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Ecology of free-ranging Aye-ayes *(Daubentonia madagascariensis)* in Madagascar in relation to morphological specializations

Ph.D. thesis

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Contents

Chapter 1

Introduction

The aye-aye *(Daubentonia madagascariensis)* is one of the most unusual species of primates. After being introduced to Western science in 1782, it was long considered a rodent rather than a primate (Sterling 1994). Aye-aye's rodent-like ever-growing incisors, thin filiform third digit, apparently well-developed sense of hearing, and unique behavior associated with the percussive foraging (Erickson 1994) is not paralleled by any other known primate, living or extinct. The only distant parallels among other mammals include the stripped possums of Australia and New Guinea (Handasyde & Martin 1996; Rawlins & Handasyde 2002) and the extinct Apatemyidae form Paleogene of Europe and North America (von Koenigswald & Schierning 1987; von Koenigswald 1990; Kalthoff *et al.* 2004, von Koenigswald *et al.* 2005).

Given its uniqueness, it may be surprising how little was the aye-aye studied. This was mainly due to difficulties of observing these elusive animals in the wild and their limited representation in captive collections. Early researchers considered aye-aye to be nearly extinct and there were only few reports on its behavior and ecology until 1990's (Petter & Petter 1967; Cartmill 1974). It was only gradually realized that the aye-aye is a wide-distributed and possibly even populous species in humid forest of eastern Madagascar (Mittermeier *et al.* 1992; Sterling 1994) but it is found in low population densities across its range of occurrence and it behaves very timidly so it is rarely encountered. Most lemurs, for example, react to an observer by freezing and staring at him/her so that the bright eyeshines can be easily detected with help of flashlights. Also the aye-aye posses the reflective layer bellow its retina, but it apparently detects the observer by the sense of hearing and it even may not look at the observer's direction before retreating or hiding, so that the eyeshines can be hardly noticed (pers. obs.). With its dark pelage, the animal may remain truly invisible to the observer.

The breaking-through research on ecology and behavior of aye-aye was a 2-year's field work by Eleanor Sterling (1993) on the Nosy Mangabe Special Reserve, an island in the Antongil Bay covered by a very old secondary forest, where aye-aye's were introduced and, at the time of Sterling's study, survived in relatively high population density. Using radio telemetry, Sterling was able to collect unique data on aye-aye feeding and ranging behavior and social organization. Her pioneering study stimulated also other researchers and in 1994, one volume of Folia Primatologica was devoted to this unique primate. The volume was introduced by Eleanor Sterling and Anna Feistner (Sterling & Feistner 1994) and included results of various small studies in captivity and in wild. But since then, only few new publications have appeared (Milliken 1995; Erickson 1995; Sterling 1998; Erickson *et al.* 1998; Simons & Meyers 2001; Soligo 2005) and the Folia Primatologica monothematic volume remains the source of most of scientific knowledge on aye-aye's behavior and ecology.

Our project was aimed to bring new detailed data on aye-ayes that inhabit a different habitat compared to the population studied by Eleanor Sterling. Our study site was a small island on Mananara River covered with an agroecosystem, predominantly composed of mixed tree orchard and plantation. Compared to Nosy Mangabe, the visibility and the level of habituation of animals were substantially better in this site. This allowed us even without use of radio telemetry to record behavioral data in details not paralleled by any previous field study. Tomáš Jůnek and I spent 7 months (April to October 2003) on this island, following several aye-ayes. The fieldwork already resulted in a Master's Thesis of Tomáš Jůnek (2005) that describes in details the feeding behavior and activity patterns if the Mananara aye-ayes.

In this thesis, I will concentrate on several specific aspects of aye-aye ecology, which are related to some of distinct morphological features of this unusual lemur. The main body of the thesis is composed of four chapters, two of them being submitted or accepted manuscripts, and the other two being provisional versions of yet unsubmitted manuscripts. Chapter 2 concentrates on the most characteristic morphological feature of the aye-aye, i.e., on its specialized fingers. The main aim is to demonstrate importance of the strong fourth finger rather than only the thin third finger, which is usually discussed in the literature on aye-aye foraging. Chapter 3 includes descriptive data on how do the aye-ayes use their hands and a quantitative analysis of lateral bias of the hand use. In Chapter 4 we evaluated context of use of body postures and locomotion relevant to distinct modifications of aye-aye's postcranial skeleton and musculature. Finally, in Chapter 5, we use information form this and other studies on the living aye-aye to re-evaluate several hypotheses concerning ecology and behavior of the extinct giant aye-aye, *Daubentonia robusta*.

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Chapter 2

Specialized use of two fingers in free-ranging aye-ayes *(Daubentonia madagascariensis)*

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Abstract

The aye-aye (*Daubentonia madagascariensis*) possesses a highly specialized hand with two fingers, the third and forth one, being used in a way not paralleled by any other primate. We observed use of the third and fourth fingers in various activities in four free-ranging aye-ayes. We found that the thin third finger was used exclusively or preferably for tapping, inserting into the mouth (probably to clean teeth), and probing for nectar, kernels and insects in bamboo, twigs and in live wood. In contrast, the robust fourth finger was used preferably when eating jackfruit (*Artocarpus heterophyllus*) and probing for invertebrates in soft plant tissues. In dead wood, both fingers were used in similar proportions. To extract contents from coconuts, the two fingers were apparently used for different tasks. From this small (686 observations), but unique, study of free-ranging aye-ayes, we conclude that the third finger appears to be specialized for use in tasks requiring high mobility, sensitivity and precision, whilst the fourth finger is specialized for tasks requiring strength, scooping action and deep access.

Key words: lemurs, *Daubentonia madagascariensis*, extractive foraging, Madagascar, hand, digits

Introduction

The aye-aye *(Daubentonia madagascariensis)* is a Madagascan lemur that is unique amongst primates in having adapted to a woodpecker- or squirrel-like foraging niche. It mainly feeds on embedded food resources such as nuts or wood-boring insects (Sterling 1994). Its hands possess elongated fingers that bear claws instead of nails (Soligo 2005). Two of these fingers are particularly specialized. The thin and bony third finger is morphologically most derived and the aye-aye does not use it in locomotion (Milliken 1995). Aye-ayes tap with this finger on various surfaces whilst foraging. Their large and membranous mobile ears apparently perceive variations in resonance which provide information on the internal structure of the object (Erickson 1994, 1995). The rodent-like ever-growing incisors can open nutshells or insect mines in tree trunks. After exposing such cavities, the third finger can further be used as a sensitive probe to inspect it and to extract its contents (Milliken 1995). It is shorter than the fourth finger, but it is functionally extended by its metacarpal, which protrudes about 18 mm from the palm (Iwano 1991). The metacarpophalangeal articulation is of the ball-and-socket type, thus allowing the finger to rotate in any direction, independently from movements of other fingers. Also, its last phalange can flex and hyperextend independently, acting as a hook that can lift larvae or another items out of cavities (Milliken *et al.* 1991). In contrast with other primates, tendons entering dorsal aponeurosis of the third finger remain largely independent and do not have substantial interconnections among their tendinous fibers (Jouffroy 1975). Furthermore, the tendon insertions on the distal phalange also extend from its dorsal aspect to the radial and ulnar side, which makes sideward movements of the last phalange possible (Soligo 2005).

While the function of the third finger is well described, relatively little is known about the use of the other specialized finger, the fourth one. Most papers do not even mention it when describing digit use during aye-aye feeding (Petter & Petter 1967; Ancrenaz *et al.* 1994; Andriamasimanana 1994; Sterling 1994). The fourth finger is the longest of the aye-aye's hand, it is strong and robust and its nail is more than twice as long and wide compared to that of the third finger (Iwano 1991). The fourth finger is regularly used for locomotion and securing positional support. The heaviest dry weight of intrinsic hand muscles attach to the fourth finger, whilst the least intrinsic hand muscle mass is attached to the second and third finger (Soligo 2005). The fourth finger has never been reported to be used for tapping but there are reports on probing and digit-feeding with the fourth finger. Iwano (1991) described its use in feeding in a single captive aye-aye. Furthermore, Milliken (1995) reported that aye-ayes sometimes use their fourth rather than third finger to probe the holes of an experimental apparatus, but the percentage of the fourth finger responses was low.

During our fieldwork with aye-ayes, we soon realized that the third and fourth fingers were used for different foraging tasks and that the fourth finger had the primary role in several

Fig. 1. The hand of the aye-aye. Note the thin third and the robust fourth finger. (Drawing courtesy of Josef Sodomka)

of these tasks. In this paper we will present descriptive data that allowed us to conclude that the third finger appears to specialize primarily in tasks requiring high mobility, sensitivity and precision while the fourth finger specializes for tasks requiring strength, scooping action and deep access.

Materials and methods

We observed free-ranging aye-ayes on a small (14 ha) island on Mananara River (S 16°10’ E 49°44’), close to Verezanantsoro National Park, eastern Madagascar. Most of the island is covered with mixed plantation, dominated by fruit trees, coconut palms and secondary forest trees (Andriamasimanana 1994). The aye-ayes were introduced onto the island in the 1980’s. During our fieldwork, there were four aye-ayes that were well habituated to the presence of observers: Lucy, an aged adult female; Rarach, her subadult son; Gomez, a young adult male; and Koulic, an aged adult male. All individuals could be reliably recognized from their distinct body features.

Aye-ayes were followed by two observers (SL and TJ) between April 2003 and October 2003. Data on finger use were collected during 58 night follows. One observer usually followed the animals during their whole active period (beginning at their emergence from the nest until retiring to the nest) and the second one only for the first half of this time (from their emergence from the nest until midnight). If possible, a single individual was followed for a given night by each observer. In the case the observer lost the animal, he attempted to re-locate the same individual. But if he instead found another individual, he continued in following the new one. We used LED headlamps and binoculars (8x30 and 8x40) to observe behavior of these nocturnal animals. The distance between the animal and the observer ranged between 2 – 30 m but it was approximately 10 m for most of the time. In case of grooming, which occurred higher in the canopy, the distance was 10-15 m for most of the time. Habituation of the four animals was highly satisfactory and we did not notice any cues of alteration of feeding or grooming behavior in response to the presence of observers.

Four recorded categories of hand use were defined as follows: (1) Tap: animal rhythmically taps on substrate with its finger in a stereotypic, species-specific way (Erickson 1994). (2) Probe: animal uses a single finger to insert it into any crevice and/or to insert the extracted food into its mouth. This term includes, but is not limited to, digit-feeding defined by Feistner *et al.* (1994) as scooping food or water into mouth with a finger. Probing does not necessarily result in consumption of food. (3) Mouth: animal inserts a single finger into its mouth. (4) Groom: animal uses one finger of its hand to scratch or to comb its fur.

Probing represents a highly variable behavior compared to tapping, putting finger in mouth or grooming fur. We therefore also recorded objects on which the animal foraged. Vegetable foods were classified into four categories: (1) Coconut: fruits of *Cocos nucifera* palms; aye-ayes foraged on the flesh after gnawing the fruit open. (2) Kernels: these were taken from *Terminalia cattappa* fruits after their stones were gnawed open; some stones contained a parasitic larva instead of the kernel, but this was extracted in the same way. (3) Jackfruit: sweet pulp from the large fruits of *Artocarpus heterophyllus* trees, extracted through a small hole gnawed through the skin of the fruit. *(4) Nectar:* taken from the banana *(Musa* sp.*)* flowers without any processing. Sources of animal food were classified into five categories: (5) Soft tissues: dead or live plant tissues other than wood, which most often included sheaths and petioles of *Cocos nucifera* palms; the most common prey were ants; (6) Dead wood: any prey from dead wood or dead bark; common prey were beetle larvae and termites. (7) Live wood: any prey from live wood or live bark; common prey were beetle larvae. (8) Bamboo: any prey from bamboo stalks, live or dead. (9) Twigs: any prey from small twigs, live or dead; eating from vines was also included here; common prey were ants and earwigs. Foraging on cankerous growths on *Intsia bijuga* trees could not be evaluated for digit use because it occurred in places with obscured visibility.

Behavioral sampling techniques were based on those described by Altmann (1974). Visibility was not always sufficient to identify fingers and recording all occurrences of finger use during a regular sampling period was therefore impossible. The main reasons for the data loss were brief duration and rapid speed of finger movements, which under conditions of obstructed visibility and limited illumination did not allow the observer to precisely identify the finger. We therefore adopted a combination of the instantaneous and *ad libitum* sampling techniques. In instantaneous sampling, we described the animals' momentary behavior at fixed 1-minute intervals; a finger use in this moment was considered a single instantaneous scan data entry. As can bee seen from an example sequence presented in Table 1, it is reasonable to consider consecutive scans collected on a same bout of foraging as statistically independent for evaluation of finger use. Finger use acts were brief relative to the one-minute sampling interval and the animals frequently switched their fingers as well as hands and body positions. We collected instantaneous data during sampling periods of 30 minutes that were separated by 30-minute breaks when the observer remained with the animal. In addition to the instantaneous data, we recorded a*d libitum* data on finger use when we were not able to distinguish the finger exactly at the point of the instantaneous scan. A continuous use of one finger (uninterrupted by other behavior) was considered as a single *ad libitum* data entry; if this act was described by an instantaneous scan, it was not recorded *ad libitum* to avoid duplication of data.

Table 2 summarizes amounts and proportions of *ad libitum* and instantaneous records for each behavior sampled. The proportion of *ad libitum* data varies between behaviors because of variability in visibility of different behaviors. However, it is not expected that visibility of the third and fourth finger use should vary in interaction with the sampling method and we therefore pooled the instantaneous and *ad libitum* data.

Table 2 also expresses number of instantaneous records of identified finger use as a percentage of total instantaneous records of hand use (when we were able to record that the animal uses either right or left hand) for the same activities. Because of the high rate of the unidentified finger-use scans, we have checked for a possible bias in identifying the finger by repeated watching of videotaped behavior. During the field study, we videotaped several bouts of feeding and grooming using SONY DCR-TRV230E video camera with infrared sensing. Additional footage of the same animals collected during the same period was provided to us by Nicolas Gabriel of St. Thomas Productions. We repeatedly watched of the videotaped sequences to in normal speed to uncover if some instances of the third or fourth finger use were lost due to a systematic bias, i.e., due to better visibility of the stronger fourth finger or due to slower movement of one of two fingers.

Following procedure commonly used in studies of lateral preferences in primates (Ward 1995), we applied binomial tests to test for finger preferences in individual acts and for individual objects, the null hypothesis being ambipreference ($p=q=0.5$). We conducted binomial tests for each individual as well as for the pooled data from all four individuals. The effect of individual identity and object being processed on finger preferences was analysed with a generalized linear model, GLM (Fahrmeir & Tutz 2002), with the numbers of records of usage of third and fourth finger as a dependent variable with binomial distribution and individual identity and object being processed as categorical predictors. Parameters were estimated with the maximum likelihood method and their significance was evaluated with difference of log-likelihood ($-2 \cdot \Delta \log L$) and its asymptotic χ^2 approximation. Two objects with no records of using the fourth finger (kernels and bamboo) were not included in the GLM analysis.

Tab. 1. One sequence of foraging on a live tree trunk transcribed from a videotaped behavior of one of the study subjects. The record describes all behaviors and also the hand used to tap and probe, time is indicated in minutes:seconds of the video record. Only third finger was uses in this sequence. The sequence is described by two instantaneous scans of tapping with the third finger. It is evident from the sequence that the two instantaneous records can be considered independent as they are separated by variable sequences of other behaviors (probing, gnawing, sniffing), changing hands and changing positions.

Minute 8	Minute 9	Minute 10
08:55 move 08:50 – 08:55 tap (right) 08:54 – 08:57 gnaw 08:57 – 08:58 tap (left) 08:58 – 08:59 gnaw 08:50 – 09:01 tap (right)	09:01 – 09:02 probe (right) 09:02 – 09:04 gnaw 09:04 – 09:09 probe (right) 09:09 – 09:11 tap (right) 09:11 – 09:19 move 09:19 – 09:25 tap (left) 09:25 – 09:30 sniff 09:30 – 09:33 gnaw 09:33 – 09:36 tap (right) 09:36 – 09:38 gnaw 09:38 – 09:45 tap (right) 09:45 – 09:57 sniff, move 09:57 – 10:00 tap (right)	10:00 – 10:04 move, gnaw 10:04 – 10:09 probe (left) 10:09 – 10:13 sniff, move 10:13 – 10:14 probe (left) 10:14 – 10:15 move, sniff 10:15 – 10:18 probe (right) 10:18 – 10:19 tap (left) 10:19 move
Minute 9 instantaneous record: tap	Minute 10 instantaneous record: tap	

Tab. 2. Sample size (number of records) for four types of finger-use behavior and two sampling techniques. The proportion of identified finger-use records is expressed as the proportion of identified hand-use records (i.e., instantaneous records, when it was identified that the animal uses its right or left hand)

	Hand use	Finger use		
	Instantaneous records	Instantaneous records (proportion of hand use records)	*Ad libitum* records	Total
Tap	209	18 (8.6 %)	45	63
Probe	1035	372 (35.9 %)	203	575
Mouth	13	0 (0.0 %)	12	12
Groom	109	8 (7.3 %)	28	36
Total	1366	398 (29.1 %)	288	686

Results

Table 3 shows results of binomial tests that compare use of the third and fourth finger for tapping, probing, putting in mouth and grooming (Fig. 2). For tapping, the animals predominantly used their third finger; the only observed case of tapping with the fourth finger involved the subadult male Rarach. For probing, three animals preferred their fourth finger; only Lucy showed nonsignificant result. Inserting fingers into the mouth occurred exclusively with the third finger. Grooming was observed being performed predominantly with the third finger, although using the fourth finger was also recorded for Lucy.

The GLM analysis shows significant effects of individual identity, objects of foraging and interaction of these two variables on finger preferences in the four aye-ayes we have observed:

Model: const + individual + object + individual*object; logL = -211.324, DF=28
-2ΔlogL (Model - object) = 216.011~ $\chi 2_{24}$, p=0.000
-2ΔlogL (Model - individual) = 130.422 ~ $\chi 2_{21}$, p=0.000
-2ΔlogL (Model - individual*object) = 130.422 ~ $\chi 2_{17}$, p=0.000

Tables 4 and 5 present data on probing with the third and fourth finger for extracting vegetable and animal food, respectively, from several different sources. Data show that feeding on coconuts is responsible for most of the observed use of the fourth finger for probing (Fig. 3). When feeding on jackfruit, the fourth finger was used almost exclusively. When feeding on banana flowers, the third finger was used almost exclusively, with the exception of a single case, where the fourth finger was used instead. In Lucy's case, only her third finger was used when extracting kernels from stones of *Terminalia catappa* fruits, but the sample size is too small to produce any significant results.

When foraging on invertebrates, finger use differed according to the substrate from which aye-ayes extracted the prey (Fig. 4). When foraging on live wood, bamboo or twigs, the third finger was used exclusively or almost exclusively. Differences between frequencies of use of each finger for probing in dead wood were not significant in any individual, but in total, the fourth finger was significantly preferred. All animals showed a significant preference for the use of one finger when foraging from soft plant tissues, except in Rarach's case where data were insufficient. But the preference for either third or fourth finger for probing in soft tissues differed between individuals.

