male CHR, which I did not consider a member of the social group A; Fig. 7; also see DISCUSSION).

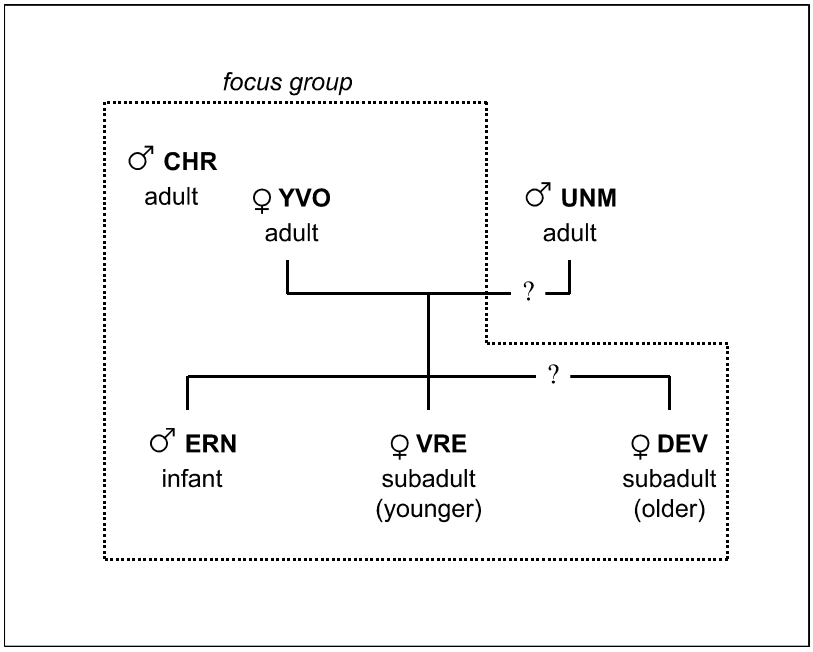

Fig. 7. Genealogical relationships between slow lorises present within the focus site during the focus period.

Radio-Tracking

I tracked members of the focus group on 64 days/nights for approximately 120 h during the focus period; 32 h at daytime and 88 h at night-time.

During the focus period I conducted a total of 150 scans of the focus group, 52 at daytime and 98 at night-time. In addition to scans, 97 location records of members of the focus group were obtained from night-time observations conducted opportunistically.

Direct Observations

During 284 locating efforts on the focus group made throughout the focus period I could visually observe slow lorises (n = 39 diurnal sightings, n = 245 nocturnal sightings). One-hundred-and-twelve of these sightings were of the infant ERN (n = 9 diurnal sightings, n = 103 nocturnal sightings). Forty-nine nocturnal sightings of ERN were independent. In 34 sightings of ERN during the focus period the scored behavior was feed; 26 feeding observations were independent. For all other members of the focus group taken together I

observed feeding 64 times with 11 ± 8 ($n = 4$) independent feeding events per individual. Of individuals not belonging to the focus group and of members of the focus group outside the focus period I obtained a total of 592 sightings ($n = 101$ diurnal sightings, $n = 491$ nocturnal sightings). Forty-four of them were of adult females with swollen teats, that is, of females which probably had suckling infants ($n = 17$ diurnal sightings, $n = 27$ nocturnal sightings). Thirty-two were of adult males sharing their home range with such females ($n = 6$ diurnal sightings, $n = 26$ nocturnal sightings). I made 12 diurnal visual observations of infants not carrying radio-collars through radio-locating other slow lorises these infants were associated with. Further, I made seven visual observations of solitary infants without radio-collars including three of ERN before he was radio-collared.

Quantitative Analyses of Dyadic Relationships

I conducted quantitative analyses of dyadic relationships only on data from the focus group collected during the focus period.

I calculated 12 different measures of association for dyadic combinations of the infant ERN with each other focus group member. One was the size of activity area overlap zones (OZs) between individuals. Sizes (and outlines) of the OZs for the members of the focus group were estimated by overlaying contours (95%) calculated with the adaptive-kernel method (Worton 1989). Calculations of activity areas were based on all independent location data on an individual collected during scans. Nine of the 12 association measures estimated proportions of time the infant ERN and each other member of the focus group spent within certain fixed distances of each other. These were calculated as simple ratios (Cairns and Schwager 1987) of the number of occurrences of a given association in independent scans to total number of independent scans. I chose three critical distances: 50 m, 10 m, and 1 m (reasons as stated in chap. 5; the viewing distance of 10 m corresponds with the furthest distance in the often dense vegetation at which a slow loris could see whether another one was feeding). I calculated associations within critical distances for three different diel segments: day, central night, and total night (definitions are given in chap. 5; note: central night is a portion of total night). Another two association measures estimated the proportions of total nocturnal time and central nocturnal time spent as nearest neighbors. Eighty-

three of the total scans, 48 diurnal scans, 45 nocturnal scans, 34 central nocturnal scans, and 15 of the nocturnal scans conducted before or after the central night were independent.

Where possible for dyadic combinations of ERN with other focus group members I tested whether observed frequencies of association within 50 m, 10 m, and 1 m differed from expected values derived from the configuration and utilization of the individuals' activity areas using binomial analyses (Zar 1996). Observed frequencies of association within fixed distances were calculated from the same data base as the proportions of time, i.e. simultaneous location data from independent scans, except that absence records were discarded. I derived expected values from the distribution of the distances between all possible pairs of locations on the two animals in question with Doncaster's (1990) DYNAMIC software. I predicted that if diet learning by young was influenced through watching older conspecifics feeding, the infant ERN of the focus group throughout the central night should have been within 10 m from at least one of the older conspecifics more often than expected (prediction 4 of the socially dependent diet learning hypothesis).

Individual-Based Quantitative Analyses

From independent nocturnal scans I calculated means and measures of dispersion for the distance between the infant ERN of the focus group and his nearest neighbour.

Further, I calculated the proportion of active time the infant ERN spent on solitary behaviors, interactions with conspecifics, co-feeding, and feeding in vicinity of conspecifics as proportions of all independent nocturnal visual observations on him. Similarly, I determined the proportion of feeding time ERN spent on different food types from all independent feeding observations (chap. 4). I defined 'feeding in vicinity' as feeding within 10 m of a conspecific, 'co-feeding' as ERN and another slow loris feeding on the same food patch within 10 m of each other, and 'feeding alone' as feeding further than 10 m away from any conspecific. The reason for choosing a distance of 10 m here, again, was my assumption that it was the furthest distance at which one loris could see whether another was feeding. A food patch consisted of a single flowering, fruiting, or sap- or gum-producing tree or two such trees of the same species adjacent to each other. Note that here as in the following I do not consider feeding in vicinity and co-feeding direct interactions.

Feeding Site Use

To determine whether the infant ERN showed concordance in frequency of use of feeding sites with other members of his social group (prediction 2 of the socially dependent diet learning hypothesis) I conducted Spearman rank correlation analyses. I based calculations of frequency distributions on location records obtained during independent nocturnal scans. I defined feeding sites as trees where lorises were seen collecting plant parts.

RESULTS

Home Range Overlap

The spatial data allowed to delineate activity areas for the infant ERN and for the three female members of the focus group: YVO, VRE, DEV (Fig. 8). ERN, YVO, and VRE were never recorded as absent, i.e. > 1,000 m outside the focus site. The activity areas determined for these individuals, therefore, equal their home ranges (Burt 1943). In contrast, the subadult female DEV was present within the focus site or was not further than 1,000 m outside the focus site only during 49% of the independent scans conducted on the focus group. The rest of the time she explored areas far away from the focus site in a typical pattern that in other subadult slow lorises preceded dispersal (chap. 5). However, DEV's calculated activity area (1.4 ha; $n = 41$ location records) was very similar in both, size and location to an activity area based on all independent fixes collected on her before the focus period (in the year 1998) when she had never left the focus site. Therefore, I consider the area used by DEV during the focus period to equal her home range too.

The adult male CHR of the focus group was present within the focus site or not further than 1,000 m outside the focus site only during four of the independent scans (5%); data were not sufficient to determine his activity area. CHR was never recorded within ERN`s home range.

The home range of the adult female YVO enclosed the other three home ranges completely (Fig. 8). YVO's, VRE's, and ERN's home ranges showed a 'Russian doll pattern' with YVO's range (4.5 ha; $n = 83$ locations) entirely enclosing that of VRE (1.7 ha; $n = 83$ locations) which in turn entirely enclosed that of ERN (0.5 ha; $n = 83$ locations). All female

members of the focus group shared substantial parts of their home ranges with the infant ERN. Absolute sizes of OZs with the infant ERN's home range were 0.5 ha for both, his mother YVO's and his sister VRE's home range, and 0.4 ha for his sister DEV's home range.

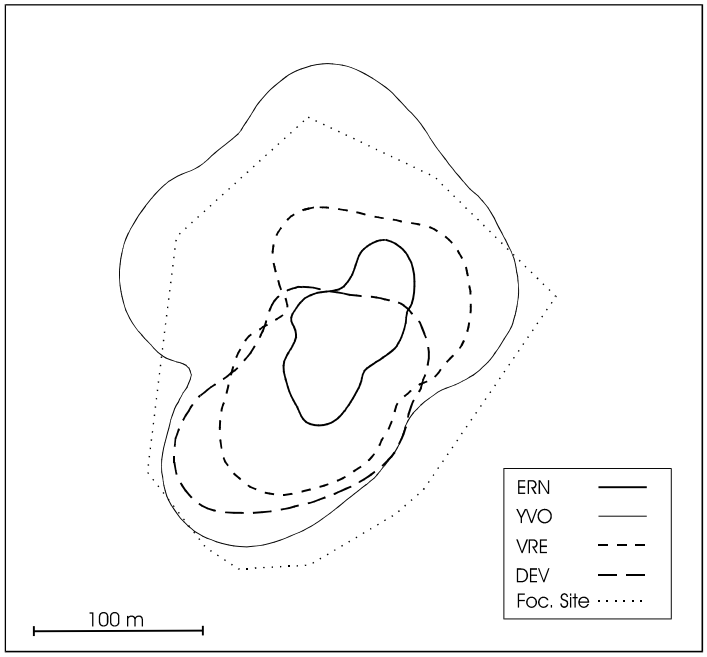

Fig. 8. Home range outlines (95% kernel isopleths) of the infant slow loris ERN, his mother YVO and two subadult female slow lorises, VRE and DEV, and border of the focus site.