Tab. 3. Sample size (number of records) for four types of finger-use behavior and two sampling techniques. The proportion of identified finger-use records is expressed as the proportion of identified hand-use records (i.e., instantaneous records, when it was identified that the animal uses its right or left hand)

	Tap			Probe			Mouth			Groom		
	3rd	4th	p	3rd	4th	p	3rd	4th	p	3rd	4th	p
Lucy	22	0	0.000***	98	86	0.080	8	0	0.008**	12	3	0.028*
Koulich	1	0	1.000	27	118	0.000***	2	0	0.500	1	0	1.000
Gomez	33	0	0.000***	41	95	0.000***	1	0	1.000	6	0	0.031*
Rarach	6	1	0.109	41	66	0.008**	1	0	1.000	14	0	0.000***
Total	62	1	0.000***	207	365	0.000***	12	0	0.000***	33	3	0.000***

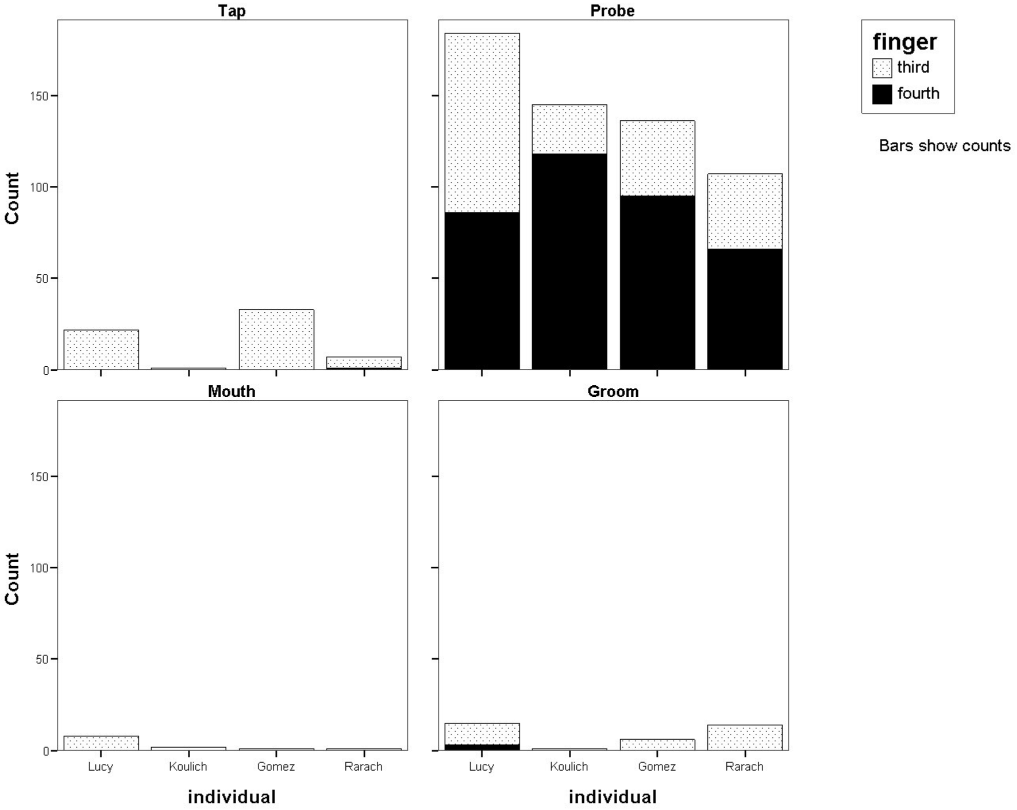

Fig. 2. Number of records of using the third and the fourth finger in four individuals and four main finger-use behaviors.

Tab. 4. Number of records and results of binomial tests for preference of the third and fourth finger for probing in four individuals and three different sources of vegetable food. Significance level indicated by asterisks: p < 0.001***, p < 0.010**, p < 0.050*

	Coconut			Kernels			Jackfruit			Nectar		
	3rd	4th	p	3rd	4th	p	3rd	4th	p	3rd	4th	p
Lucy	40	69	0.003**	5	0	0.062	0	11	0.001**	4	1	0.312
Koulic	16	72	0.000***	0	0	-	0	7	0.016*	0	0	-
Gomez	9	70	0.000***	0	0	-	0	9	0.004**	4	0	0.125
Rarach	21	49	0.001**	0	0	-	3	16	0.004**	3	0	0.250
Total	86	260	0.000***	5	0	0.062	3	43	0.000***	11	1	0.006**

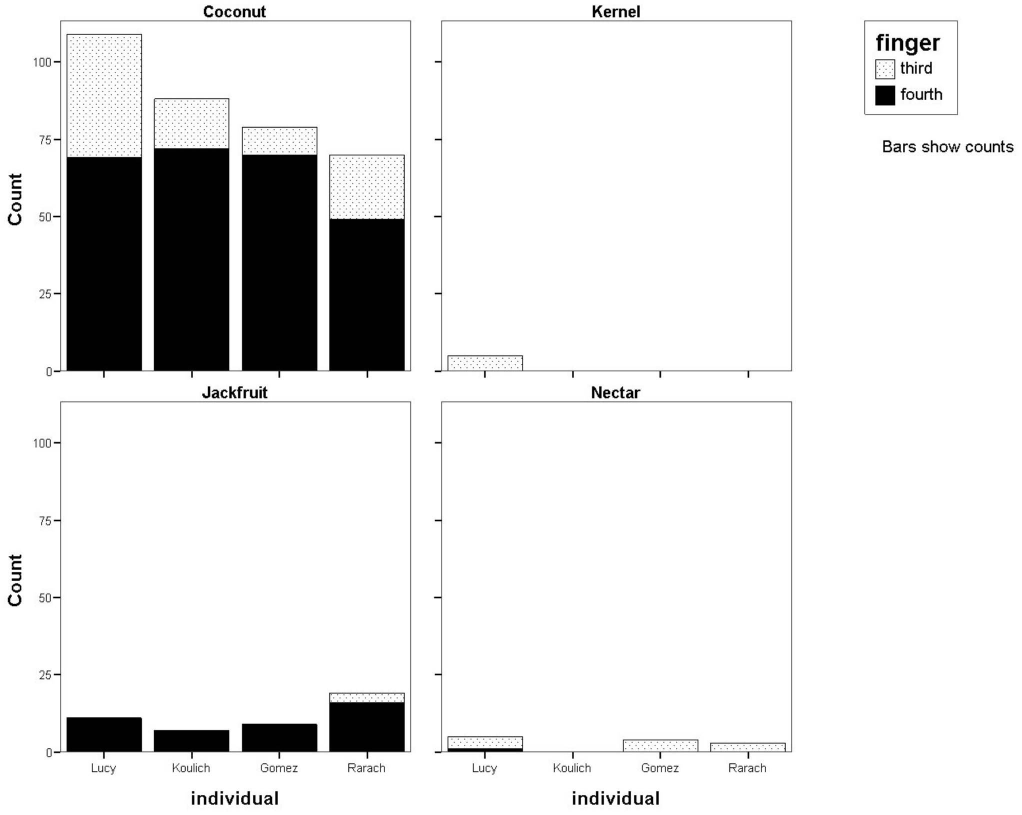

Fig. 3. Number of records of using the third and fourth finger for probing in four individuals and three different sources of vegetable food.

Tab. 5. Number of records and results of binomial tests for preference of the third and fourth finger for probing in four individuals and four different sources of animal food. Significance level indicated by asterisks: p < 0.001***, p < 0.010**, p < 0.050*

	Soft tissues			Dead wood			Live wood			Bamboo			Twigs		
	3rd	4th	p	3rd	4th	p	3rd	4th	p	3rd	4th	p	3rd	4th	p
Lucy	10	0	0.002**	6	4	0.547	22	0	0.000***	2	0	0.500	12	1	0.003**
Koulic	1	37	0.000***	5	2	0.469	0	0	-	6	0	0.031	0	0	-
Gomez	3	8	0.035*	13	6	0.142	2	2	0.750	12	0	0.000	1	0	1.000
Rarach	1	0	0.250	3	1	0.500	5	0	0.063	1	0	1.000	2	0	0.500
Total	15	45	0.000***	27	13	0.022*	29	2	0.000***	21	0	0.000	15	1	0.001**

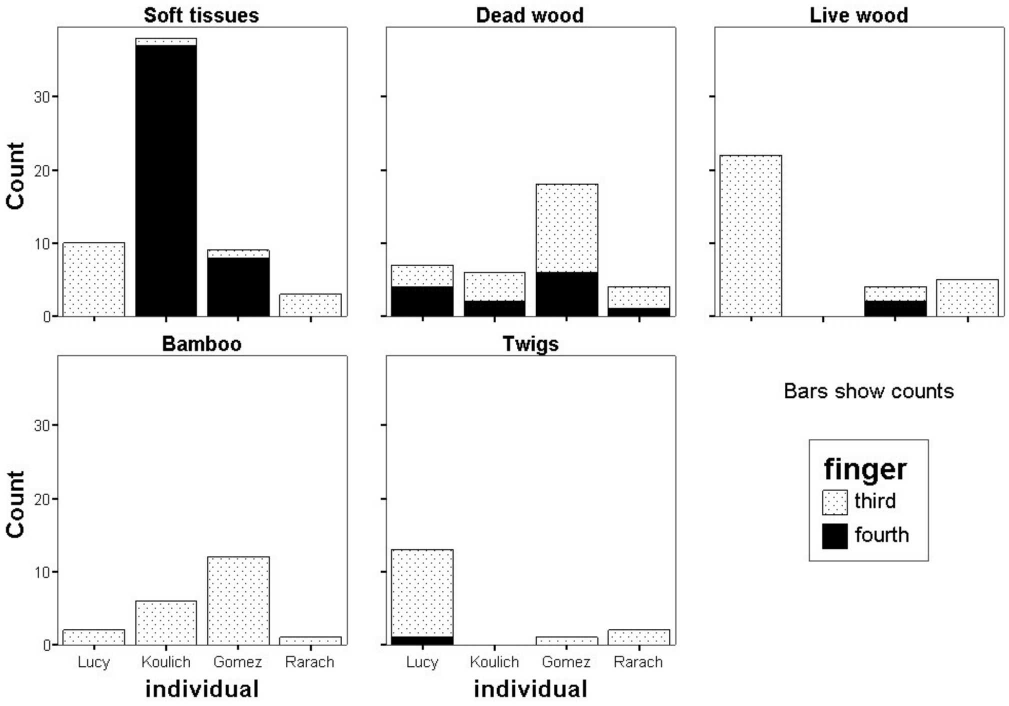

Fig. 4. Number of records of using the third and fourth finger for probing in four individuals and four different sources of animal food.

Discussion

Our data clearly show that not only the third finger but also the fourth finger of the aye-aye has been specialized for unique foraging tasks. Each of the two fingers plays a different role during the aye-aye's foraging. For most tasks, either the third or the fourth finger is preferred. When both fingers are used, they apparently have complementary roles. In general, the third finger specializes for tasks requiring high mobility, sensitivity and precision, whilst the fourth finger specializes for tasks requiring strength, scooping action or deep access.

The third finger was used for a broader range of tasks compared to the fourth finger, and was exclusively used for some activities, at least within our limited sample. Several previous reports state that aye-ayes use only the third finger for tapping (Petter & Petter 1967; Milliken *et al.* 1991; Ancrenaz *et al.* 1994; Andriamasimanana 1994; Sterling 1994; Erickson 1995). Although we did record a single instance of tapping with the fourth finger, it is probably exceptional and it is also possible that the finger was misidentified. Tapping was very common and the relatively low frequency of recorded cases does not reflect its low incidence but rather the difficulties posed by field conditions, in identifying the rapidly moving finger.

Also for inserting a finger into the mouth, we recorded only using the third finger. We suggest that this act was comprised of two different behaviors that we were unable to discriminate reliably. Following feeding with their digit, especially on coconuts, aye-ayes may put their finger into the mouth to lick the remaining contents. But the fact, that this behavior frequently occurs also outside the feeding context, suggests that aye-ayes also use their third finger to remove food remnants or dirt caught between their teeth. The third finger therefore probably serves as a tooth-cleaning member, which is unusual amongst primates.

According to our data, aye-ayes also preferred the third finger for grooming fur. But close inspection of grooming bouts that were video recorded suggests that in this case, sampling bias may have played a major role. Footage shows that aye-ayes also used their fourth fingers extensively for combing fur. But as the hand movements were quick, it was very difficult to differentiate what finger was being used and repeated watching of the video record was often required. In the field, the finger would probably not be identified and the act would not be entered into the data set. On the other hand, grooming with the third finger was often (although not always) delicate and slow, making it easier to determine and record the finger. Published descriptions of aye-aye grooming are not very explicit concerning what fingers were used. Ancrenaz *et al.* (1994) report that aye-ayes used their third finger to scratch and wipe the face and to scratch the body but they also mention grooming “using hands and feet” with no specification of fingers. Winn (1994) reports that an infant aye-aye groomed its face using the third finger but scratched/groomed its body with either the third or fourth finger. Also, Iwano (1991) reports grooming with both the third and fourth finger. It is clear that aye-ayes use both fingers for grooming, but the exact proportions and the possible differentiation of roles remain unclear.

From all our observations on aye-aye finger-use, probing was the most variable action performed by the specialized fingers. Both fingers were used for this purpose in different contexts. One of the tasks undertaken almost exclusively with the third finger was feeding on nectar. During our observations, only banana *(Musa* sp.*)* flowers were available. But the most important seasonal source of nectar for aye-ayes, flowers of *Ravenala madagascariensis*, are also exploited using the third finger, as reported by Ancrenaz *et al.* (1994) and Sterling (1994). Another example of the almost exclusive use of the third finger for soft probing may be eating eggs in captive aye-ayes (Iwano 1991) or eating ants and probably also other insects from hollow twigs as observed in our study. But besides this “soft work”, the third finger is also used to probe into cavities in hard materials that are difficult to open mechanically. This includes extracting insects from live wood and bamboo as well as extracting kernels (and parasitic insects) from fruit stones. Kernels (or parasitic larvae in stones) were eaten infrequently at our field site and the number of instances is small, but in every case only the third finger was used. Petter and Petter (1967) describe feeding on the same species, *Terminalia catappa,* and they also mention use of the third digit. In other field sites, kernels from ramy *(Canarium* sp.*)* are perhaps the most important food for aye-ayes and feeding on this fruit has been described in details. Sterling (1994), Kitko *et al.* (1996) and Iwano (1991) all state that aye-ayes use their third finger to extract kernels from the ramy locules.

There are however food resources that are preferably exploited with the robust fourth finger. When eating pulpy fruits, the fourth finger seems to be used as a scoop. It was strongly preferred for eating jackfruits in our study. It was also preferred for eating bananas and tomatoes by a captive female observed by Iwano (1991), although the same animal used both fingers for eating passion fruits *(Passiflora* sp.*)* and preferred the third finger when eating papayas *(Carica papaya).* Andriamasimanana (1994) also reports using third finger while eating fruits in wild aye-ayes, but it is not specified what kind of fruit.

Except for some fruits, the fourth finger is used for probing in sequence with the third finger. In our field site, coconuts were the most common food eaten with both fingers. Although Petter and Petter (1967) mention that only the third finger is used when feeding on a coconut, they do not describe the coconut feeding in detail and it is likely that the usage of the fourth finger was missed in this early observation with a limited use of a flashlight. Iwano (1991) also reports eating coconut with the third finger by a captive aye-aye, but these were sliced coconut pieces; when the same animal obtained and opened an intact coconut, it used both fingers to extract the flesh. In our study, both fingers were used and it appeared that their roles differed; we were able to confirm this hypothesis after watching video sequence recorded by Nicolas Gabriel (St. Thomas Productions) using an endoscope camera placed inside a coconut and presented to a captive subadult male in the Jersey Zoo. In this video one can see that the fourth finger acts as a scoop, scratching the coconut flesh with rapid movements that are audible to human observers in the field. It then collects the shavings piled inside the nut, primarily using its third finger, with slower, silent and less stereotypic movements. It is possible that a similar division of roles of the two fingers occurs when foraging for insects in dead wood or soft plant tissues, but because this behavior was more variable, we are not able to confirm this from our observations. However, in some cases the aye-ayes used their fourth finger to enlarge the cavities in the dead wood, with sawdust shed from the cavity being clearly visible.

Data of Milliken (Milliken 1995) provide some additional insights into differentiated use of the two fingers in aye-ayes, indicating that the fourth finger may be also important for accessing deep cavities. He observed an increased usage of the fourth finger in deep vertical cavities of an experimental apparatus, and the effect was stronger in relatively short-fingered females than in the long-fingered males. But in the wild, where the insect mines are not straight vertical holes, the deep access with the fourth finger can probably be reached only in soft, rotten wood. In the field, we never observed the simultaneous (instead of sequential) use of the third and forth finger as reported by Milliken (1995). But even in the Milliken's study, the combined use of two fingers occurred sometimes in deep cavities of the experimental apparatus but the incidence was low and it was not clear whether it had any functional significance in terms of improved rate of larvae extraction.

Differences in finger use correspond to differences in the third and fourth finger morphology (Soligo 2005, Milliken *et al.* 1991). The third finger is highly mobile, especially in the metacarpophalangeal joint, it is very thin and, supposedly, very sensitive. This makes it, compared to the fourth finger, a better probe to access narrow cavities in hard wood or bamboo, including irregular mines of insects like termites, where it can hook and extract an invertebrate prey. It is also well suited for collecting nectar from flowers. But it may be too fragile to resist strong bending or compressive forces. On the other hand, the fourth finger is very long, robust, and equipped with strong muscles and a big claw. These characters make it usable for penetrating in or enlarging holes in fruit pulp, rotten wood or other relatively soft materials. It is also suitable as a scratching tool to scrape solid contents of fruits or seeds. Furthermore, the fourth finger is strong enough to play an important role in securing positional support (Soligo 2005). It is likely that it was the fact that the fourth finger supplies these important roles, which allowed the aye-aye to evolve more advanced morphological specializations of the third finger.

In conclusion we may stress that the hand of aye-ayes is unique in possessing two fingers that are specialized for behaviors unparalleled by any other primate. Besides the often-discussed function of the thin third finger, the results of this study have shown that the strong fourth finger also appears to have very specialized functions.

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Chapter 3

Lateralized hand use in free-ranging aye-ayes *(Daubentonia madagascariensis)* and comparison with captive studies

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Abstract

We observed hand use in free-ranging aye-ayes *(Daubentonia madagascariensis)* on an island on Mananara River, east Madagascar. Results were compared with two conflicting studies on hand laterality in captive aye-ayes. We argue that patterns of hand preference in wild aye-ayes are comparable to those of captive animals and that discrepancies between studies are at least partly caused by different way of collecting and processing data. Aye-ayes fit Level 2 of the categories of hand laterality described by McGrew & Marchant (1997), with some individuals showing significant hand preference but with the proportion of right to left preferent animals being very close to 1 : 1. Hand preference is consistent for two of the most frequent behaviors, tapping and probing with fingers. Reaching and holding objects in hands is rare in aye-ayes. No effect of sex on hand preference was detected and it remains open whether there is an effect of age. Posture adopted by animals did not influence hand preference. Some other factors that may possibly constrain hand preferences in aye-ayes are discussed.