Time Spent within Fixed Distances from Conspecifics

ERN spent 8.9% of his total active time (total nocturnal time) within viewing distance of conspecifics. During central night ERN spent 8.8% of the time within the 10 m viewing distance of conspecifics.

The proportions of time ERN spent within 50 m, 10 m, and 1 m with each of the older slow lorises of the focus group for three diel segments (diurnal time, total nocturnal time, and central nocturnal time) are shown in Table V. The databases for three dyads - ERN-

YVO, VRE-ERN, and DEV-ERN - were sufficient to compare observed with expected frequencies of associations. The binomial test (after Doncaster 1990) gave sigificant deviations from expected frequencies, all of which were positive, only for two dyads: ERN with his mother YVO and ERN with his next eldest sister VRE. They were for diurnal time (sleeping associations) and total nocturnal time (Table V). However, for central nocturnal time none of the tests detected deviations from expected values (Table V) suggesting that positive deviations during total nocturnal time resulted entirely from movements to and from common sleeping sites. That ERN and his sister VRE associated more often than expected at sleeping sites during daytime may not indicate mutual or unilateral attraction between both individuals, but may be due to VRE being attracted to her and ERN's mother YVO. During diurnal time ERN and YVO were always within 1 m of each other.

In all cases where radio-signals showed that ERN and YVO were within 1 m from each other and I managed to see the animals they were contact sleeping with each other (n = 7). It seems likely, therefore, that any daytime association between ERN and YVO represented an occurrence of contact sleep.

In contrast to ERN who right up to an estimated age of 19 weeks seemed to contact-sleep with his mother YVO every day, his sister VRE from the very beginning of the time period she was radio-tracked (at an estimated age of 26 weeks) was observed to contact-sleep with YVO much less frequently. In the 27th week after her birth (estimated age) she contact-slept with YVO only on two of the five days both were located.

Time Spent as Nearest Neighbors

During the night (total as well as central night) ERN's most frequent nearest neighbor was his sister VRE, followed by his mother YVO and the subadult DEV (Table V).

Table V. Dyadic direct interactions (content), associations within fixed distances, and associations as nearest neighbors (both quantity) between the infant slow loris ERN, 3 older female slow lorises (YVO, VRE, DEV), and 1 older male slow loris (CHR) with whom ERN shared space. Differences between observed and expected frequencies of associations were compared using binomial analyses. Significant values are indicated by asterisks. Expected values were derived from the distribution of the distances between all possible pairs of locations on 2 animals (Doncaster 1990). Of CHR too few locations were obtained (only 2 diurnal and 3 nocturnal independent locations) to calculate deviations from expected frequencies of associations with ERN

	Dyad			
	YVO-ERN	VRE-ERN	DEV-ERN	CHR-ERN
Observed direct interactions	contact sleep, follow, alt. click call, allogroom, suckle	contact sleep, follow, alt. click call?, allogroom?	contact sleep	none
Diurnal time (sunrise to sunset)	*n* = 48 independent scans			
within 50 m	100.0%	52.1%	33.3%	2.1%
Difference observed – expected frequency	+0.351**	+0.003	+0.027	not calculated
within 10 m	100.0%	16.7%	8.3%	2.1%
Difference observed – expected frequency	+0.775**	+0.103*	+0.064	not calculated
within 1 m	100.0%	16.7%	8.3%	0.0%
Difference observed – expected frequency	+0.841**	+0.132**	+0.087	not calculated
Total nocturnal time (sunset to sunrise)	*n* = 45 independent scans			
within 50 m	26.7%	51.1%	8.9%	0.0%
Difference observed – expected frequency	+0.043	+0.142	–0.122	not calculated
within 10 m	6.7%	6.7%	0.0%	0.0%
Difference observed – expected frequency	+0.054*	+0.044	–0.046	not calculated
within 1 m	4.4%	4.4%	0.0%	0.0%
Difference observed – expected frequency	+0.041*	+0.037*	–0.012	not calculated
as nearest neighbours[1]	33.3%	57.8%	15.6%	0.0%
Central nocturnal time (sunset+2h to sunrise–2h)	*n* = 34 independent scans			
within 50 m	11.8%	44.1%	11.8%	0.0%
Difference observed – expected frequency	+0.007	+0.063	–0.144	not calculated
within 10 m	2.9%	5.9%	2.9%	0.0%
Difference observed – expected frequency	+0.026	+0.027	+0.019	not calculated
within 1 m	0.0%	2.9%	0.0%	0.0%
Difference observed – expected frequency	–0.001	+0.022	–0.006	not calculated
as nearest neighbours[1]	29.4%	58.8%	20.6%	0.0%

* $p < 0.05$; ** $p < 0.001$

[1] proportions add up to > 100% because during some scans there was more than one nearest neighbor

Distance to Nearest Neighbor during the Night

During the central night the distance between the infant ERN and the nearest older member of the focus group averaged 53 ± 30 m (*n* = 34 scans). The distances between the infant ERN and the nearest older member of the focus group during the first two hours active time (before 2130 hours) and the last two hours active time (after 0500 hours) when individuals moved away from and towards their sleeping sites respectively were significantly shorter (on average 34 ± 26 m; Mann-Whitney *U* test: $z = -2.246$; $p = 0.025$; $n = 15$ scans), but still well beyond the 10 m viewing distance. During the total night ERN was on average 49 ± 32 m (*n* = 45 scans) away from his nearest neighbor.

Feeding

I observed the infant ERN feeding on four different food types: floral nectar, plant sap, and insects. Nectar feeding accounted for 84.6% of ERN‘s feeding time; gum feeding for 7.7%. Sap feeding and insect feeding each accounted for 3.9% of feeding time. Of the older focus group members I observed only the three females feeding. Their combined diet during the focus period consisted of floral nectar and floral parts (range: 43.8 – 72.2% of feeding time), gum (0.0 – 5.6% of feeding time), sap (22.2 – 37.5% of feeding time), and fruit (5.6 – 22.2% of feeding time). I observed none of the females to feed on insects during the focus period. Fruit was the only food type consumed by the female focus group members but not by ERN.

I saw ERN feeding on one occasion before the focus period. He was then 4 weeks old and was licking up floral nectar. The first (and only) observation of insect feeding was made when ERN’s estimated age was 16 weeks. ERN was first observed to eat exudates of trees when his age was 17 weeks; he ate sap in the same manner as older slow lorises, i.e. by lapping it up from sites after opening up the bark and the superficial layer of the cambium with the lower anterior teeth.

ERN was co-feeding in three visual nocturnal observations amounting to 6.1% of his total active time. His age at these instances was 8 (first two observations), and 11 weeks respectively. In all three he was together with VRE on an inflorescence of the bertam palm *Eugeissona tristis* licking up nectar. Bertam palm inflorescences are erect, ca. 1.0 – 2.5 m tall, and consist of several hundred flowers of which a considerable number produces nectar

at the same time. One observation lasted 22 min, the other two lasted 5 min each. In all three instances ERN never looked at VRE. Instead, the two animals climbed up and down on the inflorescence ignoring the other's presence even though the distance between them was sometimes less than 0.1 m. There were no other instances of a conspecific feeding in ERN's vicinity observed apart from the three instances of co-feeding.

ERN was alone during 89.5% of his feeding time. On all occasions of ERN feeding in vicinity of a conspecific the other slow loris was also feeding (n = 3 instances of co-feeding, see above).

ERN fed on parts of three plant species, all which were also part of the diet of the other focus group members (Table VI). All trees of species consumed by the other focus group members but not by ERN were outside ERN's home range (Table VI). At least with respect to plant parts ERN was never observed to bring material to his mouth other than those also taken by at least one of the other focus group members. He once was seen catching and eating a moth. Though the three females of the focus group were not observed to feed on any insect during the focus period, at other periods their diet was known to contain insects (pers. obs.). Since insect-feeding in slow lorises generally is a rare event (chap. 7) it seems likely that the insect-feeding by the focus group females occurred during the focus period outside observation bouts.

There was a significant positive correlation between ERN's frequency of use of feeding sites and that of his older sister VRE (Spearman rank correlation analyses: r_S = 0.422; p = 0.025; n = 28). The use patterns of ERN and the subadult female DEV showed a similar correlative tendency (r_S = 0.337; p = 0.079; n = 28), while no correlation were found between the use patterns of ERN and his mother YVO (r_S = 0.175; p = 0.372; n = 28). A significant positive correlation also existed between ERN's use and that of all other female focus group members taken together (r_S = 0.437; p = 0.020; n = 28).

Table VI. Plant species and parts consumed by the infant slow loris ERN and three older female slow lorises (his mother YVO, and his sisters VRE and DEV) with whom ERN shared space

Species	Family	Type	Parts consumed	Individual			
				ERN infant	YVO mother	VRE daughter	DEV daughter
Eugeissona tristis	Palmae	Palm	Floral nectar	+	+	+	+
Gluta curtisii	Anacardiaceae	Tree	Gum	+		+	
Mangifera griffithii	Anacardiaceae	Tree	Sap	+		+	+
Buchanania arborescens [1]	Anacardiaceae	Tree	Sap		+		
Ficus sp. [1]	Moraceae	Tree	Fruit		+	+	+
Garcinia sp. [1]	Guttiferae	Tree	Flowers		+	+	
Planchonella obovata [1]	Sapotaceae	Tree	Flowers			+	
Ganua motleyana [1]	Sapotaceae	Tree	Flowers		+	+	
1 unidentified species [1]	?	Liana	Flowers			+	

[1] trees outside ERN's home range

Direct Interactions with Occurrences

I witnessed six different forms of obvious direct interactions between infants and older slow lorises during the study: contact sleep, ride/carry, suckle, allogroom, follow, alternate click calls (Table VII; note: not all of them are mutually exclusive).