Key words: *Daubentonia madagascariensis*, laterality, hand, primates, prosimians, foraging, Madagascar

Introduction

The predominant right-handedness is sometimes believed to be unique to humans (Warren 1980; McGrew & Marchant 1997). Other researchers propose that laterality in hand use is a very ancient trait that we share with non-human primates (MacNeilage *et al.* 1987; Ward 1995). Hand (or paw or foot) laterality has been reported in a diverse range of animals such as toads, parrots, chickens, cats, dogs, rats, mice, lemurs, bushbabies, monkeys and apes (for review see Hook 2004). McGrew & Marchant (1997) proposed several categories of hand laterality in primates. In this paper, we will consider the basic category, *hand preference*, which describes a significant bias in hand use in any direction (right or left) in a given animal and in a given task, which need not be stable between individuals and tasks.

Prosimians appear to show a bias towards using the left hand for visually guided reaching (Sanford *et al.* 1984; Larson *et al.* 1989). The bias was often stronger in males (Ward *et al.* 1990; Milliken *et al.* 2005). There may be an increase with age in strength of laterality but also in proportion of animals that show the right-hand bias (Ward *et al.* 1990). Predominantly right-hand preference is sometimes found in females (Milliken *et al.* 1991; Dodson *et al.* 1992) and possibly in old animals (Forsythe & Ward 1988).

The evolutionary scenario presented by MacNeilage *et al.* (1987) relates the prosimian left hand bias to the hand preference pattern they proposed for anthropoids. According to these authors, hand preferences first evolved for ballistic capture of insects in ancestral primates. The left hand was specifically used for capturing and firmly holding prey whilst the right hand was used for maintaining a tripedal positional support. When anthropoids filled more frugivorous niches, the left hand retained its role in reaching and holding fruits while the right hand changed its function and specialized in fine manipulation tasks (opening, peeling, etc.) with the food held in the left hand. This hypothesis is sometimes referred to as “the postural origin hypothesis”, thus stressing that the right hand originally specialized for maintaining postural support. It is partly supported by studies on sifakas, *Propithecus* spp., (Milliken *et al.* 2005) and indris, *Indri indri*, (Rigamonti *et al.* 2005).

Other hypotheses propose different effects of posture on hand laterality. In lesser bushbabies *(Galago senegalensis)*, patterns of hand preference emerged or were intensified whilst in the bipedal stance. It was argued that when adopting an unstable position, the need of coordination of the neural motoric systems also activates systems responsible for laterality (Larson *et al.* 1989; Dodson *et al.* 1992). Primates such as aye-ayes only rarely adopt bipedal stance (Lhota & Jůnek, pers. obs.), but a similar hypothesis may apply to other demanding postures, as may be the case in the black-and-white ruffed lemur, *Varecia variegata* (Forsythe *et al.* 1988). Contrariwise to this hypothesis, it was suggested that the need to maintain a comfortable position on branches might constrain expression of hand preference. In gentle lemurs *(Hapalemur griseus* and *H. alaotrensis)*, hand preference was stronger while feeding on a platform, compared to foraging on bamboo shoots. In bamboo feeding, the lateralization was stronger after a shoot was already detached from the stalk and the animal was free to re-position itself (Stafford *et al.* 1993).

Findings about hand preference in anthropids differ between field and captive setting: *Cebus* spp. (Panger 1998), *Semnopithecus entellus* (Mittra *et al.* 1997), *Pan troglodytes* (Marchant & McGrew 1996; McGrew & Marchant 2001). This need not be the case in prosimians. Shaw *et al.* (2004) found similar hand preference in ring-tailed lemurs *(Lemur catta)* while kept semi-free-ranging as when in winter enclosures; they suggest that if there is any effect of captivity, it may be caused by artificial food presentation. This was also shown in sifakas (Milliken *et al.* 2005) but Stafford *et al.* (1993) still found correspondence between hand preference in reaching for chopped fruits and in species-specific bamboo feeding in gentle lemurs. Aye-ayes *(Daubentonia madagascariensis)* provide us with an opportunity to compare three settings: wild, captive-naturalistic and captive-test. In addition to our field study, there is a published report by Feistner *et al.* (1994) on natural-like free feeding in captive aye-ayes in Jersey Wildlife Preservation Trust (JWPC; now Durrell Wildlife Preservation Trust, DWPC) and Duke University Primate Center (DUPC) and another paper on hand preferences in controlled test conditions in DUPC (Milliken 1995). The two captive studies lead to different conclusions. During free feeding, some animals did not show any significant hand preference while others were lateralized in both directions. In contrast, all four animals in the controlled test setting showed significant right hand bias in several preference and performance measures of digit use.

The aye-aye is a highly specialized Madagascan lemur. It forages on mechanically defended food resources such as nut kernels or wood-boring insects (Sterling 1994). Its rodent-like incisors can gnaw-open wood or nutshells. The thin third finger rapidly taps on the surface, enabling the animal to inspect the internal structure by perceiving resonations (Erickson 1994). After opening a cavity, the aye-aye probes inside with one of its two specialized fingers (third or fourth) to extract the content. Although it was never been studied in wild, it is likely that aye-ayes' specialized way of food acquisition requires a long period of learning the foraging skills (Krakauer 2004).

Being nocturnal, rare and cryptic, aye-ayes are not easily observed in the wild. We have taken opportunity to study details of hand use in four well-habituated free-ranging aye-ayes. We have collected detailed descriptive data on the patterns of hand use, tested whether there is preference of hand use in individual aye-ayes, compared the field data with those collected earlier on captive animals, and used the combined sample on wild and captive aye-ayes to test the effect of age and sex on hand preference. Finally, we tested the effect of body posture on strength of hand use laterality.

Materials and methods

Study area and subjects

We observed free-ranging aye-ayes on a small (14 ha) island on Mananara River (S 16°10’ E 49°44’), close to Verezanantsoro National Park, eastern Madagascar. Most of the island is covered with mixed plantation, dominated by fruit trees, coconut palms and secondary forest trees (Adriamasimanana 1994). The aye-ayes were introduced onto the island in the 1980’s. During our fieldwork, there were four aye-ayes that were well habituated to the presence of observers: Lucy, a mature adult female; Rarach, her subadult son; Gomez, a young adult male; and Koulic, a mature adult male. All individuals could be recognized reliably from their distinct body features. The age of Rarach was estimated to be 2 years at the beginning of our study, based on consultation with experienced aye-aye keepers from DWPT and DUPC. In addition to these, two new adults appeared on the island, apparently being released by villagers. They were not habituated but we were able to observe one of them (Darja, a young adult female) for one and a half night.

Procedure

Aye-ayes were followed by two observers (SL and TJ) between April 2003 and October 2003. Data on hand preference were collected during 83 night follows. One observer usually followed the animals during their whole active period (beginning when the animals emerged from the nest until they retired to the nest) and the other one only for the first half of this active period (ending at midnight). If possible, a single individual would be followed for a given night by each observer, but in the event that the observer lost track of the focal animal, another animal would be tracked. We used LED headlamps and binoculars (8x30 and 8x40) to observe behavior.

Behavioral sampling techniques were based on those described by Altmann (1974). There were some limitations to the data collection due to the demanding nature of nocturnal observations. Visibility was not always good enough to reliably identify which hand was used and as a result, some bouts of hand use were missed. Although we attempted to use the continuous focal animal sampling method, we had to collect data using the *ad libitum* sampling method instead. In *ad libitum* sampling, we observed the animal continuously during the sampling period but we recorded instances of hand use only when the animal was visible enough to allow recording details of its hand use. We also collected data using the focal instantaneous sampling in one-minute intervals. *Ad libitum* and focal instantaneous data were collected simultaneously during sampling periods of 30 minutes separated by 30-minute breaks during which time the observer remained with the animal.

Four recorded categories of hand use were defined: (1) *Hold:* Animal holds an object in its hands, using any form of grip with more than a single finger. It includes holding any detached object. It may also include holding an attached object if it represents manipulation rather than securing postural support. (2) *Tap:* Animal rhythmically taps on substrate with its finger in a stereotypic, species-specific way. (3) *Probe:* Animal uses a single finger to insert it into any crevice and/or to insert a food item into its mouth. This includes behavior described as digit-feeding by Feistner *et al.* (1994). (4) *Groom:* The animal scratches or combs its fur (we recorded whether hands, feet or mouth were used).

Besides recording the category of hand use and the hand (right, left or both), we have for each data entry also described the object that was being processed and the behavioral context in as many details as practicable. We were however not always able to differentiate whether the aye-aye used the third or fourth finger for probing and grooming; we have therefore pooled data for both fingers.

In addition to data on hand use, data on body posture were simultaneously collected during the focal instantaneous sampling sessions. We classified a number of postures but most of them were rare and for the present analysis, we had to lump them into two broad categories: easy and demanding postures. These categories were based on our assessment of difficulty to secure a stable position on the substrate. *Easy postures* included sitting, lying, standing or quadrupedal moving along a substrate inclined less than estimated 55°. *Demanding postures* included all suspended positions, descending head-down and clinging or moving on a substrate with an estimated inclination of 55° or more. Estimated substrate inclination was recorded to the nearest multiple of 5°; the threshold of 55° was selected *post hoc* as the value where the total frequency of the substrate-use instantaneous sampling points dropped most rapidly.

Data processing and analysis

We assigned sequences of consecutive data entries to hand use bouts that we considered independent under our assumption that the non-independence would result predominantly from specific requirements of the positioning on the substrate and the specific body posture adopted by the animal. Two sequences of data points were considered as two bouts if they were separated by either (a) the animal moving to another place while not engaged in tapping or probing or (b) the animal changing its body posture or mode of locomotion (while still engaged in hand use). Data entries were still considered to belong to a single bout if they were separated by an interval of inactivity or by a different behavioral act (e.g. gnawing, vigilance, or different hand use) without changing body posture or place. These criteria are more conservative than those used by most authors (McGrew & Marchant 1997). But still, a sequence of continuous feeding, exploration or grooming could lead to several independent hand use bouts in the event that the animal changed its place or posture.

Most of bouts of hand use were recorded as several interdependent data entries, with the beginning of the bout often noted *ad libitum* and one or several additional focal instantaneous point data recorded in case that the bout continued in the following minutes. To generate a set of independent data, we *post hoc* characterized the hand use for each bout in two ways. ‘First-noted hand’ measure was intended to enable us to use the binomial test, as has been also used in other studies. For each bout, only the first recorded hand was considered. It was an *ad libitum* record (when visibility was good to note the proper beginning of sequence) or the first instantaneous entry. The disadvantage of using the ‘first-noted’ hand may be that it may not be representative of a whole sequence of hand use, which may last several minutes (Hopkins 1999). We therefore invented a second measure, the ‘bout score’. It was based on the focal instantaneous data points collected on a given bout and represents the difference in number of instantaneous entries for the right and left hand. A positive score represents right hand preference for a given bout.

To test for lateral biases in the ‘first-noted hand’ measure, we followed a procedure applied in a number of previous studies on prosimians where data for each animal are analyzed using binomial tests. Z-scores were computed according to the formula $z = [x - (n \cdot p)] / [\text{square root } (n \cdot p \cdot q)]$, where n = total number of responses, x = number of right hand responses, and p and q are proportions of right and left responses under null hypothesis, i.e. $p = q = 0.05$ (MacNeilage *et al.* 1987; Ward 1995). Z-scores within the two-tailed confidence interval of 0.05 (i.e., $-1.95 < z < 1.95$) were considered significant. In addition to z-scores, we present also the handedness indices (HI) computed from right (R) and left (L) hand responses according to the following formula: $HI = (\#R - \#L)/(\#R + \#L)$ (Hopkins 1999). HIs are descriptive measures of the magnitude of the bias. Data for the little-observed female Darja are also included; although her sample sizes are small, it is still comparable to sample on several animals tested in the former study (Feistner *et al.* 1994).

All the following tests were performed using JMP 3.2.2.0 (© SAS Institute Inc.) software and results were considered significant at $\alpha = 0.05$ level. Non-parametric Wilcoxon signed rank test was used to detect laterality in bout scores (null hypothesis: median bout score = 0). Parametric tests were applied for comparing HIs, which did not deviate from normal distribution. To test for correlation between HIs for probing and tapping across all individuals, we used Pearson correlation coefficient. The t-test was applied to compare HIs for probing and tapping in wild animals with those computed from the published data on captive aye-ayes (Feistner *et al.* 1994). To test for strength of lateralization with no regard to its direction we also analyzed absolute values of HIs. In this case, because the Levene test detected significant differences in variance between wild and captive animals, we used instead of the t-test the Welch ANOVA, which allows variances being unequal.

After finding no significant difference in HIs, the data for wild and captive aye-ayes were pooled and HIs for probing and tapping were analyzed as continuous dependent variables in two-way ANOVA with interaction, with age and sex as the independent variables.

A log-linear model was applied to test for the effect of posture on hand preferences in four wild animals in Mnanara, excluding the less-observed female Darja. Probing bouts rather than tapping bouts were analyzed because they had more data entries; some bouts had to be omitted due to the posture not being identified. The ‘first-noted hand’ was used as a dependent nominal variable and individual and posture as independent variables, their interaction was also considered. Finally, an analogous two-way ANOVA with interaction with the ‘bout score’ as a continuous dependent variable was conducted.

Results

Description of hand use

When considering data from the four regularly observed animals only, there was a total of 1401 instantaneous point entries of identified use of right, left or both hands (Lucy: 492; Koulic: 230; Gomez: 262; Rarach: 417).

Holding objects in hands was infrequent, accounting for only 46 of 1401 hand-use scans (3.3 %). It occurred during foraging (33 scans) or grooming (13 scans). Specifically, holding during foraging accompanied gnawing (fruits, twigs or a piece bark being peeled), inspecting of or probing detached objects (fruits, twigs and galls on bark) and inserting a piece of coconut flesh or a big larva into the mouth. Holding whilst foraging was bimanual in 21 of the 33 scans, only left hand was used in 8 scans and only right hand in 4 scans. During grooming, the animals sometimes held their tail in their hands (being often suspended head-down by hind legs). They used to hold the tail with both hands when grooming it with the mouth (5 scans); the unimanual hold was adopted only when the animal used the opposite hand for the grooming (8 scans). Holding was occasionally noted outside the foraging and grooming context, such as when gnawing off twigs or leaves to build the nest or when restraining an infant.

The majority of recorded scans of hand use included using one of the two specialized fingers rather than the whole-hand grasp (1366 scans, 97.5 % of hand-use scans). This included, besides tapping (209 scans, 15.3 % of all finger-use scans), probing (1035 scans, 75.7 %) and grooming (109 scans, 8.0 %), also inserting fingers into the mouth, possibly cleaning teeth (13 scans, 0.9 %). Finger use was always unimanual and in only 0.8 % of finger use scans the other hand assisted by holding the object (whilst probing: 3 scans, whilst grooming: 8 scans). Sequential bimanual use of fingers (i.e. rapid alternations of both hands during a single bout of tapping, probing or grooming) appeared to be common; this was however not systematically quantified.

For *tapping* the aye-ayes used their third finger. The context included either exploration or feeding but these two were often indistinguishable. Objects or substrates being tapped most often were wood and bark, but the animals would tap on almost anything, including coconuts and other fruits, flowers, palm leaves or aye-aye urine marks left on branches.

Probing (including feeding with finger) was the most prevalent form of hand use among the observed aye-ayes. Compared to relatively stereotyped tapping, these were highly variable behaviors that might take form of soft probing into minute crevices as well as relatively harsh scratching inside deep holes. Either third or fourth finger could be used. Objects being probed included wood, bark, twigs, bamboo, coconuts, kernels, fruits, flowers, galls on bark, touchwood, palm sheaths and leaves. As with tapping, the context included feeding and exploration but these two were often indistinguishable.

For *grooming* the aye-ayes used their hands (77.6 % of 147 scans where details of grooming could be described), feet (17.7 %) or mouth (4.0 %); observations of grooming using the feet and mouth were not included in the hand-use scans. With the hind feet, the aye-ayes repeatedly scratched the fur in a simple, stereotypic sequence, but grooming with the hands was more variable. Besides simple scratching sequences there were also careful and attentive bouts of less stereotyped combing of the fur. In most cases, we were able to confirm that only one finger was used, either the fourth or the third one. We did not notice any differences in hand use during autogrooming of the fur and during allogrooming. As the latter was very rare (4 scans of Lucy grooming her infant), we combined both for laterality analysis.

Patterns of hand preferences

Table 1 shows results of binomial tests and handedness indices (HI) for the 'first-noted hand' measure in the wild aye-ayes in Mananara and for the captive animals studied by Feistner *et al.* (1994). The modal pattern within the sample shows no significant hand preference and a low HI of 0.2 or less. But five of the 16 animals did show significant hand preference for taping and 7 did so for probing. There are significant results in both directions across the range of sample sizes and some animals have very high values of HIs. In grooming, none of the four animals in Mananara showed significant hand preference but the sample sizes are small compared to the other measures.

The direction of hand preference (left or right) differs between individuals in the combined sample. If only significant results are considered, 4 animals show a right hand preference and 3 show a left hand preference for probing. For the tapping action, 2 animals show a right hand bias and 3 a left hand bias. If all data are considered, the counts of right (positive) to left (negative) handedness indices are 7 and 9, respectively, for probing; and 8 and 8 for tapping. Yet the hand preference does show stability between tasks; there is a marginally significant correlation between HIs for taping and probing across all individuals (r=0.49, p=0.05). In three animals with significant hand preference for both tapping and probing, these are always in the same direction (right for Patrice, left for Mina and Samantha).

Table 1. Frequencies of hand use, z-scores and handedness indices (HI) describing hand preference in tapping, probing (or digit-feeding) and grooming in aye ayes in the present study on free-ranging animals in Mananara (Man.) and in the previous study on captive animals in JWPT and DUPC (Feistner *et al.* 1994). Asterisks indicate significance of binomial tests of hand preference. Age category and sex of each animal is noted: adult male (am), adult female (af), immature male (im) or immature female (if).

	Measure	Left	Right	z-score	HI
Gomez (am, Man.)	probe	26	38	1.50	0.19
	tap	16	25	1.41	0.22
	groom	9	7	-0.50	-0.13
Koulic (am, Man.)	probe	28	12	-2.53*	-0.40
	tap	6	10	1.00	0.25
	groom	3	5	0.71	0.25
Lucy (af, Man.)	probe	53	80	2.34*	0.20
	tap	38	32	-0.72	-0.09
	groom	10	14	0.82	0.17

Rarach (im, Man.)	probe	39	46	0.76	0.08
	tap	18	25	1.07	0.16
	groom	10	12	0.43	0.09
Darja (af, Man.)	probe	9	6	-0.77	-0.20
	tap	10	6	-1.00	-0.25
Alain (am, JWPT)	probe	60	47	-1.26	-0.12
	tap	12	9	-0.65	-0.14
Patrice (am, JWPT)	probe	12	37	3.57***	0.51
	tap	4	24	3.78***	0.71
Nosferatu (am, DUPC)	probe	6	3	-1.00	-0.33
	tap	3	4	0.38	0.14
Poe (am, DUPC)	probe	8	3	-1.51	-0.46
	tap	15	28	1.58*	0.30
Juliet (af, JWPT)	probe	25	21	-0.59	-0.09
	tap	33	29	-0.51	-0.07
Mina (af, JWPT)	probe	97	65	-2.51**	-0.20
	tap	58	17	-4.73***	-0.55
Samantha (af, DUPC)	probe	18	1	-3.90***	-0.90
	tap	31	7	-3.89***	-0.63
Zaza (if, JWPT)	probe	21	53	3.72***	0.43
	tap	116	145	1.80	0.11
Fred (if, JWPT)	probe	57	73	1.40	0.12
	tap	124	112	-0.78	-0.05
Sambany (if, JWPT)	probe	88	77	-0.06	-0.07
	tap	141	73	-4.65***	-0.32
Annabellee (if, DUPC)	probe	3	15	2.83**	0.67
	tap	12	14	0.39	0.08

(Table 1, continued from the previous page)

Results of Wilcoxon signed rank tests of hand preference based on the bout scores for the four extensively observed Mananara individuals are presented in Table 2. These tests appear less sensitive in relation to the binomial tests based on the ‘first-noted’ hand use. The only significant result was the left hand bias shown by Koulic. But the directions shown by the bout scores were with no exception the same as those shown by HIs based on ‘first-noted’ hand use for tapping and probing. This suggests that the ‘first-noted’ hand measure represents well the whole hand use sequence.

Table 2. Descriptive statistics on hand use bout scores of free-ranging animals in Mananara and results of the Wilcoxon signed rank test of the hypothesis that the median bout score = 0.

Animal	Measure	n	Mean bout score	SE	Median bout score	p
Gomez	probe	64	0.28	0.26	1	0.202
	tap	40	0.23	0.17	1	0.184
	groom	16	-0.06	0.28	-1	1.000
Koulic	probe	40	-1.83	0.62	-1	0.003
	tap	16	0.06	0.36	1	0.651
	groom	8	0.38	0.38	0.5	0.531
Lucy	probe	133	0.24	0.18	1	0.098
	tap	70	-1.17	1.15	-1	0.295
	groom	24	-0.13	0.34	1	0.977
Rarach	probe	85	0.34	0.33	1	0.225
	tap	42	0.21	1.16	1	0.221
	groom	22	0.14	0.29	0	0.826

Patterns of individual hand preferences were very similar for wild and captive aye-ayes. There are no significant differences between wild and captive animals in HIs for probing (t_{14}=-0.06, p=0.95) and tapping (t_{14}=-0.52, p=0.61). When comparing absolute values of HIs, the variance was lower in wild animals in both measures (probing: $F_{1,14}$=4.31, p=0.06; tapping: $F_{1,14}$=6.59, p=0.02), so we used the Welch ANOVA. There were again no significant differences between wild and captive aye-ayes (probing: $F_{1,13.999}$=2.10, p=0.17, tapping: $F_{1,12.908}$=1.23, p=0.29).

When HIs from the combined data set (wild and captive animals) are analyzed as a function of age category, sex, and the interaction of those two variables, the whole-model test shows non-significant results for HIs for probing ($F_{3,12}$=1.56, p=0.25). It is significant for HIs for tapping ($F_{3,12}$=4.67, p=0.02) with females more left-preferent compared to males (F_1=5.72, p=0.03), the other effects being non-significant. When only the strength of lateralization is considered (i.e., the absolute values of HIs are used), the whole-model test shows non-significant results for both probing ($F_{3,12}$=1.49, p=0.27) and tapping ($F_{3,12}$=0.66, p=0.59).

Finally, the effect of posture on hand preference for probing was tested in four wild animals in Manarara. The log-linear model shows no effect of individual, posture and their interaction on the 'first-noted hand' (χ^2_7=6.59, p=0.47). An analogous ANOVA with the 'bout score' as a dependent variable has shown a significant whole-model effect ($F_{7,257}$=3.60, p=0.001). But of the independent variables, only the effect of individual identity was significant (F_3=4.21, p=0.006), with the left-handed Koulic being most divergent from the other individuals. Body posture had no significant effect on the 'bout score' either alone or in interaction with individual identity.

Discussion

It has been doubted what is the relevance of studying laterality in captive animals for understanding the natural evolution (Marchant & McGrew 1996; McGrew & Marchant 1997; Panger 1998; Rigamonti *et al.* 2005). For aye-ayes, patterns of lateralized hand use we have observed in the wild resemble what was earlier reported for the free feeding in captivity (Feistner *et al.* 1994): some animals are ambipreferent and others are biased evenly to either direction. This corresponds to the Level 2 of the McGrew and Marchant's (1997) framework. The similarity pertains despite the fact that the wild aye-ayes use their hands differently than the captive ones, which are presented mostly with detached and easy-to-process food and are subjected to more stereotypy.

Our and Feistner *et al.*'s (1994) results however differ from the findings of Milliken (1995) on four of the same animals in DUPC. When presented with two test apparatuses, these aye-ayes expressed right hand preference and performance biases in several measures of probing. Milliken (1995) concluded that the right hand bias in digit use is species-specific for aye-ayes. The sample of four animals is too small – even when all of them are right handed, this does not significantly deviate from 1 : 1 ratio on the population level using any test (if α is set at 0.05). But this does not fully account for the observed differences because Samantha, right-biased in probing when tested by Milliken, was significantly and strongly (HI = -0.90) left-biased in the other study, probably during the same year (Feistner *et al.* 1994). Milliken (1995) mentions that Samantha lost the claw on her right third finger (for a reason not related to testing) and became left hand preferent in finger use then after. But the other study took place before she lost her claw (Milliken, pers. comm.) so this cannot explain the discrepancy.

A possible explanation of Milliken's (1995) different findings is that his z-scores capture different aspects of lateralization because they are sensitive to asymmetries in probing persistence. Milliken shows that the right hand preferences in shallow cavities of the vertical cavity apparatus (VCA) were due to higher persistence of the right finger; the animals tended to use it in longer sequences of repeated probing acts. Milliken counted each entering a cavity as one event, while we have used only the first-noted entering in each such sequence. Feistner and colleagues recorded digit-to-mouth feeding on fruits that is typically represented by continuous bouts with "enterings" less distinct than while inserting the finger into a cavity. It is likely that a sequence of such "enterings" was regularly counted as a single event. Only interruptions or changes of hands were recorded as new events (this actually biases the data toward ambipreference: the direction of shifts is dependent on the preceding act – it can only be the opposite hand). When we rearrange the data from the Tab. 4 of Milliken (1995) to simulate the other two sampling designs, the differences between the three studies become less distinct, as shown in our Tab. 3. In both alternative arrangements, the HIs are relatively low and the only significantly right-preferent animal is Poe. He is the only animal with the original results significant for both apparatuses and for all cavity depths in the VCA apparatus. This also corresponds with his right-hand preference in tapping reported independently by Feistner *et al.* (1994). Leaving Poe aside, all other significant right-hand biases in probing frequency, persistence, and productivity in Milliken's (1995) paper were detected in the easiest tasks - in the two shallower holes of the VCA. Milliken states that as the complexity of the cavity increased, the aye-ayes soon switched to a variable probing strategy with alternating ways of probing into the cavity, including using the other hand.

Table 3. Comparison of various measures on lateralized finger use in four DUPC aye-ayes. Z-scores and His were computed as in our Table 1.

Name		Probe VCA[1]	Tap[2]	Digit-feed[2]	Probe VCA rearranged[3]	Probe VCA rearranged[4]	Probe HCA[1]
Nosferatu	n	419	7	9	50	84	160
	z-score	3.08**	0.38	1.00	0.85	0.87	1.11
	HI	0.15	0.14	0.33	0.12	0.10	-0.09
Poe	n	629	43	11	121	153	160
	z-score	13.44***	1.98*	1.51	3.18**	3.31***	2.21*
	HI	0.54	0.30	-0.46	0.29	0.27	0.18
Samantha	n	419	38	19	98	152	0
	z-score	2.30*	-3.90***	-3.89***	1.01	1.14	-
	HI	0.11	-0.63	-0.90	0.10	0.09	-
Annabellee	n	260	26	18	49	82	135
	z-score	2.73**	2.83**	0.39	0.71	0.00	0.26
	HI	0.17	0.08	0.67	-0.10	0.00	-0.02

Sources of data:

[1] Table 3 from Milliken (1995);

[2] Table 2 from Feistner *et al.* (1994);

[3] Data from Table 4 from Milliken (1995) rearranged to resemble design of our study where only the first-noted hand was recorded: only data from Milliken's (1995) columns Initiated Sequences Left and Initiated Sequences Right were used, data from all four cavities were pooled;

[4] Data from Table 4 from Milliken (1995) rearranged to resemble design of the study of (Feistner *et al.* 1994) where continuous digit-feeding and any change of hands were recorded: we summed Milliken's (1995) data from columns Initiates Sequences Left and Changes R→L to represent frequencies of left hand use, and data from columns Initiates Sequences Right and Changes L→R to represent frequencies of right hand use, data from all four cavities were pooled.

There are other brief reports on hand preference in aye-ayes. Ancrenaz *et al.* (1994) observed three free-ranging aye-ayes in degraded secondary forest and agroecosystems 12 km west of Mananara-Nord, close to our field site. When probing for nectar in flowers of *Ravenala madagascariesis*, a female preferred her right hand while two males preferred their left hand. These results are consistent with the above findings. Iwano (1991) reports on hand use in a wild-caught female aye-aye kept in the Tsimbazaza zoo in Madagascar. When feeding, she used more frequently the third digit of her left hand but the fourth digit of her right hand. The author however explains this as a likely artifact of the sampling method. Focal instantaneous sampling has been employed with sampling points only 30 seconds apart; such data cannot be considered independent and the sample size is likely to be inflated.

Paper of Feistner *et al.* (1994) was cited by McGrew & Marchant (1997) and Rigamonti *et al.* (2005) as contradicting the general pattern of hand preferences in prosimians reported in various studies that found the left hand preference being the most common pattern (Sanford *et al.* 1984; Larson *et al.* 1989; Forsythe & Ward 1988; Forsythe *et al.* 1988; Ward *et al.* 1990; Milliken *et al.* 2005). There are at least three reports on species-specific free foraging, which showed lack of left-hand population bias: *Indri indri* (Rigamonti *et al.* 2005), *Lemur catta* (Shaw *et al.* 2004), *Hapalemur* spp. (Stafford *et al.* 1993). But the data on aye-ayes must not be considered in the same line because behaviors under study differ. Left hand preference in lemurs has been most commonly demonstrated in visually guided reaching and holding, yet aye-ayes rarely reach for or hold objects and this is even more apparent in wild animals. Wild aye-ayes mostly forage on attached objects (often directly on the wooden substrate) that need not or even cannot be held. Even when the objects are not attached, the aye-ayes often use their mouth rather than their hands to pick up the object before transferring it to the hand (Feistner *et al.* 1994) as reported also for several other lemurs, including *Cheirogaleus medius* and *Microcebus* cf. *murinus* (Ward *et al.* 1993), *Propithecus* sp. (Milliken *et al.* 2005) and *Indri indri* (Rigamonti *et al.* 2005).

It is very likely that an important factor in development of the aye-aye's unique foraging strategy is learning. The ratio of right to left hand preferent aye-ayes closely approaching 1 : 1 indicates that the hand preference is not inborn in this species and instead develops with practice as a motoric habit, in an even direction. If this is true, then the strength of laterality should increase with age at least among younger animals. This has been shown for some other prosimians: *Lemur catta* and *Eulemur* spp. (Ward *et al.* 1990), *Otolemur garnettii* (Milliken *et al.* 1991). Feistner *et al.* (1994) indeed suggested that this was also the case for the aye-ayes they studied. But only the youngest of these captive animals, Fred (10 months old) showed ambipreference in all measures. The other three juveniles and subadults (Zaza, Sambany and Annabellee) did show hand preference in at least one measure. The three years old captive adult male Poe, which was close in age to the two years old wild subadult male Rarach, was right-handed in several measures in Feistner *et al.*'s (1994) and in Milliken's (1995) study. On the contrary, the wild animals from Mananara were ranked in their handedness just as they were ranked in age, with subadult Rarach (2 years) most ambipreferent and only two aged animals (Lucy and Koulic) showing significant hand preferences. We strongly suspect that hand preference does indeed increase with age in aye-ayes but that the process is relatively fast in captive animals. More routine in captivity may lead to faster development of motoric habits, including hand preference.

The 1 : 1 ratio of left to right preferent aye-ayes does not support the postural origin hypothesis by MacNeilage *et al.* (1987). Postural support is a very relevant issue for aye-ayes that tend to forage in a variety of demanding postures, including suspension, climbing head down or clinging to trunks of large diameters (Curtis & Feistner 1994, Lhota & Jůnek, pers. obs.). If the right hand specializes for securing postural support as suggested by MacNeilage and colleagues, then a relatively strong left hand preference in the digit-use should develop so that the function of the right hand is not compromised. But this is not the case. We have neither found any effect of easiness of position on the strength of hand preferences. It is possible that a minute effect would emerge if there were more data enabling the position to be classified in a detailed way, but we may still conclude that the postural demands are probably not the major factor that would either invoke (Larson *et al.* 1989; Forsythe *et al.* 1988; Dodson *et al.* 1992) or limit (Stafford *et al.* 1993) expressing hand preference in aye-ayes. In JWPT animals, the effect of posture was controlled by presenting food in identical dishes on a platform (Feistner *et al.* 1994) yet the animals did not substantially differ from the wild ones in their hand preference patterns.

We can however speculate about other untested factors that may limit the degree of hand preferences in aye-ayes and it is possible that more than one factor plays a role. The aye-ayes often move during foraging, especially when feeding on branches; then they need to use both forelimbs for locomotion and thus would tend to switch the hand used for tapping or probing at each step. When the aye-ayes investigate the internal structure of objects by tapping, using both hands would provide information from a wider area. When probing into a complex cavity, using both hands may enable the aye-aye to inspect it most thoroughly. When grooming fur, there is a symmetric pattern of one side of the body being better accessible with one hand and the other side with the opposite hand. Finally, there is a risk of getting one hand injured, which would have serious consequences for the animal if there were a strong efficiency bias for that hand.

If hand preferences develop slowly during maturation, as suggested by data on wild aye-ayes, it would help the animals to counteract some of the above-mentioned disadvantages. The juveniles and subadults would practice both hands during the period when most of their motoric skills are being formed. If then hand preference develops as a motoric habit in a more advanced age, the animal would still be able to use both hands efficiently. A longitudinal study on development of foraging of individual aye-ayes, preferably in the field setting, would help to address this hypothesis.

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Positional behavior in free-ranging aye-ayes, *Daubentonia madagascariensis*: the use of body postures and locomotion during foraging and traveling

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Abstract

We observed positional behavior in free-ranging aye-ayes *(Daubentonia madagascariensis)* on an island on Mananara River, eastern Madagascar. We have evaluated the context of use of positions relevant to several morphological hypotheses that explain some of modifications of aye-aye's locomotory apparatus. Our results suggest that the aye-aye's long arms have probably primarily evolved to secure a postural support during foraging for wood-boring insects, allowing the animal to cling to large-diameter, often vertically oriented trunks or branches. In contrast, the reversible feet are most employed during traveling. We propose that possessing the forelimbs highly specialized for foraging tasks influenced the compensatory specialization of the hind limbs for effective traveling, which includes frequent head-first descent. We however did not find an unequivocal explanation for the robust humerus and strong forearm of the aye-aye.

Key Words: positional behavior, feeding, traveling, *Daubentonia*, Madagascar

Introduction

The aye-aye *(Daubentonia madagascariensis)* is the most specialized of all extant Madagascan lemurs. It is known for its unusual way of foraging, which includes tapping on the surface of wood or nut shells with a thin, elongated third finger, listening to the resonations, gnaw-opening insect galleries or nuts shells with its rodent-like incisors, and extracting contents of the cavities with one of its two elongated fingers (Iwano, 1991;

Erickson, 1994; Sterling, 1994). While most of discussion on aye-aye's morphology concerned its highly unique fingers and skull (Cartmill, 1974; Milliken *et al.* 1991; Soligo and Müller, 1999; Soligo and Müller, 1999; Soligo, 2005), several authors also paid attention to unusual characters of its postcranial skeleton and musculature, such as elongated extremities, robust forelimbs, and reversible feet (Demes and Jungers, 1993; Curtis and Feistner, 1994; Runestad, 1997; Soligo, 2005). In this paper, we will address ecological context of positional behavior in which the aye-aye gains advantage form these postcranial modifications. Throughout the paper, posture refers to static or dynamic behaviors when the animal remains at place, locomotion mode or locomotion refer to behaviors when the animal changes its location, and the position refers to either of these.

The first complex of aye-aye's unique morphological characters involves its long forelimbs. These are the longest, compared to the trunk length, among primates (Curtis and Feistner, 1994). Elongated arms typify primates that move by brachiation or semibrachiation, but the aye-ayes are not reported to use any form of forelimb suspension. Furthermore, detailed proportions of its extremities differ from brachiators in two ways: the hind limbs are also markedly elongated (Curtis and Feistner, 1994) and the most elongated segment of the forelimb is the hand rather than the long bones. The hand represents 41 % of the forelimb length, which far exceeds proportions in all other primates except the tarsier *(Tarsius)* with a similar value of 38 % (Jouffroy *et al.* 1991). The most elongated part of the aye-aye hand itself is the fourth digit, which represents 71 % of the hand length and, therefore, 29 % of the whole forelimb (Jouffroy *et al.* 1991). Soligo (2005) proposed that the aye-aye's long arms represent an adaptation to vertical clinging on large-diameter substrates, such as massive tree trunks. These substrates cannot be grasped with hands; instead, the aye-aye must encircle large trunks with its arms and employ its claws to cling on it (Figure 1a). The longer the arm, the better would the animal be equipped for securing this posture.

The second set of morphological modifications includes the robust forearm skeleton and musculature. The aye-aye appears to possess not only long, but also very strong arms. The humerus shows compressive and bending strength that is unusual for a lemur of that size (Demes and Jungers, 1993). Some of muscles of the arm are remarkably well-developed and give the animal a stocky appearance (Soligo, 2005). Strong arms are required for pulling the body up during climbing, but this mode of locomotion is used by all prosimians (Gebo, 1987) so this alone should not set the aye-aye distinctly aside. There are two hypotheses explaining the aye-aye's robustly built arms. Soligo (2005) stressed the importance of lift-off forces that the aye-aye faces in two distinct situations: first, when gnawing the support, and secondly, when climbing or clinging head-up on steep supports. During gnawing, tearing the material off is mostly accomplished by the trapezius, which pulls the head against shoulders. But the effect of this is also pushing the animal off the substrate. Comparable forces result as an effect of gravity when the animal clings or climbs head-up on a steep support. The other hypothesis, proposed by Curtis and Feistner (1994), stresses the role of compressive forces during head-first descent that is frequently used by aye-ayes. Primates, which regularly descend head-first, include hapalines (callitrichines), galagonids, lorids, cheirogaleids and some lemurids (Tilden, 1990). Aye-ayes, weighting approximately 2.6 kg (Feistner and Sterling, 1995), are heavier than any of these primates. Primate hind limbs typically bear most of the body weight when walking (Franz *et al.*, 2005) but during head-first descent, the situation is apparently reversed. The robust shoulder girdle and high compressive and bending strength of the humerus of the aye-aye may be result of this high loading during head-first descent.