Table VII. Forms of direct interactions between infants and older slow lorises

Direct interaction	Description
Contact sleep	Infant sleeping in bodily contact with older individuals. Infant either clinging to the belly of an older individual or sitting directly next to one with all its hands and feet having a grip on branches, twigs or fronds (all daytime sleeping places of infants and adults observed were in trees with a minimum height above ground of 2.2 m). Sometimes an additional individual sleeping directly near such a duo making it a trio
Ride/carry	Infant clinging with all extremities to another, locomoting individual
Suckle	Infant with other individual's nipple in muzzle (may or may not be actually sucking milk)
Allogroom	Application of the tongue or toothcomb to parts of another individual's body in repetitive, frictional movements (cf. Rasmussen 1986)
Follow	Quadrupedal locomotion by at least two individuals occurring within 5 m behind one another with all of them moving in the same direction using the same substratum and matching in pace
Alternate click-calls	Sharp clicks emitted singly or in short series in turns by infants and older conspecifics with all callers within hearing range of the human observer

I saw contact sleep involving infants only during daytime. Infant slow lorises seen at daytime were always sleeping in bodily contact with other slow lorises (n = 18 separate occasions). In seven diurnal visual observations of infants not carrying radio-collars the infant was clinging to the belly of an adult female with no other loris around. In three cases the infant was clinging to the belly of an adult female with a subadult loris sleeping next to them. The adult females could be differentiated by their radio-signal; they were five. The infants probably were five too. In the remaining two cases of infants without radio-collars observed at daytime these were in contact with an adult male. One was of an adult male with an infant attached to its belly with no other loris detectable nearby. The second was of an adult male sitting near an infant. In the latter case an adult lactating female that before and afterwards had been seen in association with the respective male and also with an infant (observations included above) had been caught in one of the live-traps during the previous night and was still inside the trap at the time the observation was made (the distance between the female inside the trap and the male with the infant was about 60 m). I never made any chance observations of infants sleeping alone at daytime, nor did I ever see a lactating female at daytime that was not in bodily contact with an infant. I saw ERN of the

focus group during seven daytime scans. In all instances he was sleeping in bodily contact with his mother YVO. During the first four (made on three days) ERN was clinging to YVO's belly. In contrast, during the three later observations (made on three days too), the first of which was made when ERN's estimated age was about 17 weeks, he sat directly near YVO. I saw ERN sleeping in a trio on three days.

I observed ride/carry during the night as well as during the day. During the day I observed it only on slow lorises disturbed by me. All diurnal observations were of an adult (female or male, see contact sleep) with an infant attached to it that started climbing upwards away when I approached. When a trio consisting of an adult female, an infant clinging to the female's belly and a subadult was disturbed the subadult sometimes climbed on the back of the adult female and then the adult female fled with both, infant and subadult, attached to it. Ride/carry observed at night was apparently not a reaction to a potential danger but part of a behavioral sequence regularly occurring shortly before terminating activity as dawn approached (see further below). There were two occurrences of ride/carry observed at night and both involved the infant ERN of the focus group and his mother YVO.

I saw suckle clearly only once; the incident involved the infant ERN of the focus group and his mother YVO (at 1137 hours).

There were two cases of allogroom observed between an infant and an older individual, both during night-time. The individual being groomed in both cases was the infant ERN of the focus group. In one case the groomer was ERN's mother YVO; in the other it was either YVO, or ERN's sister VRE.

All four observed instances of follow involved the infant ERN and his mother YVO and all were made at night. In one case VRE was involved as a third individual. YVO was always the leading individual. In two cases ERN was following YVO to the sleeping place; in two he was following YVO a few meters away from the place where they had slept.

I witnessed alternate click-calls between infants and older conspecifics on seven separate occurrences in the forest. All cases involved the infant ERN of the focus group and his mother YVO. On one occasion additionally the subadult female VRE may have been involved. All cases took place at night with the older individual(s) moving towards the infant or the infant and the older individual(s) moving towards each other. The structure of ERN's click-calls compared to those of YVO appeared to be identical. It was higher pitched, however. Captured young individuals < 475 g kept in isolation before release all repeatedly

emitted the same call from shortly before dawn until late morning (n = 4 different infants, ERN included). Bigger slow lorises under identical conditions never emitted any calls.

I did not observe other obvious interactions. This holds also for forms of interactions over food that have been reported from captive slow lorises like food-stealing (Rasmussen 1986). Also I never witnessed other vocalizations. All observations of direct interactions between infants and older conspecifics made at night involved the infant ERN of the focus group. All sightings occurred either in the first 35 min after sunset or towards the end of the active period after 0500 hours. During the nocturnal hours in between I never observed any obvious interactions, even though ERN and other members of the focus group sometimes came very close to each other (see below). In the first 35 min after sunset the only interaction observed was follow. ERN always slept with YVO during the day (see below), but did not always follow her after she started moving. At least once he stayed at the sleeping place for some time after she had left. At the end of the active period after 0500 hours I observed alternate click call, follow, ride/carry, and allogroom. These behaviors seemed to form a sequence which I call the sequence of retrieving behavior and which I managed to observe in detail) on the 01.05.99. In the following is the protocol from that night:

0629 hours: ERN (not seen) emits several series of click-calls (the first heard during that full night tracking-session)

0631 hours: YVO (not seen) emits several series of click-calls; distance to ERN is 12 m

0633 hours: ERN (not seen) again emits several series of click-calls; he has moved 10 m away from his last position, but he is still 9 m from YVO‘s position at 0631 hours

0636 hours: ERN and YVO are both 0.1 m apart on the same palm frond, position as ERN at 0633 hours

0642 hours: YVO sitting on a liana with ERN clinging to her belly; they have moved 6 m from last position; YVO grooms ERN for a few seconds and then climbs up on the liana (ride/carry) and out of sight into the crown of the tree from which YVO called at 0631 hours (both individuals slept in that tree during a later daytime check)

In the seven nights in which I observed ERN and YVO meeting shortly before dawn I heard a first click call between 0504 and 0644 hours. Only in two cases I could ascertain which of the two animals was calling first: in one it was ERN, in the other YVO. In one case, VRE joined ERN and YVO during the retrieving sequence.

Infant's Solitary Behavior with Time Budget

I saw the infant ERN of the focus group at night to be engaged in the following solitary behaviors: travel, inspect, rest, stand, feed, autogroom, and jiggle. All except jiggle have been reported for captive slow lorises (Rasmussen 1986). I saw ERN jiggling only once: He was hanging under a palm frond with his body axis parallel to the frond's and all his hands and feet holding a grip to the frond; he stared at me and jerkily flexed and stretched his extremities a few times causing the fronds to rustle then moved 0.5 m under the frond and flexed and stretched his extremities again in intervals of 10-20 sec. This continued for about 10 min until he was out of sight then it stopped. My distance to ERN was 3 m (like during many observations of ERN before and after this incident) – no other stimulus was detectable.

For most of the total active time ERN indeed was active. Resting made up only 6.2% of his active time. With 40.8% he spent the biggest proportion of his active time on self-provisioning, followed by 26.5% on traveling, 6.1% on inspecting, 4.1% on autogrooming, 2.0% on standing, and 2.0% on jiggling. The remaining 12.3% of his time budget ERN spent on social interactions (click-calling included).

I never observed ERN staying at his day sleeping place for long after sunset. I conducted detailed observations of ERN during the period between 1900 and 2100 hours in eight nights. In seven he began his locomotive activity somewhere between 0 and 34 min after sunset; in one somewhere between 42 and 53 min after sunset. In contrast, I found the two smallest infants (body masses: 105 g and 119 g) observed during this study resting at night (at 0205 hours and 0035 hours) exactly at those places within a bush and a small tree (height above ground: 2.2 m and 3.5 m), where they had been seen sleeping together with their supposed mothers during daytime the previous days. Each of them was only located once when I also captured them by hand. They were easy to catch, because they did not move until after I was less than 1 m away and then they moved extremely slowly. At those

times no conspecifics were near them. The remaining two infants observed at night were bigger and, hence, probably older (body masses: 251 g and 325 g). Both were observed once only and were also captured. The behavior they were engaged in when I encountered them was travel. Another infant, VRE, regularly entered a banana-baited live-trap. At her first capture in a trap VRE's estimated age was 8 weeks (body mass: 181 g).

DISCUSSION

Summary of Socially Dependent Diet Learning Test Results

As predicted by the diet learning hypothesis the infant ERN of the focus group did not eat items outside his social group's diet. In accordance with prediction ERN showed concordance in frequency of use of feeding site with other focus group members, i.e. with his sister VRE who of all older focus group members spent the most time within ERN's home range. Contrary to prediction infants never watched conspecifics feeding. Contrary to prediction the infant ERN did not stay within viewing distance of older conspecifics more often than if he was moving independently. Contrary to prediction ERN`s feeding was not restricted to periods when a nearby conspecific fed.

ERN spent no more than 6.7% of his total active time within the 10 m viewing distance with any particular older focus group member (Table V). Taken together ERN spent 8.9% of his total active time (total nocturnal time) and 8.8% of the time during the central night within viewing distance of conspecifics.

Development of Locomotor and Foraging Independence

It has been described from captive studies on lorises and pottos that there are two different phases of infant development, an immobile and a mobile phase. During the immobile phase the young are unable or unwilling to locomote much on their own; they only climb on and off their mothers. When their mothers leave them alone they remain exactly at the site where they were dropped. This phenomenon is called infant parking. At a later age infants become mobile and start to move around on their own (Napier and Napier 1967; Rasmussen 1986; Ehrlich and MacBride 1989). Slow lorises are born fully furred with eyes com-

pletely open; within one hour after parturition they are able to cling to their mothers fur. The period between birth and first parking in captive studies on slow lorises ranged from 0 to 8 days. By 2 to 8 weeks infants in captivity became mobile. At about the same age infants ingested their first solid food (Napier and Napier 1967; Ehrlich 1974; Rasmussen 1986; Ehrlich and MacBride; 1989 Zimmermann 1989).

I never observed any of the lactating females at night carrying a young still in the immobile phase and I never saw a very young infant together with another slow loris. It is likely, therefore, that mothers start parking their young very soon after birth. Maybe even slow loris mothers under natural conditions never carry their young during the night except from the site where the young are retrieved to the sleeping place. Neither this nor any other study on lorisines has produced any evidence that older conspecifics provision young with solid food in the sense that they take active part in feeding young. Young slow lorises in the study area also did not grab food from their mother's hand or mouth as reported from captive studies on slow lorises and on African lorisines (Charles-Dominique 1977; Zimmermann 1989). Therefore, it is likely that slow lorises at Manjung obtain their first solid food by self-provisioning, i.e. not from a conspecific's hand or mouth. The largest immobile infant captured during this study weighed 119 g (estimated age 3 weeks), the smallest mobile weighed 181 g (estimated age 7 weeks). I saw the infant of the focus group licking up floral nectar on one occasion before the focus period. He was then approximately 4 weeks old. These data suggest that the minimum age of mobile infants at Manjung and also the age at which they take their first solid food is somewhere between 3 and 4 weeks. However, suckling continues for long after this. The lactation period for one mother and her daughter at Manjung (YVO and VRE of the focus group) was somewhere between 2.5 and 6 months. Reported lactation periods from captive slow lorises range from 5 to 7 months (Izard *et al.* 1988; Zimmermann 1989). The point from which slow lorises are fully independent of maternal milk appears to be the same as the point from which they no longer sleep every day together with their mothers. At that age they weigh between 350 and 400 g.

Infant-Adult and Infant-Subadult Relationships

The focus group consisted of five individuals: one male infant (ERN), its mother (YVO), two subadult females (VRE, DEV; the first a known, the other a suspected older sister of the infant), and an adult male (CHR). The only other slow loris in the focus area was an adult male (UNM) which was not radio-collared. Were these six animals all members of the same social group (see chap. 5 for the definition of 'social group' used here)? YVO, VRE, and ERN resided within the focus site (YVO's home range also included a small area adjacent to the focus site). Since they shared substantial parts of their home ranges and regularly interacted friendly with each other I consider them members of the same social group. DEV was probably also a member of that social group on the verge of dispersing to an area where she could breed. DEV spent considerable time within the focus site and interacted friendly with ERN, VRE, and YVO (contact sleep). She had never left the focus site during earlier radio-tracking periods (chap. 5). However, for 51% of the time during the focus period DEV made excursions that took her far from there. In contrast to the rest of the focus group, CHR was only rarely within or < 1,000 m outside the focus site (only 5% of the time) or any of the areas used by YVO, VRE or DEV. He was never located inside ERN`s home range and never interacted directly or associated closely with any other focus group member. Therefore, he can neither be considered a member of ERN's social group nor a model for ERN to learn from. He may not have had a fixed home range and may not have been a member of any social group. Another member of the infant's social group probably was the unmarked male UNM who once interacted directly with the infant's mother (follow). Slow lorises at Manjung usually live in extended family groups consisting of a primary pair and its not yet adult offspring (chap. 5). Of the two males present, UNM is the more likely to have been YVO's mate and ERN's father. Since I did not track UNM the content and nature of his relationships with conspecifics remains unclear. Two daytime observations of other males contact sleeping with infants and carrying the infants (after disturbance) suggest that friendly relationships between males and infants may exist. It can be ruled out, however, that UNM played an important role as a model for ERN to watch because, like CHR, he too was only very rarely near ERN.

During the night direct interactions between the infant ERN and the other members of his social group for the whole of the study period were restricted to two short periods, one just after the begin of activity, the other just prior to the end of activity. A low frequency of

close proximity interactions may be part of a strategy to reduce predation risk (Isbell 1994; Hill and Dunbar 1998; chap. 5). ERN mostly interacted directly with YVO. Suckling was the only behavior unique to this mother-infant relationship. Suckling in slow lorises, like in African lorisines, seems to take place only at daytime (Charles-Dominique 1977). Every night ERN and YVO interacted shortly before dawn in a sequence co-ordinated through click-calls. Alternate click-calling between a mother retrieving her young has also been observed in African lorisines (Charles-Dominique 1977). However, co-ordination through click-calls in slow lorises is not special to mother-infant relationships; I also witnessed it once between the two subadult females (VRE and DEV) of the focus group. Other than suckling the only special care-giving behavior towards young (infants and subadults) observed was carry (by mothers and males). Carrying after disturbance at daytime may reduce offspring mortality due to predation. Apart from that there seems to be no guarding of infants by older lorises during the night. For most of the active period conspecifics were too far away from ERN to be able to help him fight off predators. In slow lorises active maternal care seems to be limited to regular suckling, grooming, and carrying of the infant. Non-maternal infant care may be limited to occasional infant grooming and infant carrying.

A phase during which infants try to closely follow their mothers or other conspecifics virtually everywhere as observed in wild African lorisines and captive slow lorises (Charles-Dominique 1977; Rasmussen 1986; Zimmermann 1989) did not exist. It certainly did not exist in the focus group of which very detailed observations were possible, because all members, including the infant, carried radio-transmitters. I never saw other adult and subadult slow lorises at night accompanied by an infant; neither did I see other infants at night together with a conspecific. This suggests that the data from the focus group were representative of the local slow loris population.

Does Diet Learning by Young Slow Lorises Depend on Conspecifics?

Slow lorises live in a wide variety of habitats, feed on many different parts of a broad range of plant species, some of which are known to contain secondary compounds with deleterious effects on mammals, and show little overlap in food plant species between habitats (Barrett 1984; Wiens 1995; chap. 7). It is unlikely that such animals possess an entirely innate ability to recognize and ingest the appropriate food for their survival (Valsecchi *et*

al. 1994). Instead, infant slow lorises probably achieve an adult-like diet through learning. Information regarding food and foraging can be acquired by trial-and-error-learning and/or by some form of socially mediated learning. The infant of the focus group did not take to the mouth items outside his social group's diet. He further showed concordance in frequency of use of feeding sites with older group members; i.e. his next eldest sister. These results speak against trial-and-error-learning and in favor of a socially mediated form of learning. This is a tentative conclusion, however, since a social dependence of learning can only be demonstrated positively by experimentation under controlled conditions (Galef 1990).

No Diet Learning by Young through Watching Conspecifics

Social transmission of food and foraging information has been proposed in numerous studies and mammal species, primates and non-primates, and birds (Hall 1962; Ward and Zahavi 1973; Watts 1985; Whitehead 1986; Hauser 1988; Galef 1990; Boesch 1991; Langen 1996; Rapaport 1999). Many instances appear to operate through direct observation: one individual, the model, through its activities, draws the attention of a nearby second individual to a particular event or stimulus, which is followed by incidental learning (Laland and Plotkin 1991). Food transfer between individuals (e.g. scrounging) or any other direct interaction over food are not necessarily part of this process. But if, indeed, infants learn about diet by such a mechanism we should expect that they watch conspecifics feeding, and that they feed exclusively synchronous with potential models at least during a certain period (Whitehead 1986). I tested these expectations on the infant and the three females of the focus group. These females were the only potential models for the infant, because other slow lorises apparently spent only very little time in the infant's home range. None of the expectations was fulfilled, however.

Diet learning may be restricted to only a short phase in the infant's life and, theoretically, the period when the focus group infant learned from conspecifics could have been prior to the focus period (in the up to 5 weeks between first solid food intake and the begin of the focus period). There are several points that speak against this, however. Firstly, the fact that I never saw a very young infant together with another slow loris (see above). Secondly, the observation of ERN alone licking nectar at an estimated age of only 4 weeks

which is about the age when captive slow lorises take there first solid food. Thirdly, reported phases when infants closely follow their mothers in African lorisines beginning from an age of 3 to 4 months and up to an age of 6 months (Charles-Dominique 1977). Since a following phase seems to be non-existent and since ERN managed to fulfill his nutritional demands without showing predicted behavior patterns, I suggest that young slow lorises at Manjung do not learn about diet through visual observation of or direct interaction over food with conspecifics.

Do Infants Learn about Diet from Conspecifics by Indirect Communication?

Learning through direct observation is not the only way of learning from contemporaries, maybe not even the most common for mammals. So far, four more modes have been discovered in rats and demonstrated in cases of diet learning by young: (1) Rats form preferences for food flavors based on experiences *in utero* (Hepper 1988). (2) Weaning rats select solid food eaten by their mothers after transmission of cues through maternal milk (Galef and Henderson 1972; Galef and Sherry 1973). (3) An adult rat‘s breath contains olfactory cues that allow young rats to identify and induce them to prefer the food the recently fed adult has eaten (Galef and Wigmore 1983). (4) Marks left by adult rats around feeding sites bias young rats to feed both in the areas where adults have eaten and on the foods they have ingested (Galef and Heiber 1976; Galef and Beck 1985). All four modes may play a role in diet learning by wild slow lorises. The fourth mode seems to be especially appropriate in a species under strong selection pressure for minimum inter-individual direct contacts and high risk of errors due to noxious diet as the slow loris. Urine marking indeed is a frequently displayed behavior by captive slow lorises (Seitz 1969; Daschbach *et al.* 1983; Rasmussen 1986), but is extremely difficult to discern by eye in the field. Probably it does occur and then information transfer between conspecifics through these marks is predicted (chap. 5). Further study is required to prove that this information is incorporated into foraging decisions.

SUMMARY

Lorises and pottos (subfamily Lorisinae; Schwartz *et al.* 1998) are among the least gregarious primates and mothers start to leave their infants alone for considerable periods of time during the night, when they are active, as early as the day of birth. However, it has been reported from captive studies that weaning young lorisines follow their mothers in close distance nearly all the time and obtain their first solid food through scrounging. Based on these observations it has been suggested that young lorisines depend on their mothers to obtain information on diet and that they do so by watching their mothers feeding or interacting directly with their mothers over food. This study describes the social relationships between an infant and older conspecifics in a group of wild slow lorises *Nycticebus coucang* and for the first time for any nocturnal primate tests for a social dependence on diet learning by infants. There was no phase during which the infant tried to follow its mother to places other than the sleeping site. All infant-adult and infant-subadult relationships were characterized by extremely low frequencies of direct interactions and close proximity associations during the active period. Active maternal care seemed to be limited to regular suckling, grooming, and carrying of the infant. Non-maternal infant care may have been restricted to occasional infant grooming and infant carrying. Data from other individuals indicate that such patterns were representative of the local slow loris population. The infant of the focus group only took food items to the mouth which were also part of its social group's diet and showed concordance in the frequency of use of feeding sites with other members of its group. These results speak against diet learning by trial and error. They indicate that diet learning by infants probably does depend on information obtained from older conspecifics. However, the infant of the focus group was not involved in direct interactions with conspecifics over food and fed mostly alone (89.5% of its feeding time). It was not within a distance where it could see older conspecifics feeding more often than expected from the configuration and utilization of the individuals` home ranges. When feeding in vicinity of other slow lorises the infant never looked at them. This suggests that, contrary to expectations, visual observation or direct interaction over food are not the mechanisms by which information on food resources is passed from older individuals to young, but that other ways of obtaining such information are used by immature wild slow lorises.

Chapter 7

Diet

Fast Food for Slow Lorises: Is Low Metabolism Related to Secondary Compounds in High-Energy Plant Diet?