Finally, the aye-aye is characterized by its reversible feet (Curtis and Feistner, 1994). Jenkins and McClearn (1984) described that in several species of primates, carnivores and rodents, foot reversal is achieved by crurotalar plantarflexion, subtalar inversion and midtarsal supination (Figure 1b,c,h,i). Amongst primates, this mode of foot reversal occurs in ruffed lemurs *(Varecia variegata)* (Meldrum *et al.*, 1997) and in the slow loris *(Nycticebus coucang)* (Jenkins and McClearn, 1984). The skeleton of the aye-aye foot shares several characters with that of the lorids (Curtis and Feistner, 1994) suggesting also a similar mode of the hind foot reversal. But regardless of the common mechanism, the actual use of the hind foot reversal differs between primate species. The ruffed lemurs only rarely descend head first (Pereira *et al.*, 1988), showing instead a high frequency of postural hind limb suspensions (Pereira *et al.*, 1988; Meldrum *et al.*, 1997). The low loris and aye-aye, on the contrary, employ the foot reversal besides the postural suspensions also for locomotion, i.e., for the head-first descent. In ruffed wild ruffed lemurs, the hind limb suspension is used exclusively in the context of foraging although in captivity, it is also employed in other contexts including grooming, play, investigation or hanging for no apparent objective (Meldrum *et al.*, 1997). In aye-ayes, the context of use of the hind limb suspension was never systematically addressed.

In her comparative study of procyinid carnivores, McClearn (1992) asked the question how do adaptations for two important tasks in animal's life, foraging and locomotion (traveling), interact to influence the animal's limb morphology. Based on her comparison of coatis *(Nasua narica* and *N. nasua)*, raccoons *(Procyon lotor)* and kinkajous *(Potos flavus)*, she concluded that forelimbs of coatis and raccoons possess adaptations for food gathering and processing that preclude their use in locomotion on slender terminal branches and therefore restrict the animals' ability to feed on a tree crown periphery and to travel through the canopy horizontally from tree to tree. We may similarly ask how do these two important life demands, foraging and traveling, interact in modifying the limb structure of the aye-aye.

This question is especially interesting in the light of findings from previous field studies, which show that several aspects of foraging and traveling sets the aye-aye apart from the other nocturnal primates. Specific features of the aye-aye foraging include collecting wood-boring insect larvae from live or dead tree trunks and branches (Erickson, 1995). These are often large-diameter vertical substrates that may be hardly accessible for a primate of the aye-aye's size. The horizontal branches may be sometimes exploited even from the underside (pers. obs.). Furthermore, when the aye-aye uses its specialized fingers to tap on surface and probe into the insect galleries, it is forced to cling tripedally to the trunk (Soligo, 2005). Traveling also poses some specific demands on the aye-aye. For a nocturnal primate, the aye-aye has unusually large home ranges (over 200 ha for a male) and night ranges, and much of the nighttime is spent traveling (Sterling, 1993). In addition, due to its feeding site selection (tree trunks), it has to frequently travel between forest strata from the canopy down the trunk and back.

There are no gross body postures or modes of locomotion that the aye-ayes use exclusively for foraging or for traveling (Curtis and Feistner, 1994). Most of positions are used in variety of behaviors, but in varying proportions that were not yet documented for free-ranging animals. Inspecting proportions of time spent in specific positional behaviors during different activities may help us to explain what selective forces were responsible for evolving morphological modifications associated with these postures. Therefore, our aim is to find out in what activities (foraging, traveling, or another activity) the aye-ayes employ body positions that are facilitated by (I) elongating of forelimbs, (II) increased robustness of forelimbs and (III) possessing reversible feet.

Methods

We observed free-ranging aye-ayes on a small (14 ha) island on Mananara River (S 16°10' E 49°44'), close to Verezanantsoro National Park, eastern Madagascar. Most of the island is covered with mixed plantation, dominated by fruit trees, coconut palms and secondary forest trees (Andriamasimanana, 1994). This habitat differs from the nearby primary rainforest in structural properties (substrate availability) as well as in food resources. Aye-ayes are however known to exploit a wide range of primary and secondary habitats around Mananara (Ancrenaz *et al.*, 1994; Andriamasimanana, 1994) and the data collected in secondary habitats may be therefore considered reasonably valid when studying the gross adaptations of the aye-aye's locomotory apparatus. During our fieldwork, there were four aye-ayes that were well habituated to the presence of observers: a mature adult female, her subadult son, a young adult male, and a mature adult male. All individuals could be recognized reliably from their distinct body features.

Two of us (Lhota and Jůnek) studied the aye-ayes between April 2003 and October 2003. We have started collecting data using a preliminary ethogram of positional behavior, that was subsequently improved based on our field experience. We prepared a new detailed ethogram on the July 15th; it is presented in Appendix I. In this report, we consider the first half of the study as a reconnaissance observations period and for the purpose of quantitative analysis, we include only data collected by one observer (Lhota) since the July 15th. The observer usually followed the animals during their whole active period (beginning when the animals emerged from the nest until they retired to the nest), using LED headlamps and binoculars (8x40) to observe behavior. If possible, the observer followed a single individual for a given night. In the case he lost the animal, he attempted to re-locate the same individual. But if he instead found another individual, he continued in tracking the new one.

To record positional behavior, we employed the focal instantaneous sampling technique as described by Altmann (1974). The observer collected the instantaneous data at 1-minute intervals during sampling periods of 30 minutes, which were separated by 30-minute breaks during which time he remained with the animal. The focal instantaneous data were collected during 39 night follows. The observer collected data on positional behavior (posture or mode of locomotion) simultaneously with data on substrate characteristics (height, support diameter and support angle) and animal's activity. The categories used to describe the animal's activity are defined in Appendix II. He estimated animal's height to the nearest meter, the support diameter to the nearest centimeter, and the substrate inclination to the nearest multiple of 5°. Unusual positions, including the acrobatic postures, were described in details and/or sketched.

Data collected by the instantaneous sampling at 1-minute intervals represent a valid estimation of the percentage of time spent in various behavioral states (Altmann, 1974) but they cannot be considered as independent data entries for positional behavior that often lasts for several minutes and they should not be subjected to formal statistical testing. We therefore directly compared percentages of instantaneous points. We excluded from analysis all instantaneous points when the animal was in the nest, hidden in the canopy or otherwise invisible for the observer (so that its positional behavior could not be observed). In some cases, the observer was not able to classify the position or activity with full confidence due to limited visibility. When it was not possible to decide between two similar options (for example, inactivity and rest), both options were noted and the sampling point was considered as undecided. For purpose of the present analysis, we used only the decided sampling points. Only in case of foraging, which was classified in relatively fine details, we included the undecided cases within the category 'Unspecified foraging' in order to avoid ignoring a significant proportion of the foraging time. The total sample of instantaneous points analyzed for this report is 4560. In a degree, the sample sizes differed for the four aye-ayes (i.e., 1332, 1247, 1059 and 922 instantaneous points). But we consider the sample sizes sufficiently balanced to combine the data for all individuals and to present the total counts.

After examining the raw data, we have grouped selected positions into broader, mutually overlapping categories according to criteria relevant to three complexes of aye-aye postcranial morphological modifications: (I) elongating of forelimbs, (II) increased robustness of forelimbs and (III) possessing reversible feet. As we were considering two different hypotheses concerning the adaptive value of the aye-aye's robust forearm (lift-off forces and dead-first descent), there are also two criteria relevant to this morphological trait (IIa and IIb). The four grouping criteria were as follows:

Criterion I. Positions in which the long forelimbs facilitate holding on large-diameter trunks or branches by embracing the support.

Criterion IIa. Positions in which the forelimbs apparently resist lift-off forces, which originate from gnawing onto substrate or from head-up body orientation vertical substrates.

Criterion IIb. Positions in which the forelimbs bear increased stress due to head-down body orientation.

Criterion III. Positions in which the aye-aye reverses its feet.

Positional behavior relevant to the above-defined groups was selected according to Table I. There is however no definite rule concerning relevance of individual positions defined in the ethogram (Appendix I) because characteristics like the degree of embracing a large support (Figures 2a,d), the strength employed by the arms or the degree of foot reversal (Figure 1h,i) are not related to any of the positions unequivocally. In Table I, we have based our selection on the most typical patterns of individual positions, based on our field experience. Only the highly variable acrobatic positions were evaluated case-by-case referring to detailed descriptions and/or drawings in observer's field notes. Transitional positions were excluded from these summarizations. Some data on positional behavior had to be omitted in the case of behaviors grouped by Criterion I because classification of relevant positions depended on substrate diameter, which was not noted for 55 data points.

For this analysis, activities were also grouped into broad categories: (1) traveling, as defined in the ethogram, Appendix I, (2) foraging, that was comprised of the four categories of the ethogram: tapping, gnawing, probing or eating, and unspecified foraging, and (3) other activities.

Table I. Criteria of selection of positional behaviors relevant to adaptive modifications of aye-aye limb morphology. (Note: The threshold substrate diameter of 35 cm was selected *post hoc* as the value where the frequency of use of instantaneous sampling points for positions relevant to Hypothesis I dropped most markedly. The threshold substrate angle of 55° was selected *post hoc* as the value where the total frequency of the instantaneous sampling points dropped most rapidly.)

Criterion	Positions grouped by Criterion
Criterion I: Positions in which the long forelimbs facilitate holding on large-diameter trunks or branches by embracing the support.	Following positions whenever on a support of diameter larger than 35 cm: clinging, head-down clinging, pronograde suspensions, climbing, descending (all types) and moving in suspension; Additionally, genital dragging and chest sliding on substrates of at least 35 cm in diameter and inclined at least 55°
Criterion IIa: Positions in which the forelimbs apparently resist lift-off forces, which originate from gnawing onto substrate or from head-up body orientation vertical substrates	All postures employed during gnawing the support or large objects (jackfruit, coconut, big palm leaves or sheaths), but not softer plant tissues, twigs or detached objects; pronograde suspensions, moving in suspension, climbing, clinging (head-up), tail-first and lateral descent; genital dragging on a support inclined at least 55°
Criterion IIb: Positions in which the forelimbs bear increased stress due to head-down body orientation.	Acrobatic positions with hands on lower support (evaluated case by case), head-first descent, head-down clinging, lateral descent, bridging; Following positions on a substrate inclined at least 55°: walking down, chest-sliding or standing facing-down
Criterion III: Positions in which the aye-aye reverses its feet	Head-down acrobatic postures (evaluated case by case), head-down clinging, head-first descent, hind leg suspension, bridging (due to animal's weight, the body usually declined down during bridging)

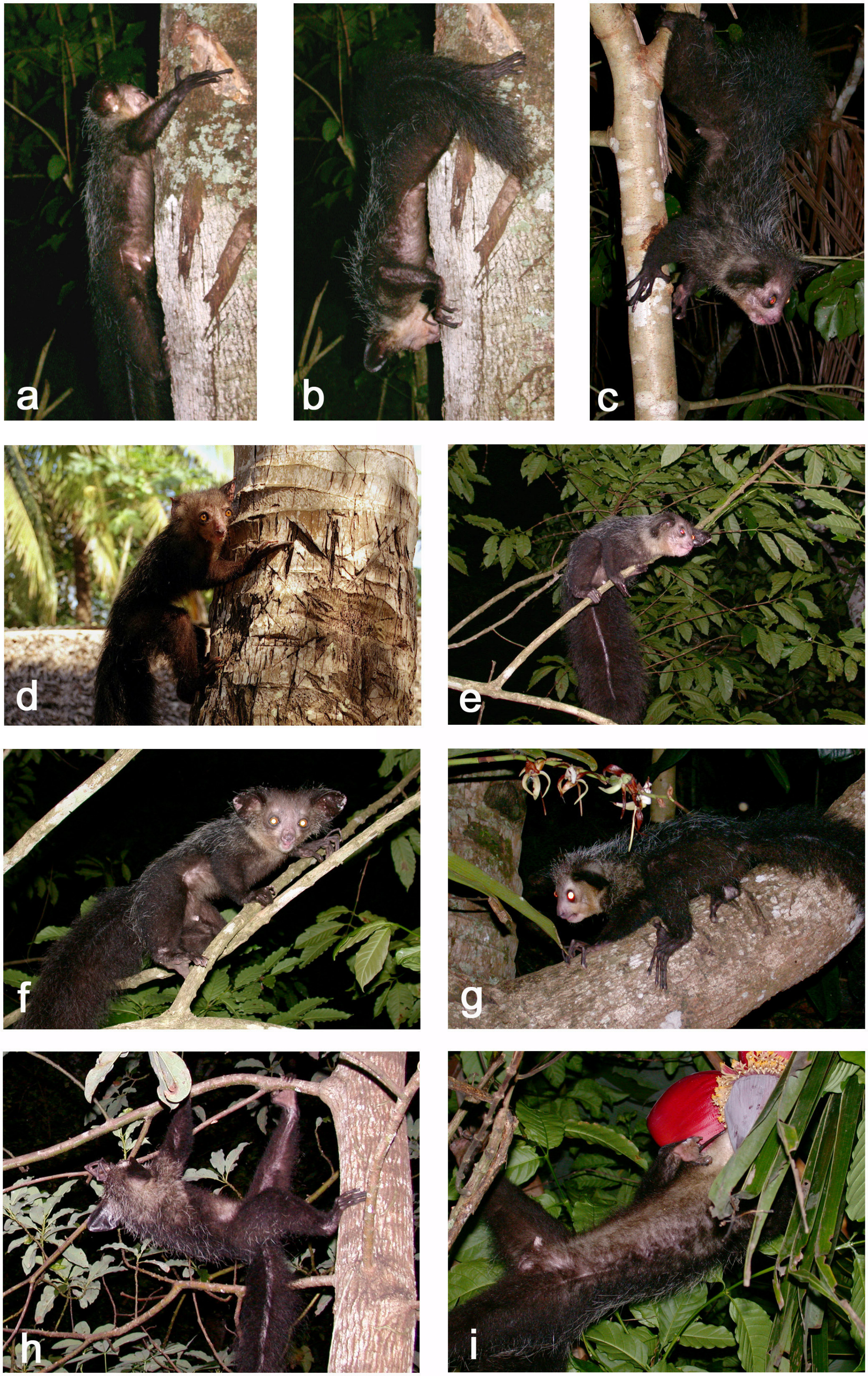

Figure 1. Selected examples of positional behavior of aye-ayes. See next page for the legend.

Figure 1. (preceding side) Selected examples of positional behavior of aye-ayes.

a. Clinging on a large-diameter trunk whiles gnawing the support. The arms embrace the support and the animal clings by its claws; two principal points of support are the long fourth finger and the highly opposable thumb. Note the extreme dorsiflexion of the foot.

b. Head-down clinging on the same trunk whilst (the raised third finger of the left hand is visible). Note that feet embrace smaller diameter than the arms and that both hands are placed relatively high, showing much less dorsiflexion, compared to the feet on the previous picture. There is a high degree of foot reversal.

c. Head-down clinging during traveling. In contrast to the previous picture, the feet grasp the branch rather to clinging to it with claws. There is also less complete foot reversal.

d. Clinging during vigilance (watching surroundings). The fourth finger again form a principal point of support, although there the arms are not particularly extended to embrace the substrate. There is again an extreme feet dorsiflexion.

e. The preparatory phase of leaping during traveling. Until lifting off, the posture is classified as standing.

f. Standing on an oblique branch whilst vigilant (watching the observer).

g. Walking on an oblique branch during traveling. Note that the less-inclined position of trunk when walking head-down compared to the head-up position on a similarly oriented branch on the previous figure. This postural adjustments has been described by Krakauer *et al.* (2002). Also note the full-curl position of the fingers of the left hand.

h. Moving in suspension whilst foraging. The right foot dorsiflexed whilst the left foot shows an incomplete foot reversal, which includes plantarflexion and inversion.

i. Pronograde suspension whilst probing and eating nectar from a banana flower, using the third finger. The posture is close to being classified as acrobatic. There is again only incomplete reversal of one (right) foot that involves plantarflexion and inversion. All photos by Tomáš Jůnek.

Results

Table II shows the raw data, pooled for four aye-ayes, before the positions were lumped according to Table I. Figures 2-5 represent usage of positions grouped according to Criteria I, IIa, IIb and III during foraging, traveling and other activities.

Table II. Total counts (for all four animals) of instantaneous data points for different postures and locomotions during different activities: traveling (tra), body care (bca), resting (res), inactivity (ina), vigilance (vig), investigation (inv), tapping (tap), probing or eating (pbe), unspecified foraging (unf), nest building (neb), play (pla), social interactions (soc), calling (cal), and excretion (exc)

	tra	bca	res	ina	vig	inv	tap	gn	pbe	unf	neb	pla	soc	cal	exc	Total
walking	1051				9	118	1			12	24	1	12	10		1238
chest-sliding	3					1										4
genitals-drag															19	19
climbing	55					5	1		1	4				1	4	71
head-first descent	39					4				1			1			45
lateral descent	18					1				1						20
tail-first descent	3					1				1						5
leaping	33															33
sitting	11	103	23	68	121	8	5	66	217	15			5	13		655
squatting		3			1		2	4	130	5						145
perching	1	7		1	1	4	1	29	72	2				1		119
liyng		18	67	1	7			3	13	3			3			115
standing	130	22		93	143	68	58	110	228	44	6	5	4	27		938
crouching															30	30
upright	1	6			5	10	18	62	128	11			2			243
clinging	40	3		32	27	15	46	51	31	37				3	1	286
head-down clinging	4			5		3	4	2	1	3				1		23
hind limb suspension	2	61		3	1	2	1	2	4	2	3	2				83
pronograde suspension	10	157	1	9	7	8	18	35	48	22		11	1			327
move in suspension	29					7		1		9				1		47
bridging	57													1		58
acrobatic		2					1	3	15	1	3	17				42
transitional	1									13						14
Total	1488	382	91	212	322	255	156	368	888	186	36	36	28	58	54	4560

Positions grouped by Criterion I (i.e., when the long forelimbs facilitate holding on large-diameter trunks or branches by embracing the support) are disproportionately more used during foraging, whilst they are underrepresented during traveling (Figure 2). The most represented traveling position, walking (Figure 1g), which represents 1051 of 1488 traveling sampling points (71 %), does not fit to the criterion regardless of the substrate diameter. The most represented relevant traveling position is climbing, which accounts for only 55 of 1488 sampling points (4 %). Furthermore, detailed inspection of the data showed that only 10 of these occurred on the substrate diameters of 35 cm or more. Albeit the most represented foraging position, standing, also does not fit to the Criterion I, it accounts for only 28 % of the total foraging time (440 of 1598 tapping, gnawing, probing or eating and unspecified foraging data points). The most represented relevant foraging position, clinging (Figure 1a), accounts for 165 of the foraging data points (10 %) and of these, 43 occurred on supports of diameters of 35 cm or more. Pronograde suspensions (Figure 1i) were the next most represented relevant position during foraging, accounting for 123 foraging data points, but only 3 of these occurred on substrates diameters of 35 cm or more. Therefore, clinging on large diameter supports accounts for most of the overrepresentation of the positions grouped by Criterions I during foraging.