INTRODUCTION

A slow pace of life in endothermic animals is characterized by low activity rates, low daily energy expenditure (DEE) and low basal metabolic rates (BMRs). Endotherms living a 'slow life' may be under strong selection pressure to conserve energy, e.g. if the acquisition of energy through their diet is exceedingly expensive. Specifically, a slow lifestyle has been interpreted as a mechanism for dealing with a diet that is either poor in energy content (McNab 1980, 1983, 1986), becomes scarce during extended, but unpredictable periods (McNab 1980, 1983, 1986; Lovegrove 2000), or contains high concentrations of toxic compounds or digestion inhibitors (McNab 1980, 1983, 1986). The first and the third form of these limitations in energy supply have been cited as factors selecting for low metabolic rates in leaf-eating and ant- or termite-eating species, respectively (McNab 1978, 1984). Leaves, ants, and termites are supposed to yield few calories relative to the ingested volume (McNab 1978, 1984). Furthermore, they often contain high concentrations of chemical compounds with deleterious effects on foragers (Schmidt 1990; Deligne *et al.* 1981; Swain 1979). The hypothesis that low energy requirements are advantageous to deal with unpredictable periodic food shortages may explain why species from geographic regions experiencing climatic extremes brought about by El Nino Southern-Oscillation (ENSO) events tend to have lower metabolic rates (BMRs) than species from other geographic regions (Lovegrove 2000). One of the regions where ENSO often has marked climatic effects, causing failures of monsoon rains and therefore dramatic droughts, is Southeast Asia (Harger 1995; Stone *et al.* 1996; Chang 1997). ENSO events are considered unpredictable, because they occur in intervals between 2 to 10 years (Glantz 2001).

All members of the primate subfamily Lorisinae (lorises and pottos; following Schwartz *et al.* 1998) are nocturnal and arboreal and have a peculiar mode of locomotion: Their movements are always smooth and deliberate and most of the time rather slow, they never jump (Ishida *et al.* 1992). This slow lifestyle is related to low rates of energy expenditure. All lorisines examined have BMRs lower than 60% of the predicted value (Kleiber 1932; Hildwein 1972; Hildwein and Goffart, 1975; Whittow *et al.* 1977; Goffart 1978; Müller 1979; Müller *et al.* 1985). No estimates of DEE are available on any lorisine species, but I expect it to be low as well (Ricklefs *et al.* 1996). Although the food habits of lorisines are still poorly known Rasmussen and Nekaris (Rasmussen 1986; Rasmussen and Nekaris 1998; Nekaris 2000) suggest that their low metabolism and their slow movements are functionally related to a diet containing a high amount of toxic insects.

The slow loris *Nycticebus coucang* (body mass 0.5-1.5 kg) has the lowest BMR of all lorisines (40% expected value, Whittow *et al.* 1977; Müller 1979). Only few eutherians have similarly low relative BMRs, e.g. sloths (*Bradypus*, *Choloepus*; Irving *et al.* 1942; McNab 1978, 1984). Prior to this study the only information available on the natural diet of the slow loris stemmed from a few chance observations by Elliot and Elliot (1967), Lim *et al.* (1971), and Medway (1978), an analysis of four stomach contents by Fooden (1967, 1976), direct observations of one radio-collared female and an analysis of five of its feces by Wiens (1995), as well as 21 observed feeding events plus the feces of two live captures by Barrett (1984). These data sets were probably not representative of slow lorises natural diets, but suggested that slow lorises eat primarily fruit, and supplement their diet with invertebrates (including ants), vertebrates, leaf parts, and possibly plant gums, nectar, and bark.

I studied whether the slow loris indeed faces any of the three forms of limitation in energy supply proposed as main factors in the evolution of a slow lifestyle. To assess potential dietary energy constraints, I observed the foraging behavior of slow lorises in the wild and analyzed feces. I compared rainy- and dry season data to determine whether unpredictability in food supply potentially affects slow loris lifestyle.

METHODS

Dietary Measures

I determined diet from direct observation and analysis of feces. I conducted quantitative analyses of observational data on instantaneous observations of feeding (n = 168) from 15 intensively tracked adult and subadult slow lorises (>20 location records). To avoid possible bias from irregular sampling intervals I included only instantaneous feeding observations on any animal that were independent (separated by > 2 h; chap. 4). I used the remaining n = 139 instantaneous feeding observations to determine percent feeding times on different food items. I pooled all independent instantaneous feeding observations for each of the 15 individuals (total such observations per individual 9 ± 12) and calculated an average feeding time per individual for each food type (Fig. 9, Table IIX).

I collected a total of 118 complete fresh fecal pellets (combined dry mass: 135.6 g) of 25 captured animals (adults and subadults) from traps and from cages where animals were kept shortly before and after immobilization. Feces containing banana bait were not collected. Feces were stored in 70% ethanol. I treated pellets from the same catch as one sample. Forty-seven fecal samples were included in the analysis (1-6 per animal). Fecal samples from the same loris were collected at least 5 days apart (average: 149 days) and, therefore, considered independent samples. Before analysis I softened feces by soaking in water, then I dissected them. I examined component parts using binocular microscope and grossly assigned them to one of the following categories: fruit part (whole seed, seed part, fruit fiber), wood/bark, flower part (pollen grain, anther, petal, receptacle), gum, arthropods. While for seeds and flower parts it was often obvious that they came from different species, their scientific names were only rarely determined. Larger remains from arthropods sometimes allowed identification to ordinal level. Results of fecal analysis are expressed in terms of percentage of total number of fecal samples in which food items occurred. I recorded numbers of prey individuals per sample only for ants and lepidopteran larvae (by counting heads).

Data Analyses

For comparison between seasons, I treated months with less than 200 mm rainfall as dry season, the remainder as rainy season. To compare feeding behavior between seasons I only

used eight individuals for which I obtained > 5 independent sightings per season. I tested potential seasonal changes in diet composition among six individuals that inhabited the primary forest part. I used only those individuals because my data were most complete for the primary forest. I applied Wilcoxon tests (Zar 1996) to compare foraging behavior and χ^2 tests (Zar 1996) to determine differences in the occurrences of food remains in feces.

RESULTS

Foraging Behavior

Feeding accounted for an average of $20.5 \pm 12.1\%$ ($n = 15$) of the active time of slow lorises at Manjung (chap. 5). The diet consisted of five food types: plant saps, plant gums (a group of water-soluble exudates that seal wounds, Bearder and Martin [1980]), floral nectar and flowers, fruits, and arthropods. Slow lorises spent most of their feeding time ingesting phloem sap floral and nectar or nectar-producing parts (Fig. 9). I never observed slow lorises feeding on items other than those scored for quantitative analysis.

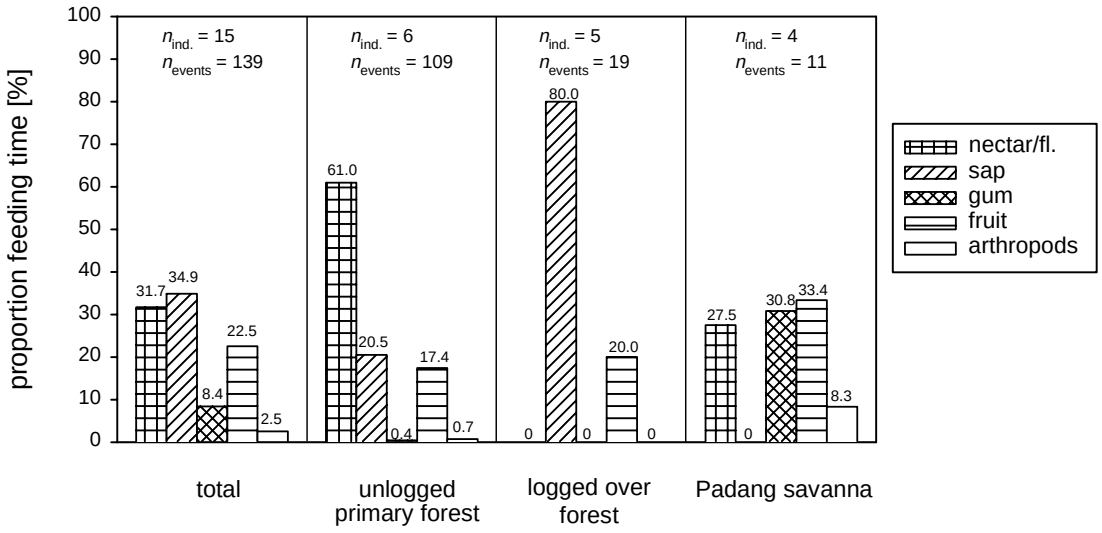

Fig. 9. Proportion of feeding time slow lorises at Manjung spent on the intake of five different food types (values given are medians)

Sap Eating

When slow lorises ate sap they perforated the superficial layer of the cambium of trees or lianas (see Table IIX for a list of identified species) by using their lower anterior teeth and lapped up the exposed saps. Slow lorises spent only a short time at one particular sap hole (< 2 min) and then quickly moved a few meters within the same tree to gouge the next hole. Preferred trees were riddled with hundreds of small holes. On thinner twigs sometimes the bark was chewed off from large areas.

Gum Eating

Slow lorises collected gums mostly from sites where they had already exuded (due to prior injury) and solidified by using their lower anterior teeth as scoops. The quantity of available gum was usually large (the size of a chicken egg and larger) and slow lorises spent a substantial amount of time (up to 10 min) at one particular site.

Floral Parts

The single most frequently consumed food item was floral nectar of the bertam palm *Eugeissona tristis* (Table IIX). This stemless palm is growing in dense clusters with fronds reaching up to 7 m in length. Its inflorescence is erect, ca. 1.0-2.5 m tall, and consists of several hundred flowers. Nearly all above ground parts of the palm bear spines. Each inflorescence produces two types of flowers: first staminate, then hermaphrodite flowers, both about 5 cm long with three hard woody petals. At any given time the flowers of one inflorescence are all roughly in the same developmental state. From both types of flowers nectar oozes out in thick droplets through the suture between the closed petals producing a strong smell. The amount of nectar available from one inflorescence was usually large. Lorises spent up to 30 min slowly climbing up and down on a single inflorescence to inspect several flowers and lap up nectar. Before lapping nectar slow lorises often bit off one of the three petals of the flowers.

Table IIX. Food plants of slow lorises at Manjung

Food type or species	Family	Plant type	% instant. feeding obs.	% occurrence in feces
Nectar/floral parts				
Eugeissona tristis	Palmae	Palm	41.0	21.3
Grewia paniculta	Tiliaceae	Tree	2.9	?
Planchonella obovata	Sapotaceae	Tree	2.9	?
Ganua motleyana	Sapotaceae	Tree	2.2	?
Ilex sp.	Aquifoliaceae	Tree	1.4	?
Garcinia sp.	Guttiferae	Tree	0.7	?
total			51.1	44.7
Sap				
Buchanania arborescens	Anacardiaceae	Tree	7.9	-
Chisocheton macrophyllus	Meliaceae	Tree	7.2	-
Mangifera griffithii	Anacardiaceae	Tree	5.8	-
Buchanania sessifolia	Anacardiaceae	Tree	3.6	-
Prunus polystachya	Rosaceae	Tree	2.2	-
unidentified	Leguminosae	Liana	0.7	-
Reinwardtiodendron humile	Meliaceae	Tree	0.7	-
Ocrantomelon dao	Anacardiaceae	Tree	0.7	-
Dacryodes rugosa	Burseraceae	Tree	0.7	-
Neo-Uvaria foetida	Annonaceae	Tree	0.7	-
total			30.2	51.1[1]
Gum				
Anacardium occidentale	Anacardiaceae	Tree	2.9	?
Gluta curtisii	Anacardiaceae	Tree	0.7	?
total			3.6	55.3
Fruit				
Ficus spp.	Moraceae	Tree	6.5	?
Diospyros kingii	Ebenaceae	Tree	2.9	?
Artocarpus heterophyllus	Moraceae	Tree	0.7	4.2[2]
Pometia pinnata	Sapindaceae	Tree	0.7	?
Ixonanthes icosandra	Annoniaceae	Tree	0.7	?
Grewia laevionata	Tiliaceae	Shrub	0.7	?
unidentified	unidentified	Shrub	0.7	?
Rhodomyrtus tomentosa	Myrtaceae	Shrub	0.7	16.7[3]
Elaeis guineensis	Palmae	Palm	0.7	2.1[3]
total			12.9	70.2

[1] as indicated by pieces of bark and wood
[2] identified from fiber
[3] identified from seeds

Fecal Analyses

I could not directly trace nectar and plant saps in feces. However, 51.1% of fecal samples contained pieces of bark and wood. Since slow lorises are likely to ingest small fragments of fresh bark or wood each time they gouged holes or peeled off bark I considered the occurrence of these items as indicators for sap eating. Flower parts indicative of nectar eating were present in 44.1% of all feces (only flower parts of *Eugeissona tristis* could be identified to the species level; Table IIX). Chitinous remains of arthropods were present in 91.5% of fecal samples. Parts of fruit were found in 70.2% of fecal samples. I found slimy translucent masses of reddish brown color that swoll up enormously after soaking in water in 55.3% of fecal samples. I assumed this to be mucilage from plant gums (Bearder and Martin 1980).

Seeds, seed parts, and fruit fiber found in feces belonged to 19 plant types. Single fecal pellets contained up to four types of seeds. However, only three types of fruit remains could be identified to the species level (Table IIX).

Arthropods found in feces were overwhelmingly insects: Coleoptera, Orthoptera, Lepidoptera (larvae, imagi), and Hymenoptera; the remainder being spiders. Ant remains (heads) were present in 40.4% of fecal samples. Only one fecal sample contained a substantial number of ants (23). All other samples contained < 6 ant individuals. Remains from lepidopteran larvae were present in 12.8% of fecal samples with no sample containing more than one. Feces did not contain any termite remains

Comparisons between Seasons

The total feeding time, calculated as the proportion of time active, did not differ between rainy- and dry season (Wilcoxon test: $n = 8$, $z = -1.400$, $p = 0.161$). I did not find seasonal differences in the proportions of feeding time spent on the five different food types (Table IX). Similarly, I did not detect seasonal differences in the frequencies of occurrence of food remains in feces (Chi-square test: $\chi^2 = 1.225$, $df = 4$, $p = 0.874$).

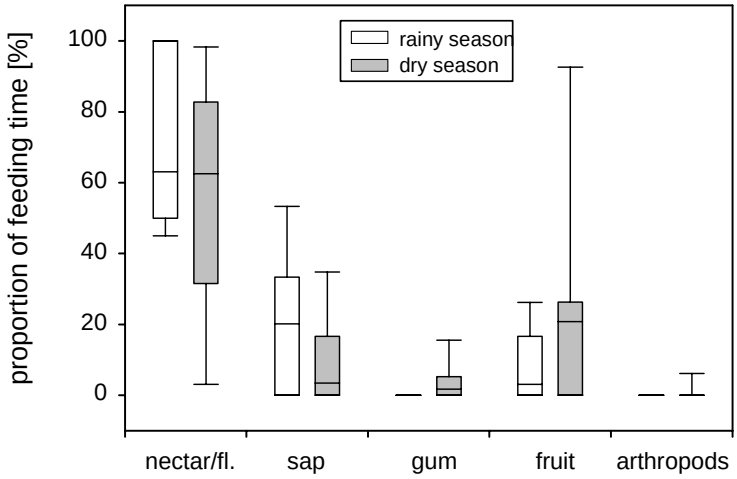

Fig. 10. Comparison of proportions (%) of feeding time spent by slow lorises on the intake of five different food types between rainy season and dry season. Paired data for the $n = 6$ individuals living in primary forest (medians, 10^{th}, 25^{th}, 75^{th}, and 90^{th} percentiles as boxes with error bars). For none of the food types proportions differed significantly (Wilcoxon tests).

DISCUSSION

My behavioral observations showed that slow lorises concentrated most of their feeding effort on the intake of floral nectar and nectar-producing parts, followed by phloem saps and fruit. The fecal analysis confirmed those trends. This suggests that the data were not biased towards observing certain food types over others, and that fruit, floral nectar and phloem sap indeed constituted a major part of the slow lorises' diet. Sap- and gum-eating have been reported from many primate species (prosimians, callithrichids, and African cercopithecines), but only a few of them use sap or gums as a major source of nutrients. These species have been referred to as members of an exudate-feeding guild (Sussman and Kinzey 1984; Nash 1986). The slow loris, apparently, is another member of this guild. Most exudate-eating primates lick and/or scrape gum or sap from surfaces after prior insect infestation or breakage. Specialized gouging behavior to elicit sap or gum flow was so far only found in three genera: *Callithrix*, *Cebuella* (Callitrichidae) and *Phaner* (Cheirogalei-

dae) and seems to be rare among vertebrates in general (Coimbra-Filho and Mittermeier 1976; Petter *et al.* 1971).

Dietary habits in the wild are only known for two other lorisine species, the similar-sized African potto *Perodicticus potto* and the smaller slender loris *Loris tardigradus* from South India and Sri Lanka. Stomach and cecum contents of 41 pottos contained on average 65% fruits, 21% gums and 10% insects, mainly ants, the remainder being leaves and fungi (Charles-Dominique 1977). Pottos have also been observed to feed on floral nectar (Grünmeier 1990) and are known to eat small vertebrates, such as bats (Charles-Dominique 1977; Jones 1969), birds (Charles-Dominique 1977), as well as geckos (Walker 1969). Information about slender lorises' diet in the wild stem from the direct observation of feeding behavior (Petter and Hladik 1970; Nekaris 2000). They indicate that this species relies mainly on animal food of which ants and termites form a large part. Other foods observed being consumed by slender lorises are molluscs, small vertebrates, and plant gums (Nekaris 2000). Recently, there is indirect evidence that the pygmy slow loris (*Nycticebus pygmaeus*) like the slow loris is a tree-gouger and exudate-eater (Tan and Drake 2001).

It has been suggested that animals generally operate on an intensity close to maximum potential metabolism set by the rate of energy assimilation from food (McNab 1980). Hence, diet should profoundly influence the pace of life animals live. Species with permanent access to high-energy diet are expected to have a fast pace of life. Why do slow lorises who mostly eat nectar, sap, and fruit, have a slow lifestyle? Three proximate explanations for a slow lifestyle have been put forward: (1) food items are low in energy content; (2) high-energy food is not available during extended, unpredictable periods; (3) secondary compounds in the diet reduce assimilation of energy from the diet.

Is Slow Loris Diet Energy-Poor?

Fruit, floral nectar, and phloem sap provide high amounts of easily digestible mono- and disaccharides (Crafts 1961; Percival 1961; Zimmermann 1961; Baker 1975; Waterman 1984) and/or lipids (Waterman 1984). Thus, I conclude that the answer is no; slow-living slow lorises ingest a high-energy diet similar, for example, to that of fast-living sunbirds, honeyeaters or nectarivorous bats (McNab 1983, 1988).

Gums also generally contain high concentrations of carbohydrates (Anderson *et al.* 1972; Anderson and Leon de Pinto 1985; Coimbra-Filho and Mittermeier 1977; Bearder and Martin 1980). For example, the gum of the cashewnut tree *Anacardium occidentale*, (Table VII) consisted of 84% carbohydrate (Machado and Leite 1957, cf. Coimbra-Filho and Mittermeier 1976). However, gums may not be a high-energy type of food. Gums, but not sap, nectar, and fruits, may often be largely indigestible for mammals that lack microbial fermentation (owing to the presence of 1-4-ß-linkages between sugar residues in gums; Waterman 1984; Nash 1986). The slow loris is reported to lack a chambered site for microbial fermentation in its digestive tract (Osman-Hill 1953). Remains of gums found in feces indicate that slow lorises were not able to completely digest gums of some tree species.

Does High-Energy Diet Come Seasonally?

The second form of limitation in energy supply suggested to be functionally related to a slow lifestyle in endotherms is that of an unpredictable and long period of shortage in food- and hence in energy supply. However, my observational data showed that nectar of the bertam palm, the major food source for slow lorises in the primary forest part, was available year-round. Nectar-producing bertam inflorescences were even available during the ENSO induced periods of extreme drought in 1997 and 1998. This is consistent with observations by Wong (1959) suggesting that bertam palms flower year-round at a fairly constant rate. Bertam palm inflorescences attracted a variety of insects that slow lorises readily consumed. Sap and gum are also constantly available (Bearder and Martin 1980), although their chemical composition may fluctuate (Stewart *et al.* 1973). Only fruit may become scarce during certain times in evergreen tropical forests (Whitmore 1988). Yet, I did not find any evidence for seasonal differences in fruit availability in slow lorises' diets. Another way to detect longer lasting periodic food shortages is by looking at the nutritional state of the animals themselves. The radio-tracked individuals seemed in good physical condition during all captures; a female slow loris even successfully raised offspring during the 1997-1998 ENSO event (pers. obs.). I conclude that these animals did not face extended periods of food shortage.