Figure 2. Percentage of time spent in positions grouped by Criterion I and other positions during foraging, traveling and other activities. Numbers in bars refer to total number of instantaneous data points.

Positions grouped by Criterion IIa (i.e., when the forelimbs apparently resist lift-off forces, which originate from gnawing onto substrate or from head-up body orientation vertical substrates) represent the highest absolute number of sampling points for both traveling (155) and foraging (533). In relative terms, however, foraging is represented disproportionately more, whilst traveling is underrepresented when compared to not-relevant positions (Figure 3). Including a wide range of positions associated with gnawing the substrate is primarily responsible for this result. Gnawing the support (Figure 1a) accounts for 311 of 533 relevant foraging data points (58 %), the most often employed position being standing (70 points) and sitting (56 points), which would otherwise not be considered relevant. In traveling, climbing accounted for most of the relevant data points (55, i.e. 35 %).

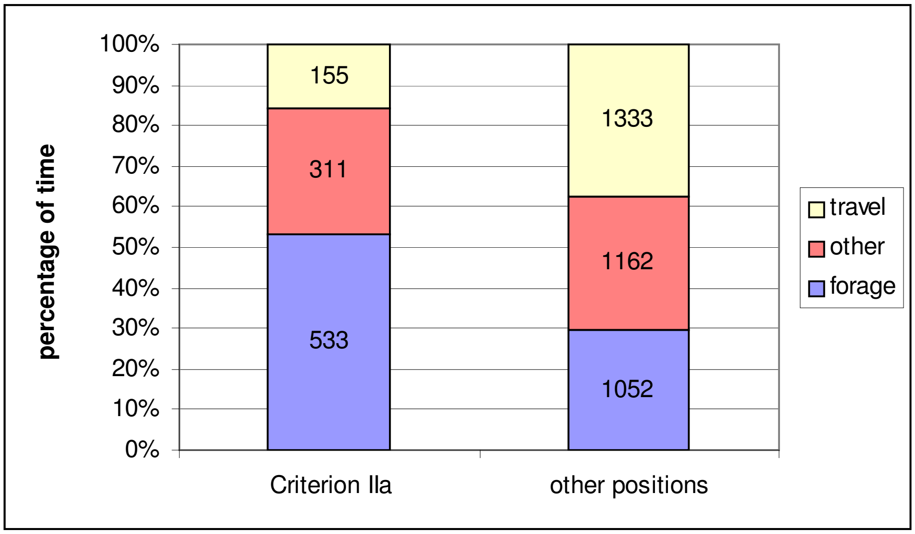

Figure 3. Percentage of time spent in positions grouped by Criterion IIa and other positions during foraging, traveling and other activities. Numbers in bars refer to total number of instantaneous data points.

Positions grouped by Criterion IIb (i.e., when the forelimbs bear increased stress due to head-down body orientation) show the opposite pattern, they are underrepresented during foraging whilst they are overrepresented when traveling (Figure 4). The most represented relevant traveling positions are bridging (57 points) and head-down descent (39 points, Figure 1c), representing 41 % and 28 % of the total of 140 relevant traveling data points, respectively. Of 25 relevant foraging points, acrobatic (13 points) and head-down cling (10 points) postures accounted for most of the data (note that not all acrobatic postures included in Table II were evaluated as relevant to Criteria IIb and III).

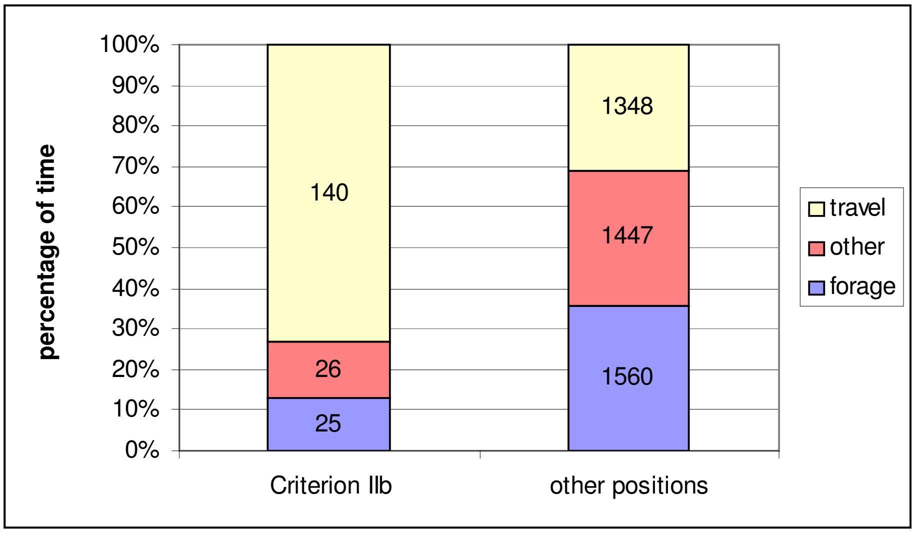

Figure 4. Percentage of time spent in positions grouped by Criterion IIb and other positions during foraging, traveling and other activities. Numbers in bars refer to total number of instantaneous data points.

Positions grouped by Criterion III (i.e., that hind foot reversal is employed for hanging, clinging and descending head-down) are also underrepresented during foraging whilst they are overrepresented when traveling (Figure 5). Again, bridging (57 points) and head-first descent (39 points) are the most represented relevant positions, accounting for 56 % and 38 % of the total of 102 relevant traveling data points, respectively. In foraging, the hind limb suspension (9 points) adds to acrobatic (13 points) and head-down cling (10 points) postures to account for most of the total 33 data points.

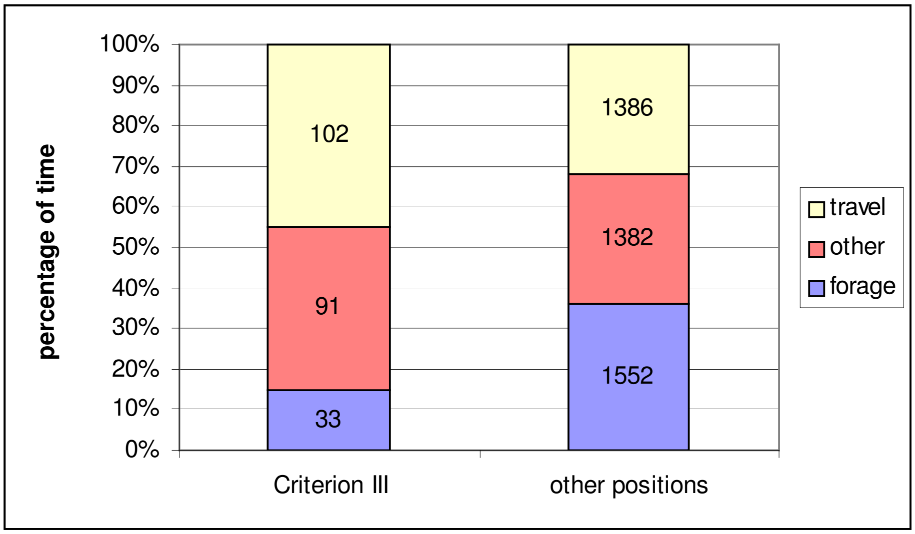

Figure 5. Percentage of time spent in positions grouped by Criterion III and other positions during foraging, traveling and other activities. Numbers in bars refer to total number of instantaneous data points.

Discussion

Overall, our data support the view of Curtis and Feistner (1994) and Runestad (1997) who consider the aye-aye to be a generalized arboreal quadruped rather than a locomotory specialist. The aye-ayes showed a wide range of positional behaviors, including several motorically demanding ones. But for most of their activities, they preferred to use the less demanding ones, namely walking, standing, sitting, squatting, perching, lying, and the supported upright posture. Only two of the more difficult positions, namely pronograde suspensions and head-up clinging, were used in a comparable proportion of time, followed by less frequently employed hind limb suspension, bridging and climbing. Preference for the less demanding positions was clear for all activities except body care, which was more often performed in hind limb or pronograde suspension compared to sitting or other less demanding postures. It is possible that the suspended grooming posture enables the aye-aye to access all parts of its body more easily compared to sitting.

Given the overall preference for less demanding positions, only a small percentage of time was spent in postures or locomotory modes relevant to any of the proposed morphological adaptations hypotheses. However, the percentage of time alone is probably not a sufficient measure of importance of these positions. It is likely that even less-frequently employed positions may result in morphological modifications of the musculo-skeletal apparatus if they enable the animal to access some key resources.

The complex of positional behaviors that employ the long arm to embrace large-diameter supports (Criterion I) appears to be more relevant to foraging than to traveling or to any other activity. These positions (i.e., clinging, climbing) are strongly preferred for feeding when compared to analogous positions when the hind limbs are used to support the body from above (head-down clinging, head-first descent). The positions relevant to Criterion I are most often employed when the aye-aye clings to large trunks during foraging activities, including tapping, gnawing, probing and eating. The aye-aye typically feeds on wood-boring insects in these positions. Although field studies proved that insects do not represent the dominant food resource for the aye-ayes in terms of foraging time and the amount of ingested matter (Ancrenaz *et al.*, 1994; Andriamasimanana, 1994; Sterling, 1994, Sterling *et al.* 1994), our data still suggest that the aye-aye's forelimbs are indeed morphologically adapted to access this food and that that these adaptations are not limited only to possession of the highly specialized fingers.

Soligo (2005) proposed an advanced version of this hypothesis, in which he stresses the need of assuming tripedal (one-hand-two-feet) postures during the specialized foraging of the aye-aye. When tapping, probing and extracting larvae, one hand is being occupied with these tasks so that only the other hand is available for securing the positional support. With our data, we did not specifically address the context of use of the tripedal positions. It was in order to avoid an overwhelmingly circular argumentation, as most of tripedal clinging positions are defined by using one hand for foraging tasks (tapping, probing or holding food) and they therefore necessarily occur almost exclusively during foraging. But the possibility that the need of assuming tripedal position might have been a crucial selective pressure leading to the elongation of the aye-aye's forelimbs would even strengthen the arguments that this morphological modification results primarily form needs of the aye-aye's foraging.

It must be stressed that the most-elongated segment of the aye-aye's forelimb is the fourth finger. While this finger plays an important role for embracing large-diameter supports when adopting some body postures (Figure 1a), it is also important in the aye-aye's foraging. Compared to the thin third finger, which is used for tapping and sensitive probing, the fourth finger is specialized for probing that requires strength, scooping action and/or deep access (Chapter 2). It is therefore necessary to consider how did the selective pressures related to positional behavior and to foraging interact in evolving the long fourth finger. Soligo (2005) suggested that the initial selective advantage related to the need of securing postural support rather than to digit-feeding. This is questionable, however, because foraging in relevant positions (collecting wood-boring insects on large-diameter trunks and branches) might have already required also some extent of the specialized finger use in feeding. It may be more likely the probing and support-maintaining function of the aye-ayes strong fourth finger have co-evolved together as a single complex of adaptations. We however fully agree with the other Soligo's (2005) statement, i.e. that it was the possession of the strong elongated fourth finger that enabled the aye-aye to further evolve the other specialized finger, the third one, which is freed from the support-maintaining role and specializes morphologically as a soft an sensitive probe. We therefore support a slightly modified Soligo's (2005) evolutionary scenario with the aye-aye first evolving one (the fourth) or two (the third and fourth) fingers specialized for both tasks, feeding and maintaining the support, and subsequently further evolving one (the third) finger to serve solely as the foraging member.

Several authors have addressed the question how does possessing of the elongated hands limit the repertory of positional behavior of the aye-aye. Krakauer *et al.* (2002) and Soligo (2005) described several modifications of the stride pattern that possibly serve to decrease stress impacted on the delicate fingers during the phase of the stride when the highest pressure shifts from the heel of the palm to the fingers. Our finding that the positions when the aye-aye reverses its feet (grouped by Criterion III) are most employed during traveling extends the arguments that the aye-aye's locomotory apparatus may be modified to compensate for possessing the elongated forelimbs. We propose that having long hands with fine and relatively susceptible fingers (their injury could have fatal consequences for the animal's foraging efficiency) increases the relative importance of the hind legs in securing position, bearing animal's weight and propelling the body during locomotion in contexts other than foraging, particularly during traveling. Head-first descent is a strongly preferred mode of aye-aye's descent during traveling, followed by lateral descent, whilst the tail-first descent in employed only infrequently. In contrast to its high use in traveling, the head first-descent and its postural parallel, the head-down clinging, is only infrequently employed during foraging, when the aye-ayes strongly prefer using the head-up positions. This shows that the forelimbs and the hind limb of the aye-aye tend to specialize for complementary tasks – while the forelimbs are modified to securing head-up positional support when foraging, the hind limbs specialize to increase traveling options by employing the head-down positions.

Explaining the remarkably robust arm (the humerus and arm musculature) of the aye-aye is less straightforward. The aye-aye frequently use the positions that heavily load the shoulder girdle (grouped by Criteria IIA and IIB) both during foraging (when lift-off forces predominate) and during traveling (when compressive forces predominate). Based on the present literature, it cannot be conclusively decided whether the robustness of the upper extremity adapts the animal to resist the lift-off forces or rather the compressive forces. It is likely that some aspects of robustness (such as the humerus compressive strength) are advantageous in both situations. Adaptive modifications for resisting lift-up forces might therefore represent pre-adaptations to resist the compressive forces, and *vice versa*, and the two sets of modifications might have co-evolved. Furthermore, we should also consider the possibility that the robustness of the aye-aye humerus is a mere allometric product of increasing body size while pertaining the body built of a generalized arboreal quadruped (Runestad, 1997). In conclusion, we are so far unable to identify a specific set of activities that may be responsible for the evolving a strong, robust arm and shoulder girdle of the aye-aye.

Overall, our results suggest that the need to adopt specific body positions used during foraging and during traveling have modified different extremities (and their girdles) of the aye-aye. While the specific modifications of the forelimb serve primarily the demands of foraging, the hind limb modifications serve primarily the traveling purposes. But ultimately, the specialized foraging might played a more complex role in shaping of the locomotory apparatus of the aye-aye. It is likely that even the hind limb adaptations for traveling (reversible feet) resulted from the necessity to compensate for possessing the elongated forelimbs specialized for foraging tasks, and from the need to move frequently between canopy layers in order to access the feeding sites. These broad connections with the specialized way of foraging may help to explain why did the aye-aye evolved (or retained) morphological adaptations for traveling modes that are otherwise characteristic only for primates of smaller body sizes.

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Appendix I. Categorization and description of body postures and modes of locomotion

Any position observed can be classified to one of the following categories:

Walking (Figure 1g). Quadrupedal locomotion above a horizontal or oblique support with a relatively regular footfall pattern. When walking on an oblique support, the limbs do not pull the body up in a visibly increased tension. We included within this category also receding, that occurred rarely during social interactions.

Chest-sliding. The animal slides down a medium to large-diameter oblique support propelled by its hind legs, dragging the chest on the substrate. (Note: We were unable to interpret this behavior; it superficially resembles a scent marking but it occurs only rarely and may represent only an unusual form of descending oblique branches.)

Genitals-dragging. The animal moves as when walking or climbing but it lowers its hindquarters and drags its genitals on or near the substrate. (Note: Whenever well visible, the animal was urinating and spread the urine mark along the substrate.)

Climbing. Quadrupedal head-first ascent above an oblique or on vertical support with body weight being pulled up by limbs in a visibly increased tension.

Head-first descent. The animal moves down above an oblique support or on a vertical support, the body is primarily hung by the hind limbs during the locomotion.

Lateral descent. The animal descents above an oblique support or on a vertical support by clinging across the support and alternately lowering its fore- and hindquarters.

Tail-first descent. The animal moves down above an oblique support or on a vertical support by receding in the locomotory mode that otherwise resembles climbing.

Leaping. The animal leaps, jumps or drops down from a support, with a phase of no contact with the substrate. Only the in-air phase was considered a leap, preparatory phases they may take place are classified as standing (Figure 1e), clinging or hind limb suspension.

Sitting. The animal sits with the hind limbs flexed and hands placed on a similar level as feet.

Squatting. This represents an extreme semihunched posture (in terms of Pereira *et al.*, 1988) when the animal did not place its hands on substrate or placed them on a higher-elevated support.

Perching (Curtis 1992). This is a specific hunched sitting posture (in terms of Pereira *et al.*, 1988) when the animal sits across a support, maximally flexes its legs, so that the belly touches the substrate, and the shoulders and arms are held lowered compared to the hindquarters.

Lying. The animal's body weight rests apparently primarily on ventrum rather than on legs.

Standing (Figure 1f). Quadrupedal or tripedal standing on a horizontal or oblique support in position (notably the degree of limb flexion) characteristic for walking. When on an oblique support, the limbs are not in a visibly increased tension.

Crouching. A stereotypic quadrupedal standing posture, when the animal lowers its hindquarters close to the substrate. (Note: The position is associated with defecation or urination; it is probably identical to "crouching" described by Curtis (1992), interpreting it as being associated with scent marking.

Upright. Static postures that typically occurred in the form of supported bipedal standing, when the animal's weight rested primarily on hind legs but the hands helped in keeping the posture by holding to or by being placed on an elevated support. (Note: Unsupported bipedal standing, when body weight rested only on legs, was extremely rare).

Clinging (Figure 1a,d). The animal remains in a position characterized for climbing but with no locomotion.

Head-down clinging (Figure 1b,c). The animal remains in a position characterized for head-first descent but with no locomotion.

Hind limb suspension. A specific hanging posture, when the animal suspends itself by its feet.

Pronograde suspension (Figure 1i). A hanging posture when the animal's body remains parallel with the support rather than perpendicular to it. It may be bipedal, tripedal or quadrupedal.

Moving in suspension (Figure 1h). The animal moves quadrupedally whilst suspended pronogradely bellow the support.

Bridging. Any locomotory mode wherein the animal applied extreme extension of its forelimbs in order to cross between two supports without losing contact with the substrate.

Acrobatic. An unusual and apparently demanding postural mode that cannot be easily classified to any of the above categories. It also includes a single recorded case of hand suspension.

Transitional. The animal is in the process of changing from one position to another.

Appendix II. Categorization and definition of general activities

All behavior recorded in adult aye-ayes while visible could have been described within following categories:

Traveling. Progression, which is not apparently related to other ongoing behavior; it includes the chest-sliding descent where we were not able to confirm a scent-marking function. Traveling includes brief (up to several seconds) stationary stops or initial phases of progression, when the animal apparently looks for the next direction, prepares itself for a leap, hesitates or spins before leap or when it briefly stops moving with no specific intention apparent. It does not include brief stops when the animal sniffs or taps the substrate or pais attention to stimuli not related to the direction of travel.