Is Energy Turnover Compromised by Plant Secondary Compounds?

A slow pace of life has further been linked to a diet containing high amounts of digestion inhibiting compounds or toxins (McNab 1980, 1983, 1986). Digestion-inhibitors exert energy-assimilation rate reducing effects in the gut by binding with the substrate to be digested, inhibiting digestive enzymes, or being antimicrobial (Rhoades and Cates 1976; McArthur *et al.* 1991). Toxins include all compounds that interfere with specific physiological processes within cells (Brattsten 1979; Waterman 1984). Insects are potential animal food items often containing toxic and digestion inhibiting substances. Such substances have been found in species from many different insect and other arthropod orders (Teuscher and Lindequist 1994). Rasmussen and Nekaris (Rasmussen 1986; Rasmussen and Nekaris 1998; Nekaris 2000) explicitly mention ants, termites, and butterfly or moth larvae as 'toxic groups' and suggested that the low BMRs of lorisines have evolved in relation to insectivory. Arthropods regularly appeared in the feces of slow lorises in small amounts. However, ants, termites, and lepidopteran larvae did not constitute major proportion of these arthropods (contrary to what was found in *A. calabarensis*; Jewell and Oates 1969; Charles-Dominique 1977). Ants found in feces of lorises were mostly aggressive diurnal species of the genus *Oecophylla* that likely attacked the lorises and were subsequently ingested during grooming. The occurrence of arthropod ingestion did not allow me to test whether such arthropods were toxic or repugnant.

Like animal matter, plant matter can also contain toxic or digestion inhibiting compounds. Bark, sap, gum, and flowers of many plant species and families are known to contain secondary compounds with proven or suspected negative implications for mammals (Rosenthal and Janzen 1979; Gartlan *et al.* 1980; Wrangham and Waterman 1981; Waterman 1983, 1984; Nash and Whitten 1989; Wink 1999). Even floral nectars can contain toxic constituents (Baker 1978). At least seven important plant genera of which sap or gum were consumed by slow lorises during my study contain toxins or digestive deterrents (search in CD ROM database 'Dictionary of Natural Products', Chapman and Hall; Table X). Some of these plants are known to be dangerous for humans: the exudates of *Gluta* spp. and *Mangifera* spp. produce sores on the skin. The saps of some species of *Mangifera* have sometimes been used criminally to injure an enemy by causing vomiting and purging after intake. The bark of *Gluta* spp., dry, powdered, and given in water, even kills humans. The gum of *Anacardium occidentale* also is capable of blistering the skin,

and, if taken internally, causes gastro-enteritis with loss of control of the muscles and interrupted respiration (Burkill 1935). Thus, I hypothesize that slow lorises indeed did consume toxic and/or digestion inhibiting secondary compounds along with their high-energy diet.

Table X. Plants of which slow lorises consumed exudates with their known secondary compounds (according to CD ROM database 'Dictionary of Natural Products', Chapman and Hall)

Genus	Parts	% instant. feeding obs.	Secondary compounds
Buchanania	Sap	11.5	Hexahydroxyflavones
Chisocheton	Sap	7.2	Steroids with furan- and pyran rings
Mangifera	Sap	5.8	Steroids, spirolactones, furanones, farnesanolid, Glucosyl-pentahydroxy-benzophenon, heptadecenyl-1,3-benzendiol, Pentahydroxy-xanthenone, tannins (trigallic acid)
Anacardium	Gum	2.9	Phenolics with long-chained carbohydrates, flavonoids
Prunus	Sap	2.2	Tannins, cyano-glycosides
Reinwardtiodendron	Sap	0.7	-
Ocrantomelon	Sap	0.7	-
Dacryodes	Sap	0.7	Triterpenes
Neo-Uvaria	Sap	0.7	-
Gluta	Gum	0.7	3-heptadecenyl-1,2-benzendiol

Slow lorises may depend on plant parts containing toxic or ingestion inhibiting not only for satisfying their need for energy, but also their need for nutrients like calcium, magnesium, and potassium (Bearder and Martin 1980).

A mechanism to deactivate toxins involves their conjugation with sulphate, hippuronic, or glucoronic acid (Häussinger *et al*. 1988; Scheline 1991). The conjugates are then excreted via urine or bile. An upper limit to detoxification rate is apparently set by the supply of cosubstrate for the conjugation (Foley et al 1995; Illius and Jessop 1995). Thus, animals must balance intake rate of foreign compounds with nutrient intake rate (Provenza 1997). The main cosubstrate used in many mammals is glucoronic acid (Baldwin *et al.* 1980; Scheline 1991) which is derived from glucose. Excretion of glucoronic acid conjugates is thus often a drain on glucose reserves (Jessop and Illius 1997). Cork (1981) estimated that glucoronic acid excretion due to absorption of allelochemicals from *Eucalyptus* spp. foliage might increase glucose requirements of koalas *Phascolarctos cinereus* by 20%. High requirements for glucose not only as a source of energy but also as a cosubstrate for detoxifi-

cation, could explain why even slow lorises with their very low metabolic rate might be compelled to rely on a sugar-rich diet. I suggest that slow lorises have high-energy diet available year-round. However, they may not assimilate more energy from their high-energy diet than they need to maintain their slow lifestyle. Their slow lifestyle may largely be determined by the need to detoxify plant secondary compounds in their diet.

SUMMARY

The slow loris *Nycticebus coucang* is a slow-moving arboreal mammal known to have a very low basal metabolic rate relative to other eutherian species of its body mass. A slow pace of life has been causally linked to a low intake rate of usable energy due to a diet that (1) is generally low in energy, (2) is unpredictably periodically scarce, and (3) contains high amounts of toxins or digestion inhibitors. In order to assess whether the slow loris faces any of these three kinds of limitation in energy supply I studied its dietary habits by direct observations of feeding behavior of radio-collared individuals and by fecal analysis. The diet was composed of five distinct types of food: floral nectar and nectar-producing parts, phloem sap, fruits, gums (another group of plant exudates), and arthropods. The largest proportion of feeding time was spent on phloem sap (34.9%), floral nectar and nectar-producing parts (31.7%), and fruits (22.5%). These food types should provide the slow lorises with high amounts of easily digestible sugars indicating that slow lorises at Manjung did not face an energy-poor diet. Furthermore, I found no evidence for seasonal food shortages: dietary habits were indistinguishable between rainy- and dry seasons, even though most dry season data were collected during periods of extreme drought induced by the 1997-1998 El Nino Southern-Oscillation event. However, many genera of food plants are known to contain secondary compounds that are toxic or reduce digestibility. I suggest that low metabolism in slow lorises is at least partly related to the need to detoxify secondary compounds in high-energy plant diet.

Chapter 8

Synopsis

In der vorliegenden Dissertationsschrift beschreibe ich die soziale Organisation, das Jungenaufzuchtsystem und die Nahrung des Plumploris *Nycticebus coucang*, einem nachtaktiven baumlebenden Halbaffen, im malaiischen Regenwald. Die Basis dazu sind Ortsdaten, die ich während der insgesamt 1000stündigen radio-telemetrischen Verfolgung von Plumploris sammelte, Verhaltensdaten von der direkten Beobachtung besenderter Tiere, morphometrische Daten sowie Kotanalysen.

Bezüglich seiner sozialen Organisation charakterisiere ich den Plumplori als solitäre gruppenlebende Art. Manche adulte oder subadulte Plumploris hatten großflächig überlappende Wohngebiete, aber selbst solche Individuen begegneten sich nur äußerst selten. Im Durchschnitt waren Plumploris während 93.3 % ihrer nächtlichen Aktivitätszeit alleine. Die täglichen Ruhezeiten verbrachten sie an 7 von 10 Tagen alleine. Alle vier beobachteten sozialen Gruppen bestanden aus jeweils einem adulten Weibchen, einem adulten Männchen und einer unterschiedlichen Zahl von jüngeren Tieren. Diese Gruppenzusammensetzung in Verbindung mit Daten zur Hodengröße und dem Abwanderungsverhalten weisen darauf hin, dass Plumploris monogam sind. Gruppen kamen anscheinend durch ein verspätetes Abwandern des Nachwuchses aus dem elterlichen Wohngebiet zustande. Die Tiere schienen keinen wesentlichen kooperativen Nutzen direkt aus gemeinsamen Handlungen mit Artgenossen oder Interaktionen mit Artgenossen über kurze Entfernung zu ziehen; das einzige offensichtlich kooperative Verhalten, das ich beobachtet habe, war Fremdputzen. Es sind eine Reihe von Säugerarten bekannt, die offensichtlich sozial sind, ohne daraus einen erkennbaren Vorteil zu ziehen. Ich diskutiere mögliche Szenarien, die Säugetiere dazu bringen können, ein soziales Leben zu leben.

Das Jungenaufzuchtsystem zeichnete sich ebenfalls durch eine sehr geringe Häufigkeit von direkten Begegnungen zwischen den Tieren aus. Während ihrer ersten Lebenstage wurden die Jungen von ihren Müttern nachts ‘geparkt’. Später bewegten sie sich selbstständig und unabhängig von Artgenossen. Die aktive mütterliche Fürsorge schien sich auf das

Tragen der Jungen zum Schlafplatz und regelmäßiges Säugen und Putzen zu beschränken. Nicht-mütterliche Fürsorge war anscheinend auf gelegentliches Putzen und Tragen der Jungen begrenzt. Es ist behauptet worden, dass junge Loris auf ihre Mütter angewiesen sind, um Informationen zur Nahrung zu bekommen. Angeblich erhalten sie solche Informationen, indem sie ihren Müttern beim Fressen zuschauen oder mit den Müttern in direkte Interaktionen verwickelt sind, die in Zusammenhang mit der Nahrung stehen. Ich habe diese Hypothese an einer Gruppe von Plumploris getestet. Die Fokusgruppe bestand aus einem abhängigem Jungen und vier älteren Individuen. Das Junge aus der Fokusgruppe nahm nur Nahrung ins Maul, die auch Teil des Nahrungsspektrums der älteren Mitglieder seiner sozialen Gruppe war, und es zeigte mit den Älteren Übereinstimmungen in der Häufigkeit der Nutzung von Nahrungsplätzen. Diese Ergebnisse sprechen gegen ein Lernen durch Versuch und Irrtum. Sie deuten darauf hin, dass das Junge beim Erlernen des Nahrungsspektrums tatsächlich auf Informationen zurückgreift, die ältere Artgenossen liefern. Allerdings war das Junge nicht an direkten Interaktionen mit Artgenossen beteiligt, bei denen Futter eine erkennbare Rolle spielte, und fraß meistens alleine (während 89.5% seiner Fresszeit). Es hielt sich auch nicht öfter innerhalb einer Entfernung, in der es Artgenossen sehen konnte, auf, als auf Basis der Beschaffenheit und Nutzung der Wohngebiete zu erwarten war. Wenn es in der Nähe von Artgenossen fraß, schaute es diese nie an. Das spricht dafür, dass, anders als postuliert, Beobachten oder direkte Interaktionen, die in Verbindung mit Futter stehen, nicht die Mechanismen sind, mit denen Information zur Nahrung von Älteren auf Junge übertragen werden. Ich diskutiere alternative Möglichkeiten wie junge Plumploris an diese Informationen gelangen können.

Meine Daten zur Nahrung des Plumploris setze ich in Beziehung zu seinem eigentümlichen Lebensstil. Der Plumplori ist wie die anderen Arten aus seiner Unterfamilie ein Tier mit einer im Vergleich zu anderen Eutheriern der gleichen Körpermasse sehr niedrigen basalen Stoffwechselrate, das sich langsam bewegt. Ein langsamer ‘Lebenstakt’ ist unter anderem darauf zurückgeführt worden, dass die Nahrung nur eine niedrige Rate der Energieaufnahme erlaubt, weil sie (1) allgemein einen niedrigen Energiegehalt hat, (2) unvorhersehbar periodisch knapp werden kann, oder (3) einen hohen Anteil an Giften oder verdauungshemmenden Stoffen aufweist. Um zu beurteilen, ob der Plumplori einer oder mehrerer dieser Limitierungen in der Versorgung mit Energie ausgesetzt ist, habe ich seine Ernährungsgewohnheiten durch direkte Beobachtung des Fressverhaltens und durch Ana-

lyse des Kotes untersucht. Die Nahrung setzte sich aus fünf unterschiedlichen Typen zusammen: Blütennektar und nektarproduzierenden Pflanzenteilen, Phloemsaft, Früchten, Milchsaft (eine weitere Gruppe von Pflanzenexudaten), und Arthropoden. Der größte Teil der Zeit, die die Tiere fürs Fressen aufbrachten, entfiel auf Phloemsaft (34.9%), Blütennektar und nektarproduzierende Pflanzenteile (31.7%) und Früchte (22.5%). Diese Nahrungstypen sollten Plumploris mit einer großen Menge von leichtverdaulichen Zuckern versorgen; die Nahrung der Plumploris scheint somit nicht generell energiearm zu sein. Weiter fand ich keine Hinweise auf saisonale Nahrungsengpässe: Die Ernährungsgewohnheiten während der Regen- und der Trockenzeit waren statistisch nicht voneinander unterscheidbar und das, obwohl die meisten Trockenzeit-Daten während einer extremen Dürre gesammelt wurden, die durch das El Nino-Ereignis in den Jahren 1997/98 hervorgerufen worden war. Viele Pflanzengattungen, die der Plumplori frisst, enthalten toxische oder verdauungshemmende Stoffe. Ich vermute daher als Grund für die niedrige Stoffwechselrate des Plumploris zumindest teilweise die Notwendigkeit zur Entgiftung von Stoffen, die mit der energiereichen pflanzlichen Nahrung aufgenommen wurden.

Synopsis

In this thesis I describe the social organization, infant care system, and diet of the slow loris *Nycticebus coucang*, a nocturnal arboreal prosimian primate, in the Malaysian rainforest. accordingly. Data collected are locational data obtained during 1,000 h of radio-tracking slow lorises, behavioral data from visually observing radio-collared individuals, morphometric data, and records on food remains from fecal analysis.

With respect to its social organization, I characterize the slow loris as a solitary group-living species. Some adult and subadult individuals had broadly overlapping home ranges, but the frequencies of close-proximity association between individuals were always extremely low. Individuals on average were alone for 93.3 % of their active time at night and slept alone on 7 out of 10 days. Four social groups observed each consisted of a single adult female, a single adult male, and a varying number of non-adult individuals. This group composition in conjunction with data on testis size and dispersal suggests a monogamous mating system. Groups apparently formed through delayed dispersal of a primary pairs offspring. Slow lorises seemed not to derive substantial co-operative benefits directly from joint actions or close-proximity interaction with conspecifics; the only obvious co-operative behavior I observed was allogrooming. They were also not 'forced' to share space with conspecifics by a limited availability of shelter sites. There exists a number mammal species which are apparently social, without deriving any obvious benefit from it. I discuss possible scenarios which may lead to individuals' decision to live a social life.

The infant care system was also notable for the very low frequency of direct encounters between animals. During the first days after birth young were 'parked' by their mothers. Later they locomoted on their own and independent of conspecifics. Active maternal care seemed to be limited to carrying the young to the sleeping place and regular suckling, and grooming of the infant. Non-maternal infant care appeared to be restricted to occasional infant grooming and infant carrying. It has been suggested that young lorises depend on their mothers for information on diet and that they obtain this information by watching their mothers feeding or interacting directly with their mothers over food. I tested this hypothesis on a group of slow lorises including one infant and four older individuals. The infant of the

focus group only took food items to the mouth which were also part of its social group's diet and showed concordance in the frequency of use of feeding sites with other members of its group. These results speak against diet learning by trial and error. They indicate that diet learning by infants probably does depend on information obtained from older conspecifics. However, the infant of the focus group was not involved in direct interactions with conspecifics over food and fed mostly alone (89.5% of its feeding time). It was not within a distance where it could see older conspecifics feeding more often than expected from the configuration and utilization of the individuals' home ranges. When feeding in vicinity of other slow lorises the infant never looked at them. This suggests that, contrary to expectations, visual observation or direct interaction over food are not the mechanisms by which information on food resources is passed from older individuals to young, but that other ways of obtaining such information are used by immature wild slow lorises.

I set my data on the diet of the slow loris in relation to its peculiar lifestyle. The slow loris like the other members of its subfamily is a slow-moving animal known to have a very low basal metabolic rate relative to other eutherian species of its body mass. A slow pace of life has been causally linked to a low intake rate of usable energy due to a diet that (1) is generally low in energy, (2) is unpredictably periodically scarce, and (3) contains high amounts of toxins or digestion inhibitors. In order to assess whether the slow loris faces any of these three kinds of limitation in energy supply I studied its dietary habits by direct observations of feeding behavior and by fecal analysis. The diet was composed of five distinct types of food: floral nectar and nectar-producing parts, phloem sap, fruits, gums (another group of plant exudates), and arthropods. The largest proportion of feeding time was spent on phloem sap (34.9%), floral nectar and nectar-producing parts (31.7%), and fruits (22.5%). These food types should provide the slow lorises with high amounts of easily digestible sugars indicating that slow lorises did not face an energy-poor diet. Furthermore, I found no evidence for seasonal food shortages: dietary habits were indistinguishable between rainy- and dry seasons, even though most dry season data were collected during periods of extreme drought induced by the 1997-1998 El Nino Southern-Oscillation event. However, many genera of food plants are known to contain secondary compounds that are toxic or reduce digestibility. I suggest that low metabolism in slow lorises is at least partly related to the need to detoxify secondary compounds in high-energy plant diet.

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Acknowledgements

Helga Schulze introduced me to the art of observing lorises. She also provided the cover drawing. Annette Zitzmann abducted me to Malaysia and showed me the tropical rainforest. When Holger Preuschoft suggested that Annette and I should start fieldwork on slow lorises and pentail tree shrews under his sponsorship there was no stopping us. He has been a benevolent mentor ever since. I am afraid I did not know the logic of science before I read 'Logik der Forschung' by Sir Karl Popper and I did not know how to translate that knowledge into groundwork before I met Bernhard Meier. The hammock discussions with Bernhard will have to be blamed if one day they bury me on the cemetery of Heknewhow-on-Butdidnotachieve. Before we set off for fieldwork Simon Bearder and Pierre Charles-Dominique also provided advice on methods for this project. In Malaysia we were attached to the Forest Research Institute of Malaysia. I am most grateful to the current Director-General Abdul Razak bin Mohd. Ali and his predecessor Mohd. Salleh bin Mohd. Noor for hosting our research. We received not only official, but also intellectual and practical support from Lim Boo Liat, Louis Ratnam, and Nor Azman Hussein. I further wish to thank two other FRIM staff for identification of herbarium material: Saw Leng Guan and Mat Asri bin Ngah Sanah. Special thanks for their commitment go to my field assistant Tedung bin Uia and the trapper-team Mat Nor bin Mohamad Akhir, Alias bin Soh, Mohd. Azuar bin Othman, Wan bin Marzuki, Tiee bin Sipang, Chagok, Jumpon bin Hitam, and Wa bin Katan. I am grateful to all residents of Labuan Bilek for their warm hospitality, in particular Haji Kamal bin Haji and his wife Haji Indon binti Hamzah. The late Haji Kamarruddin bin Ahmad was not only our landlord, but became a source of information regarding all aspects of life in Malaysia. I deeply miss him. Other friends in Malaysia who provided help and moral support are Chai Koh Shin, Gary Lim, Gerd Weinland, and Christoph Muziol. Authorization to conduct research in Malaysia was kindly granted by the Economic Planning Unit at the Prime Minister's Department in Kuala Lumpur. I thank my advisor Dietrich von Holst for his continuous support. Wolf Stöhr kindly repaired the last and crucial transmitter. Andreas Jürgens helped with the identification of plant remains from fecal samples. Michael Wink provided information on secondary plant compounds. This

dissertation has benefited greatly from discussion with a number of people, some of whom also commented on drafts of one or more chapters, including: Annette Zitzmann, Martin Wikelski, Michaela Hau, Heiko Rödel, Peter Waser, and Cornelia Kraus. Adrienne Hogg polished my English. To Annette I say: 'I am proud that we did it'.

This research was sponsored by the Deutsche Forschungsgemeinschaft (grant Pr 58/21 to H. Preuschoft), the Fazit Foundation (graduate student fellowship), the Universitätsverein Bayreuth, and the Daimler-Benz AG.

Declaration

I hereby declare that I wrote this thesis on my own and used only those sources and tools reported. Further, I declare that I did not try, with or without success, to submit this thesis anywhere else. I have not failed in any other doctoral examination at any other university.

Bayreuth, 19th February