Body care. Scratching or combing own fur or skin (using hands, feet or mouth), licking hand, inserting the third finger into mouth (presumably to clean teeth), stretching body and sharpening teeth by inserting a twig into diastema and rubbing it against the inner side of incisors.

Resting. The animal is either sleeping or dozing, with eyes closed, half-opened or opened but not directed to any apparent stimulus, and with body visibly relaxed. It does not include presumed resting in places where the animal is not visible and positional behavior cannot therefore be recorded.

Inactivity. The animal is fully awake but it does not move, does not pay visible attention to any external stimulus and does not show any behavior that could be described by any other category; it includes ceasing activity caused by rain and staying in proximity or contact with an infant with no other infant-related behavior.

Vigilance. Visual (or visual and auditory) monitoring of any direction or object, which is not in a close proximity (a reaching distance); it includes both unfocused looking around and concentrated watching. It may occur during breaks in traveling, resting, foraging or other activities, but only in case that it is not focused on objects of these behaviors.

Investigation. Sniffing and close visual inspection of any object except another aye-aye, whilst hands and teeth are not specifically used.

Tapping. A species-specific fast tapping on surfaces with the third finger.

Gnawing. It includes, besides proper gnawing, also using the incisors whilst peeling off a material and scrapping contents from a surface. It does not include using incisors for ingesting food or in connection with nest building (including collecting nesting material), body care or social interactions.

Probing or eating. Using third or fourth finger to probe-inspect any crevice, to scrap food or to bring food into mouth. Using mouth to pick up and ingest (or nibble with a possible intention to ingest) any food item

Unspecified foraging. It includes any foraging activity, which cannot be described as investigation, tapping, gnawing, probing or eating. It includes repositioning, brief breaks during foraging with no obvious interpretation, and instances when the observer was not able to identify details of foraging due to limited visibility, transitional nature of behavior or combination of both. It does not include breaks in foraging caused by vigilance to external stimuli (this is classified as vigilance).

Nest building. Includes biting off twigs or parts of big leaves as a nest material, carrying them to the nest and building a new or reconstructing an old nest; it does not include behaviors when animal is inside the nest and therefore not visible to record positional behavior

Playing. It includes locomotory play (fast running with interspersed frequent leaps), playful manipulation with objects, play fighting with objects (in this study, playing with coconuts transitional between foraging and fighting) and social play (playful chasing, attacking and wrestling)

Social. Agonistic or affiliate interactions with another aye-aye, including an infant. It does not include play interactions, calling without direct interaction with another animal, mere watching another animal or its direction, and mere staying in proximity or in contact with an infant without paying any further attention to it.

Calling. Emitting any call when not in a direct interaction with another aye-aye. It may occur simultaneously with other behaviors; the animal's behavior is when scored as calling when it calls during traveling, vigilance, rest or inactivity but not when it calls during foraging, nest building, body care or excreting. (Note: Frequent snorting was not considered as a call in this study so it did not fit to this category).

Excretion. Defecating, urinating or urine-marking by spreading the trail of urine along trunks or branches.

Chapter 6

What can the living aye-aye *(Daubentonia madagascariensis)* tell us about the extinct giant aye-aye *(D. robusta)*?

Introduction

Some 1000 – 2500 years ago, the island of Madagascar was inhabited by a rich megafauna, which included large non-flying aepiornitid birds, giant land tortoises, a pygmy hippopotamus, and several genera of giant lemurs. Most of these lemurs, such as koala-like megaladapids, sloth-like palaeopropithecids, or monkey-like archaeolemurids (Godfrey *et al.* 2006), became extinct without leaving any surviving close relatives. But two genera of the giant lemurs do have relatives among the surviving smaller forms: the ruffed lemurs *(Varecia* spp.*)* are a sister taxon to the extinct *Pachylemur* (Crovella *et al.* 1994) and the living aye-aye *(Daubentonia madagascariensis)* is a close relative of the extinct giant aye-aye *(D. robusta).*

The giant aye-aye was discovered at the beginning of last century in the dry southwest of Madagascar. The first-found fossil remains, three human-drilled incisors found in 1901 by Grandidier in Lamborahana. One of these is already lost but the remaining two were rediscovered in a museum collection and restudied by MacPhee and Raholimavo (1988). Although the fossil teeth were noticeably larger than those of the living species, it was only after Lamberton (Lamberton 1934) excavated near Tsirave associated bones that formed a near-complete skeleton of an unusually robust aye-aye. The skeleton, which regrettably missed the skull, has been described as *D. robusta*. The teeth found by Grandidier are now also assigned to this species (MacPhee & Raholimavo 1988). Third, and the last, fossil finding of the giant aye-aye consists of two humeri found near Anavoha (Lamberton 1934).

Simons (1994) reviewed what was known about the giant aye-aye to that date. He concluded that the animal was 3 - 5 times larger than the extant aye-aye. He stressed fact that in contrast to the living species, the giant aye-aye inhabited the most arid parts of Madagascar and that it remained a mystery how did it find enough food in this harsh habitat. He hypothesized that it might extend its feeding niche by increased terrestriality and by ability to dig in substrate or to tear rotten logs with its strong arms. He also proposed that it probably had low population densities and wide-spaced interbirth intervals, and that it might be an easy target to human hunters, who might eventually bring it to extinction.

Since Simons (1994) review, no new fossils of this species were discovered and the giant aye-aye remains one of the least known subfossil Madagascan lemurs. But during the intervening 13 years, new information accumulated on the other aye-aye species, the extant *Daubentonia madagascariensis*. It includes data on its ecology and behavior (this thesis), on morphology and function of its locomotory apparatus (Runestad 1997; Soligo & Műller 1999; Krakauer *et al.* 2002; Soligo 2005, this thesis) as well as on its geographical distribution (Sterling 1998).

In this paper, we attempt to exploit the new data on the living aye-ayes to bring additional insights in reconstructions of the life of the extinct giant species. We first address the problem of its body size and robustness, asking how much it differed from the living species and what selective forces might be responsible for the difference. We will then turn to the problems of how did it move and what did it eat, addressing also the possibility of increased terrestriality and digging behavior of the giant aye-aye. Finally, we will consider what habitat it probably occupied in the arid southwest Madagascar and what was the likely cause of its extinction in the recent past.

Body weight and robustness

Was the giant aye-aye really giant? This may be expected *a priori* from the fact that all other Malagasy lemurs, which are known to be extinct, were larger compared to all extant species (Godfrey *et al.* 2006). A threshold weight of approximately 10 kg seems to be a very good predictor of the recent past extinction risk: all lemurs with estimated body weight above 10 kg disappeared, whilst all that weight less than 10 kg still survive. But in the case of the limited fossil material of *Daubentonia robusta*, it is very difficult to consider the body weight. The current estimates range widely, between 6.7 and 13.5 (Simons 1994), which is 2.5 – 5 times the weight of the living *Daubentonia madagascariensis*.

Whilst the issue of body weight of the giant aye-aye has proven difficult to tackle, the robusticity of its skeleton has received detailed treatment. As its name implies, the postcranial skeleton of *Daubentonia robusta* is remarkably massive. In general, this is again to be expected as also the other extinct lemurs found in Madagascar were robustly built compared to the extant species. But the long bones of the giant aye-aye are highly massive even than compared with the other extinct lemurs, although it is one of the smallest of them. This applies most to the humerus, as demonstrated by Simons (1994). The robusticity index, calculated from the ratio of midshaft diameters ([mediolateral diameter + anteroposterior diameter] x 100) to the maximal length of the bone, shows the highest value among all lemurs so far measured. It is comparable only with some mammals that are clearly several times heavier than was the giant aye-aye, such as the black bear, moose or saiga.

The robustness of the giant aye-aye's humerus may be considered as an exaggeration of a pattern, which is also found in the smaller extant species. Demes & Jungers (1993) found several measures of the humeral compressive and bending strength to be remarkably high in *Daubentonia madagascariensis*, when compared with some other extant prosimians. Robustness of the forearm skeleton and musculature of this species has been discussed by several other authors (Curtis & Feistner 1994; Krakauer *et al.* 2002; Soligo 2005, Chapter 4). The robustness index of the giant aye-aye's humerus is nevertheless by 33 % higher than that of the extant species and besides the relatively broader shaft (reflected by the index), there are also other differences in its shape: the tubercles on the proximal end and the wing-like lateral flange on the distal end (crista supinatoris) are relatively oversized, whilst the size of the humeral articular head is relatively small in the giant species (Simons 1994).

Other long bones of the giant aye-aye, though still massive, show less extreme robustness compared to the humerus. Whilst the forearm bones are distinctly longer than in the extant aye-aye, their shape is relatively similar, except for the less curving of the ulna and the broader distal part of the radius. Also the difference in the shape of the femur is less pronounced, except of a proportionally small femoral head, situated on a shorter and thicker neck. The robusticity index of the giant aye-aye's femur is exceeded by several large primates, namely by the extinct sloth lemurs *(Palaeopropithecus, Archaeoindris*, and *Babakotia)*, koala lemurs *(Megaladapis)* and the gorilla *(Gorilla)* (Simons 1994).

Regrettably, the skull of the giant aye-aye is not available to see whether it also fitted to the pattern of general robustness. Only the human-modified incisors from Lamboharana may give us some cues. Interestingly, they are not as different from those of *Daubentonia madagascariensis* as might be expected from postcranial measurements. They are wider than mean values for the extant aye-aye teeth measured by MacPhee and Raholimavo (1988), the lower incisor being 13.6 % wider and the upper one being 11.5 % wider. They are also slightly thicker but this measure is already within the range detected for the extant species. It is difficult to consider the length of the teeth as their roots were apparently cut during the process of ancient trimming. With no doubt, they were larger than those of the extant aye-aye, but the exact size is unknown. Sterling (1993) increased the MacPhee and Raholimavo's (1988) sample by adding teeth measurements collected on live aye-ayes in Nosy Mangabe. She now found both width and thickness of the fossil teeth within the range for the extant species. Based on the incisors morphology, MacPhee & Raholimavo (1988) concluded that

Daubentonia robusta was larger but otherwise probably not very different from the extant *D. madagascariensis*; no unusual robustness of the skull was therefore demonstrated.

Runestad (1997) has questioned the basic issue of robustness of the living aye-aye in her comparative study of selected extant primates. Referring to a different comparative sample than which was used by Demes & Jungers (1993), she argued the humerus of *Daubentonia madagascariensis* is not unusually strongly built for a generalized climbing primate of a given size. To calculate the regression line, she included the aye-aye within a sample composed of generalized quadrupeds represented by two prosimian families (Cheirogaleidae, Daubentoniidae) and selected Platyrhine monkeys. The aye-aye did not prove to be an outlier in any of the measures of the humerus and femur compressive and bending strengths. Instead, it fitted close to the similarly sized Platyrhine species, the black bearded sakis *(Chiropotes satanas)* and white-fronted capuchin *(Cebus albifrons)* males.

The unusual robustness of the humerus of *Daubentonia madagascariensis* reported by Demes & Jungers (1993) may therefore result from the composition of their comparative sample. Although the aye-aye humerus (and not femur) showed remarkably high relative compressive and bending strengths, it was evident only within a subsample of prosimian species weighting over 1.2 kg. Most of them are more-or-less specialized leapers rather than generalized quadrupeds. When the relative compressive strength of the humerus was compared with that of the femur, the aye-aye fitted very close to the line indicating isometry while all other species weighting above 1.2 kg (lemurids and indriids) shifted below that line toward a relatively higher strength of femur (Demes & Jungers 1993). When similarly comparing bending strengths, the aye-aye deviated from isometry toward higher humeral bending strength, as however also lemurids did, while indriids were again shifted toward a higher femoral strength.

The questionable nature of the aye-aye robustness may be of crucial importance for estimating the body weight of the giant species. Its skeleton was apparently forelimb-dominated and the most robust part of the forelimb was the upper arm, especially parts where the flexors and extensors of the forearm attach. We have however shown that this may result from an allometric relation specific for generalized arboreal quadrupeds, and may differ from that in the leaping or slow climbing species. The two weight estimates given by Simons (1994) originate from regressions calculated by Godfrey (pers. comm. to Simons, 1994), using her extensive comparative database. The lower estimate (6.7 kg) was based on the surface area of the femoral head, while the upper one (13.5 kg) was based on the average of values based on regressions for the humerus and femur midshaft circumferences. Simons

(1994) preferred the latter measure, arguing that the femoral head of *Daubentonia* is small relative to other dimensions. But we rather argue in the opposite way, i.e., that within the comparative sample of differently specialized large lemurs, the midshaft diameter of the aye-aye's long bones, notably the humerus, may tend to overestimate the body weight.

Of the other lemurs, the ruffed lemurs *(Varecia)* are probably most similar to the extant aye-aye in their positional behavior, with walking and climbing as the dominant mode of locomotion but also high frequency of leaping and suspension by their reversible feet (Gebo 1987; Pereira *et al.* 1988; Meldrum *et al.* 1997). It is possible that there was a similar parallel also between the giant aye-aye and *Pachylemur*, an extinct giant lemur known to be closely related (Crovella *et al.* 1994) and probably also ecologically similar (Godfrey *et al.* 2006) to the extant ruffed lemurs. Is notable in this respect that although it is one of the smallest extinct lemurs, *Pachylemur* also possesses a highly robust humerus, with the robusticity index value approaching that of the giant aye-aye. *Daubentonia, Varecia* and *Pachylemur* are rather unusual among the medium-sized to large lemurs in being generalized quadrupeds rather than specialized leapers or slow climbers. In a comparative sample composed primarily of leapers and slow climbers, measures of humerus circumference may lead to an erroneous estimation of the body weight of these species.

While we prefer the low body weight estimate of *Daubentonia robusta*, which is based on the femoral head surface area, we must consider the possibility that also this measure may be biased. *Daubentonia madagascariensis* did not deviate from regression lines for the generalized quadrupeds, as calculated by Runestad (1997). Relatively small size of articulations in the aye-aye may therefore result from allometry and as such, it should not be considered unusual. But this again depends on composition of the comparative sample. In Runestad's (1997) analysis, the slow-climbing lorids had relatively larger articulations of the humerus and femur compared to the generalized quadrupeds. These primates do not leap and may need highly mobile shoulders and hips to cross between branches by limb extension and bridging. If this also applied for the extinct slow-climbing lemurs included in the Godfrey's comparative sample, then the regression based on the femoral head surface may indeed underestimate the giant aye-aye's body weight, as suggested by Simons (1994). But at the current state of knowledge, we consider the low estimate of the giant aye-aye (i.e., 6.5 kg) to be the better supported.

The conclusion that the apparent robustness of the aye-aye may result from allometry suggests that robustness itself may have no specific adaptive value for either of the *Daubentonia* species. Indeed, in our behavioral study of free-ranging aye-ayes, we were unable to identify any consistent context (such as foraging or traveling) when the aye-ayes typically use body postures and locomotory modes associated with possessing the strong arms (Chapter 4). Rather than being selected for robustness, there might been a selection for maintaining the generalized quadruped pattern of the body built whilst increasing the body size; the robust forelimb may be only an allometric consequence of this.

Locomotion

A highly complete skeleton discovered by Lamberton (1934) is larger and more robust than the skeleton of the extant aye-aye but in other respects, it does not appear very different. Isolated metacarpals and phalanges show the same specialization of the hand, notably of the third finger, as described in *Daubentonia madagascariensis* (Erickson 1994, Chapter 2). This alone strongly suggests that also positional behavior (body postures and locomotion) of the giant aye-aye basically resembled that of the extant species. Notion of the allometric nature of the increased robustness and the possibility that the body weight of the two species might not extremely differ only add to this argument.

But on the other hand, the larger size of the giant aye-aye probably posed some constraints on its locomotory abilities. Research on positional behavior and substrate use of the living aye-ayes (Curtis 1992; Curtis & Feistner 1994, Chapter 4) suggests that it may already approach a body weight limit to some of locomotory modes. Most notably, *Daubentonia madagascariensis* is the largest primate that is known to regularly descend trunks and branches head-first. Our data (Chapter 4) showed that this locomotion is important especially when traveling between feeding sites. The ability to use the reversible feet to descend head-first may compensate for limitations brought up by the highly elongated forelimbs, specialized rather for securing clinging postures on large vertical supports during foraging on wood-boring insects. Ruffed lemurs *(Varecia)* have also reversible feet and they frequently use the hind legs suspension but they only rarely descend head-first (Pereira *et al.* 1988; Meldrum *et al.* 1997). The humerus of ruffed lemurs was not described as remarkably robust (Demes & Jungers 1993). With the body weight of approximately 3.6 kg (Pereira *et al.* 1988), which is approximately 1 kg more than in the extant aye-aye (Feistner & Sterling 1995) and with no special adaptations of the forelimbs, the head-first descent may be too demanding for the ruffed lemurs. But the highly robust humerus of the giant aye-aye strongly suggests that this species was able of this locomotory mode. This might also apply for *Pachylemur*, the giant relative of ruffed lemurs, which is also reported as having an unusually robust humerus (Simons 1994). There are animals in the extant fauna as big or bigger than the giant aye-aye, that are able to descend head-first, notably the raccoons, *Procyon lotor,* (McClearn 1992) or the binturong, *Arctictus binturong* (pers. obs.). The extant aye-aye therefore does not represent the upper weight limit to this locomotory ability.

A detailed description of the muscle attachments of the extant aye-aye (Soligo 2005), together with description of bone anatomy of the giant extinct species (Simons 1994) may bring further insights to the question how did the extinct species move. Apparently, there was disproportionally more muscular tissue attached to the giant aye-aye's humerus. Proximally, the insertions of the supraspinatus, infraspinatus and subscapularis (which attach to the prominent humeral tubercles) might be well developed. These muscles act to abduct, adduct, rotate and stabilize the arm. Notably strong must have been muscles attaching to the distal part of the humerus. Both species of *Daubentonia* are distinct by a well-developed, wing-like flange along the lateral side of the distal humerus, the crista supinatoris. As shown by dissections of the extant species (Soligo 2005), this flange is functionally extended by a strong ligament connecting it with the humeral neck. Compared to the living species, the flange is disproportionally developed in the extinct giant aye-aye (Simons 1994).The principal muscle that attaches to this region in *D. madagascariensis* is the medial head the triceps brachii (Soligo 2005), originating on the dorsal aspect of the flange. Also the lateral head of the triceps might be well developed becausein the extant aye-aye (Soligo 2005), it originates on the proximal part of humerus, which is very broad in the giant species. The triceps is an extensor of the forearm and, due to its third head being attached to the scapula, also an adductor of the shoulder. It is therefore highly important during the head-first descent, suggesting that the giant aye-aye was indeed able of this locomotory mode. Ventrally, the principal muscles attached to the humerus at the broadened distal part in the extant aye-aye include the brachialis and brachioradialis (which also attaches to the ligament that extends from the flange), which are both flexors of the forearm and are important for pulling the body up during climbing and for securing clinging postures. Soligo (2005) also stresses that the relatively proximal and lateral origin of the brachiordialis (due to the lateral flange and ligament) increases the ability to supinate the forearm, but this is more important for digit-feeding than for securing a body position. In summary, the muscles most disproportionally developed in the giant aye-aye included flexors and extensors of the forearm and possibly also the muscles that stabilize the arm and shoulders. It is suggestive of an animal, which moved by climbing, clinging and descending head-down. This would fit to an animal with a similar repertory of positional behavior as described in the extant aye-aye (Chapter 4).

Substrate use and foraging

The puzzle of what did the giant aye-aye eat in dry southwestern forests may be approached indirectly, by asking: If the giant aye-aye moved similarly as the extant species, why it was larger?

The most pronounced differences in size between the two aye-aye species can be found in the long bones of the arm. This can be seen when comparing their humeri and femora (Figures 1 and 2 in Simons, 1994). This disproportion may be just due to the need to bring the center of mass close to the substrate in large climbing animals (Runestad 1997). But as the anterior extremities of aye-ayes are longest among primates when compared to the trunk length (Soligo 2005), it is more likely that there has been a specific selection force for evolving long forelimbs. Our data on positional behavior in free-ranging aye-ayes (Chapter 4) demonstrate that the principal context when they benefit from possessing elongated forelimbs is foraging for wood-boring insects on large, often vertically oriented trunks and branches. They typically cling to these substrates head-up, embracing the support with the long arms and hooking to the bark with claws. The reach of the forelimbs may be a significant constraint that limits exploitation of large logs by medium-sized mammals. McClearn (McClearn 1992) for example describes that free-ranging coatis *(Nasua narica)* are too small to encircle trunks of more than ca. 80 cm in diameter with their hands and that they have to climb lianas or adjacent trees in order to access fruits on such large-diameter trees. The aye-aye, which otherwise resemble these procyonid carnivores in several aspects of its morphology and positional behavior (pers. obs.), may be very acrobatic on large trunks, frequently alternating position when inspecting insect galleries, clinging only tripedally whilst using one hand for tapping or probing, and resisting apparent lift off-forces when gnawing the support (Soligo 2005). It is likely that the longer the forelimbs, the more secure is the posture adopted on a large vertical log; and an increase in body size further adds to an increase of the arm reach.

The increase in the whole body size may be a consequence of selection for increasing the embrace size of the forelimbs. There is however an alternative way of adapting to foraging on large-diameter trunks and branches, and it is dwarfism. Many marsupials, squirrels and primates that forage on large trunks are small bodied. They are equipped by claws, which are in case of primates modified nails (Soligo & Műller 1999), their thumb is not highly opposable and they cling to the bark by hooking with claws instead of grasping the support. Many of them feed on exudates and the marmosets have even evolved specialized dentition to penetrate the bark and to incite the exudates flow (Ankel-Simons 2000). But none of these species gnaws deep into the hard wood to forage large insects such as the cerambycid larvae.

This is even case of the often discussed stripped possums of Australia and New Guinea. These animals, weighting approximately 310 g *Dactylopsila palpator)* or 448 g *(D. trivirgata)* (Flannery 1995), compare in size with the clawed monkeys. Regardless of their small body size, they show convergence with the aye-aye in using their modified incisors and fingers to extract wood boring larvae (Rand 1937; Rasmussen & Sussman 2007). But they are much less specialized compared to the aye-aye. They large lower incisors are not ever-growing and they are typically not used for gnawing into hard wood but rather for tearing off rotten wood and bark (Handasyde & Martin 1996). Besides beetle and moth larvae, there is also high proportion of other insects in their diet, including ants, termites, earwigs, crickets, cockroaches and other arthropods (Rawlins & Handasyde 2002). Foraging on deep wood-boring larvae such as those of horned beetles probably requires substantial strength, which cannot be put forth by a small animal clinging only by its claws. The larvivorous aye-aye must therefore follow different evolutionary path, having increased its size rather than dwarfed. Even the extant aye-aye is an unusually big nocturnal primate and the giant species might only evolve this pattern further.

This may partly explain why the aye-aye so not follow the general pattern found in Malagasy lemurs, with the larger of the closely related species or subspecies found toward north of the island (Albrecht *et al.* 1990, cited in Simons 1994). If larvivory were responsible for the increased size of aye-ayes, than such selection force would be specific for this genus and not relevant to any other lemurs.

The larger species of aye-ayes was found in the driest part of Madagascar. If large size facilitates preying for wood-boring insects, is it possible, that insects represented relatively more important food resource in this type of habitat? Although Lanberton (1934) presumed that a large larvivorous animal such as *Daubentonia robusta* could not have found enough insect prey in the dry south, there is no *a priori* reason to believe that there is a scarcity of the insect prey in dry tropics compared to the humid regions. MacPhee and Raholimavo (1988) note that in West Indian islands like Puerto Rico, the insect density in areas comparably dry to the southwestern Madagascar may be twice as high as in rainforests. Furthermore, the wood-boring insects represent less seasonal resource the vegetable food. Larvae of cerambycid beetles typically develop several years and they are therefore available year-round (Erickson 1994). In contrast, flowering and fruiting is highly seasonal in the dry southwestern Madagascar. At present, *Daubentonia madagascariensis* in humid forests of east Madagascar largely depends on seeds. In Nosy Mangabe, the year-round available kernels of ramy *(Canarium* sp.*)* fruits represent the major food item for the aye-aye in terms of foraging time as well as in terms of ingested matter (Sterling *et al.* 1994; Sterling 1994). While collecting larvae on large logs, like those of baobabs *(Adansonia)*, may require large body size, feeding on seeds is likely to impose constraints on the body weight because too heavy animal would be unable to access smaller sized terminal branches where fruits tend to be most available. There is a reason to believe that the giant aye-aye was more dependent on the insect prey compared to the extant species and that this was an important factor in evolving its larger body size.

Terrestriality

The living *Daubentonia madagascariensis* frequently uses terminal branches to bridge between tree trunks (Chapter 4); this ability was probably compromised by the larger weight of *D. robusta*. This is also suggested by morphology of the femoral neck of the giant species. Compared to the extant aye-aye, it is situated on a short and thick neck, and more distally compared to trochanter (Simons 1994). This shows limited ability to extend the hind limb in various angles and therefore also limited abilities to adopt acrobatic bridging positions. The extant aye-aye also frequently leaps between branches, with some of leaps being of large-descent (up to 6 m deep), with high-impact landing to terminal twigs (Lhota & Jůnek, unpublished data). Although it is very likely that *D. robusta* also leaped (Simons 1994), this was probably limited to leaping between thicker branches that more easily bear the animal’s weight.

An alternative way of traveling through forest might involve occasional terrestriality. Sterling (1993) has stressed importance of terrestriality even for the smaller extant species; the aye-ayes on Nosy Mangabe spent 25 % of their time on the ground, which is more than for any other lemur except some populations of *Lemur catta* (Sterling 1993). But this is probably exceptional, as the aye-ayes studied by other authors were never observed on ground or only rarely (Petter & Petter 1967; Ancrenaz *et al.* 1994). Extremely high level of terrestriality reported by Andriamasimanana (1994) in Mananara is clearly due to a mistake in a figure legend. Based on our data from the same field site (Lhota & Jůnek, unpublished data), the proper values of the time spent on ground, as reported for two aye ayes in the Figure 4 by Andriamasimanana (1994) were most likely 1.52 % and 1.32 % instead of 43.34 % and 52.81 %. Aye-ayes therefore use the ground level but in a highly variable degree.

Simons (1994) mentions several cases when *Daubentonia madagascariensis* apparently crossed long distances in areas with no trees. This may possibly account for the unusual pattern of distribution of *Daubentonia madagascariensis* over an extensive geographic range, yet with no subspecies definitely identified (Groves 2001). But during their normal ranging, aye-ayes do not descend to ground merely to move between trees, even in secondary ecosystems with a discontinuous canopy (Lhota & Jůnek, unpublished data). Foraging, rather than traveling, seems to be the typical context of the aye-aye's terrestriality. In nosy Mangabe, most of the time spent by the aye-aye on ground was due to foraging on kernels of fallen ramy *(Canarium sp.)* fruits. In our field site in Mananara, where terrestriality was relatively rare, the typical context was similar, foraging on fallen coconuts (Lhota & Jůnek, unpublished data). In the highly seasonal environment of the southwestern Madagascar, the ability to exploit seeds fallen on the ground would probably much extend the season of availability of this food for the aye-aye. Furthermore, as discussed by Simons (1994), there might have been also additional insect food resources in the southwestern Madagascar available for the giant aye-aye on the ground. Besides fallen logs and branches, there are for example giant burrowing crickets or termite mounds.

Sterling (1993) measured limb proportions in would-caught *Daubentonia madagascariensis* and found a very high value of the intermembral index (IMI) that exceeds values for all lemurids. As a possible explanation, she put forward the high degree of terrestrial locomotion she has found in Nosy Mangabe aye-ayes. We disagree with this interpretation because it is the aye-aye's long hand that may explain most of forelimbs length disproportion; the high value of the IMI of the extant aye-aye may be better explained by the above-described adaptations for head-up clinging on large-diameter vertical supports. A more meaningful measure of adaptations for terrestriality would be length of the long bones of the arm and legs. When we compare the long bones proportions of the two *Daubentonia* species, we can see that *D. robusta* fits to the Steling's (1993) hypothesis better because its humerus, radius and ulna are relatively more elongated compared to its femur (Figures 1, 2 and 3 in Simons 1994). It must be repeated that having proportionally short hind limbs may be advantageous in large animals also for climbing, as it brings the body mass closer to substrate (Runestad 1997), but regardless the origin of these limb proportions, they seem to equip the giant aye-aye better for terrestrial locomotion, compared with the extant species.

Digging in soil and tearing wood

The possibility that the aye-aye exploited ground dwelling insects and logs and nuts fallen to the forest litter brings us to another hypothesis. Simons (1994) suggested that its robust forelimbs and muscles attached to the lateral flange of distal humerus might helped the animal to dig in the ground and to tear apart the rotten wood in search for food. We suggest that if the giant aye-aye used its hands in this way, it would probably result in a disproportional increase in robustness of the fourth finger. In the living aye-aye, the fourth finger is used for some of strength-requiring tasks in the extant species (Chapter 2) at it is very likely that it served a similar purpose in the extinct species. Unfortunately, the skeleton of hand of the Lamberton's (1934) specimen is known only incompletely. But so far, no specific development of any of the fingers has been stressed. There is a good reason to believe that the use of hands was basically similar in the two aye-ayes species. In the living aye-aye, we can see a very strong preference toward using mouth as opposed to hand for reaching for, tearing off, holding, and manipulating objects whilst the hand us almost exclusively used for tasks, which involve the use of the two specialized fingers, i.e., for tapping, probing, digit feeding and grooming (Chapter 3). It is possible that the aye-aye avoids risk of getting the delicate fingers injured by using mouth instead of teeth for other tasks, including tearing rotten wood (digging was not described for this species).

Preference for reaching and manipulating using mouth rather than hands is widespread among lemurs (Ward *et al.* 1993). But in aye-ayes it seems to be even more fixed than in other species. Most captive lemurs use hands (or both mouth and hands) to pick up pieces of chopped fruits presented in a dish (Pereira *et al.* 1988; Ward *et al.* 1990; Stafford *et al.* 1993). But aye-ayes almost always use their mouth even in this context (Feistner *et al.* 1994). When the wild aye-ayes use their hands whilst tearing materials, they typically only hold it by hands, putting forth the levering force by their teeth (pers. obs.). There is a slight indication in incisors morphology that supports the hypothesis that also the giant aye-aye used teeth, rather than fingers, to tear apart tough materials during the food excavation. If the two available teeth of *D. robusta* belonged to the same or similarly sized individuals, then the lower incisor is relatively larger in the giant species than it is in the living one: it is slightly thicker (in the extant species, the upper incisor is always thicker) and, in one of several variants of the length reconstruction, it also appears more disproportionally longer (MacPhee & Raholimavo 1988). The extant aye-aye typically uses its upper incisors as an anchor and the lower ones as a lever when tearing off material (pers. obs.). If the lower incisors of the giant aye-aye were in fact disproportionately developed, then *D. robusta* might use the teeth for tearing tough materials even more than the living species, leaving hands free to remain specialized for the finer finger work.

Habitat use and extinction

Our reconstruction shows that the giant aye-aye was probably similar to the extant smaller species in its basic ecology, except that it might be better adapted for preying on wood-boring insects on large tree trunks and for collecting various foods on ground. This would extend its feeding niche but on the other hand, the large-sized giant aye-aye probably had to find more food to survive. Could the dry forest habitat of southwestern Madagascar provide a large aye-aye with enough food resources?

Two of the three sites that yielded giant aye-aye's fossils (Lamborahana and Anavoha) were coastal wetlands located within zone, which is now covered by the driest thorn scrub. The third site (Tsirave) is a river valley located within the less extreme zone of the dry deciduous forests. Some 2000 years ago, the area was probably inhabited by apparently arboreal lemurs such as *Palaeopropithecus*, *Archaeolemur*, *Pachylemur*, or *Megaladapis* (MacPhee & Raholimavo 1988). It is likely that such fauna did not occupy the dry thorny scrub forest but rather the more humid basins and gallery forests. MacPhee and Raholimavo (1988) argued that even today, there are patches of such mesic vegetation along water courses and water bodies in the southwestern Madagascar and that these might have been just somewhat more extensive in a recent past due to proposed slightly more humid climate. Therefore, rather that being adapted to the harshest xeric vegetation formations, the giant aye-aye more likely lived in habitats comparable to those few western Madagascan dry forests, which probably until today host the extant aye-ayes (Sterling ; Simons 1994; Sterling 1998). These dry-forests aye-ayes are extremely rare and practically nothing is known about their life. But their research would be highly valuable to understand the ecological niche of not only this, but also the extinct giant species.

The giant aye-aye gone extinct perhaps some 1000 years ago (Sterling). Our re-evaluation of the body size suggests that it probably was the smallest of all extinct lemurs and perhaps the only one that which falls within the range of body sizes of the lemurs that survived until today, although it was still larger than the extinct lemurs that today inhabit the southwest Madagascar today. It is possible that the original rarity of the species made this species more prone to extinction compared to other medium-sized sized lemurs, the lemurids and indriids. The living aye-ayes are at present found over an extensive geographic range, which probably includes most of the island of Madagascar (Groves 2001). But throughout this area, it appears to be rare (Mittermeier *et al.* 1992). Even in Nosy Mangabe, where the population density was relatively high at the time of the Sterling's study (Sterling 1993), the aye-ayes inhabited large home ranges and moved long distances each night, for a nocturnal primate. Low population density may represent a natural characteristic of this genus. The scarcity of fossil remains finding fossil of both aye-aye species may indicate that these animals were already rare between 1000 and 2500 years ago, during the period to which most of the Madagascan lemur fossils date (MacPhee & Raholimavo 1988).

Although arrival of humans to Madagascar was probably a key factor in extinction of giant lemurs, the exact role of humans remains disputable (MacPhee & Raholimavo 1988; Godfrey *et al.* 2006). There is a lot of traditional beliefs associated with the living aye-aye, and some of these lead to killing the animals (Simons & Meyers 2001). The fact that the only found *D. robusta* incisors were drilled by humans, apparently to be worn as an ornament, suggests that the native people might have considered the animal rather unusual. For its large size, it might have been also hunted for meat. The giant aye-aye was probably nocturnal (Godfrey *et al.* 2006) but if it was more terrestrial and if it showed less antipredatory behavior due to its body size and strength, it might be an easier target to humans compared to the living species. But on the other hand, if the original habitat of the giant aye-aye (mesic forests) was limited in extent and fragmentary in nature, the habitat loss due to land-burning practices of early agriculturalists may alone bring this animal to extinction.

We can possibly see a parallel with the extant species even in respect to the extinction process. In humid eastern Madagascar, the living aye-ayes tend to adapt well to a range of secondary habitats, including agroecosystems (Andriamasimanana 1994; Ancrenaz *et al.* 1994) and they do not appear to be under immediate threat. But the situation is very different in the dry forests of western Madagascar, where the sightings of aye-ayes (or their feeding signs) are only rare, and sometimes only historical (Sterling ; Sterling 1998). *Daubentonia madagascariensis* may be in an advanced stage of the extinction process in dry forests of western Madagascar, north from the presumed former geographical range of *D. robusta*. This may mean that the two species of aye-ayes might have indeed not only adapted to similar niches in dry forests, but also that they are facing the same fate in these niches.

Conclusions

The giant aye-aye, *Daubentonia robusta,* might not differ from the extant *D. madagascariensis* in its morphology and ecology as much as could be inferred from its robust skeleton and geographical distribution in the dry southwest. This conclusion echoes that of Godfrey *et al.* (2006) who argued that in general, the extinct giant lemurs in Madagascar resembled the extant species in the principal aspects of their ecology and life history.

The giant aye-aye was probably no more that 2.5 times larger than the extant species and its robustness might result from allometry rather than from specific selective forces. It probably had a similar repertory of postural and locomotory behavior a the extant species, including the ability to descend trunks head-first. Also in feeding ecology, it might resembled the extant aye-aye, perhaps except a higher importance of wood-boring insect larvae in its diet. The need to collect this prey from large-diameter trunks might be the principal selective force for increasing the forearm reach and therefore also the body size. It was probably more terrestrial than the extant species and it probably used ground for occasional traveling as well as for foraging. It is however unlikely that it possessed specific adaptations for digging. It was probably a rare solitary animal with large home ranges and long night paths; this may have contributed to its eventual extinction. It the possible that an advanced process of extinction of the common aye-aye in dry forests of western Madagascar has similar causes as the completed extinction of the giant aye-aye in southwestern Madagascar in a recent past.

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Chapter 6

Conclusions

This thesis presents and discusses data on several specific aspects of ecology of the aye-aye *(Daubentonia madagascariensis)*, which are related to several of the numerous distinctive morphological features of this unusual lemur. Our project was conducted on a small island on Mananara River, eastern Madagascar. Exceptionally good habituation of aye-ayes that inhabit the island, together with a very good visibility in the agroecosystem habitat, allowed us to record behavioral data in details not paralleled by any previous field study.

Our data on the use of two modified fingers show that both third and fourth finger have specific, partly complementary roles. The third finger is specialized for tapping and for probing tasks requiring high mobility, sensitivity and precision, whilst the fourth finger is specialized for tasks requiring strength, scooping action and deep access.

We show that reaching and holding objects in hands is rare in aye-ayes and that aye-ayes preferably use their mouth for any manipulation that would not involve the specialized finger work. We demonstrate that some wild and captive aye-ayes show significant preference to using one hand for some tasks but with the proportion of right to left preferent animals being very close to 1 : 1; hand preference is consistent for two of the most frequent behaviors, tapping and probing with fingers.

Our results suggest that the aye-aye's long arms have probably primarily evolved to secure a postural support during foraging for wood-boring insects, allowing the animal to cling to large-diameter, often vertically oriented trunks or branches. We also propose that possessing the forelimbs highly specialized for foraging tasks influenced the compensatory specialization of the hind limbs for effective traveling, which includes frequent head-first descent.

Finally, in our comparative review of recent data available on the living and extinct aye-ayes, we conclude that the extinct giant species, *Daubentonia robusta*, probably did not differ from the extant *D. madagascariensis* in its ecology as much as could be inferred from its robust skeleton and geographical distribution in the dry southwest Madagascar, except that it might be more insectivorous and more terrestrial then the living aye-aye.