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RESEARCH ARTICLE

Specialized Use of Two Fingers in Free-Ranging Aye-Ayes (*Daubentonia madagascariensis*)

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The aye-aye (*Daubentonia madagascariensis*) possesses a highly specialized hand with two fingers, the third and the fourth, being used in a way unparalleled by any other primate. We observed the use of the third and the 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 for cleaning the teeth) and probing for nectar, kernels and insects in bamboo, twigs and live wood. In contrast, the robust fourth finger was used preferably when eating jackfruit (*Artocarpus heterophyllus*). When probing for invertebrates in soft plant tissues and in dead wood, both fingers were used in high proportions. To extract the 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, whereas the fourth finger appears to be specialized for tasks requiring strength, scooping action and deep access. Am. J. Primatol. 70:786–795, 2008. © 2008 Wiley-Liss, Inc.

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

INTRODUCTION

The aye-aye (*Daubentonia madagascariensis*) is a Madagascan lemur that is unique among 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 (Fig. 1). 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 while foraging. Their large and membranous mobile ears apparently perceive variations in resonance, which provide information on the internal structure of objects [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 (distal) phalange can flex and hyperextend independently, acting as a hook that can lift larvae or other 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].

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

Although 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 articles do not even mention it when describing digit use during aye-aye feeding [Ancrenaz et al., 1994; Andriamasimanana, 1994; Petter & Petter, 1967; Sterling, 1994]. The fourth finger is the longest on the aye-aye's hand; it is strong and robust and its claw is more than twice as long and wide compared with 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, whereas the least intrinsic hand muscle mass is attached to the second and the third fingers [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 the third finger to probe the holes of an experimental apparatus, but the percentage of fourth finger responses was low.

During our fieldwork with aye-ayes, we soon realized that the third and the fourth fingers were used for different foraging tasks and that the fourth finger had the primary role in several of these tasks. In this study we present descriptive data that allow us to conclude that the third finger appears to specialize primarily in tasks requiring high mobility, sensitivity and precision, whereas the fourth finger specializes in 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 1980s. 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 (S. L. and T. J.) 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), whereas the second observer followed only the first half of this time (from their emergence from the nest until midnight). If possible, on a given night, a single animal was followed by each observer. In cases where the observer lost the animal, he attempted to relocate the same individual. However, if he instead found another individual, he continued in following the new one. We used light-emitting diode headlamps and binoculars (8 × 30 and 8 × 40) to observe the behavior of these nocturnal animals. The distance between the animal and the observer ranged between 2 and 30 m but it was approximately 10 m for most of the time. In the case of grooming, which occurred higher in the canopy, the distance was 10–15 m for most of the time. All four animals were well habituated to human observers. They occasionally reacted to the noise caused by the observer's progression through the vegetation, but this typically occurred when the animal traveled and the observer had to follow it. In this situation, the animal sometimes increased the traveling speed or changed the direction of progression away from the observer. However, during feeding or grooming, when the animal did not move far and the observer remained noiseless, we did not notice any cues of alteration of 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 inserts a single finger into a crevice and/or inserts 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. Before fieldwork, the two observers spent a training period by practicing collecting data from video recordings and live aye-ayes in the Vincennes Zoo (Paris, France) until they reached a high level of agreement in identifying the finger (total agreement for close distance video recordings).

Probing represents a highly variable behavior compared with tapping, putting finger in mouth or grooming fur. We therefore also recorded the 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 catappa* fruits after their stones were gnawed open; some stones contained a parasitic larva instead of a 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 *C. nucifera* palms; the most common prey they contained 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 live or dead bamboo stalks. (9) Twigs: any prey from small live or dead twigs; 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 individual 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-min intervals; a finger use in this moment was considered a single instantaneous scan data entry. Finger-use acts were brief relative to the 1-min sampling interval and the animals frequently switched their fingers as well as hands and body positions. As can be seen from an example sequence presented in Table I, it is reasonable to consider consecutive instantaneous scans collected from the same bout of foraging as statistically independent for evaluation of finger use as they are separated by variable sequences of other behaviors (probing, gnawing, sniffing), changing hands and changing positions. We collected instantaneous data during sampling periods of 30 min that were separated by 30-min breaks when the observer remained with the animal. Besides the instantaneous data, we recorded additional instances of finger use by ad libitum sampling. 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. In the field notes (Table I), series of same-type behaviors were entered using one- or two-letter abbreviations with fingers coded as numerals (e.g., t3 for tapping with the third finger) and each single act was then entered using a single-letter code (l or r, depending on whether the left or the right hand was used). Compared with filling a code sheet, this continuous recording procedure required only brief glances at the field notebook thus allowing almost continuous viewing of the animal.

Table II summarizes the number and proportion of ad libitum and instantaneous records for each behavior and expresses the number of instantaneous

TABLE I. Sample Sequence of Foraging on a Live Tree Trunk Transcribed From Videotaped Behavior of One of the Study Subjects

Minute 8	Minute 9	Minute 10
08:55 move	09:01–09:02 probe (right)	10:00–10:04 move, gnaw
08:50–08:55 tap (right)	09:02–09:04 gnaw	10:04–10:09 probe (left)
08:54–08:57 gnaw	09:04–09:09 probe (right)	10:09–10:13 sniff, move
08:57–08:58 tap (left)	09:09–09:11 tap (right)	10:13–10:14 probe (left)
08:58–08:59 gnaw	09:11–09:19 move	10:14–10:15 move, sniff
08:50–09:01 tap (right)	09:19–09:25 tap (left)	10:15–10:18 probe (right)
	09:25–09:30 sniff	10:18–10:19 tap (left)
	09:30–09:33 gnaw	10:19 move
	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)	
Ad libitum record:	Ad libitum record:	Ad libitum record:
t3 r l	pb3 r r - t3 r l r r	pb3 l l r - t3 l
Instantaneous record:	Instantaneous record:	
t3 r	t3 r	

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 the third finger was used in this sequence. For analysis the sequence is described by 12 ad libitum records and two instantaneous scans (abbreviations used: t3 and pb3 introduce a series of consecutive records of tapping or probing, respectively, with the third finger; l and r mean a single record of probing and taping using the left or the right hand, respectively). It is evident from the sequence that the two instantaneous records can be considered independent.

TABLE II. Sample Size (Number of Recorded Incidences) for Four Types of Finger-Use Behavior for the Two Sampling Techniques

		Finger use		
	Hand use Instantaneous records	Instantaneous records (proportion of hand-use records (%))	Ad libitum records	Total
Tap	209	18 (8.6)	45	63
Probe	1,035	372 (35.9)	200	572
Mouth	13	0 (0.0)	12	12
Groom	109	8 (7.3)	28	36
Total	1,366	398 (29.1)	285	683

The number of instantaneous records with identifiable finger use is also shown as a proportion of the total instantaneous records with identifiable right/left hand use.

records of identified finger use as a percentage of total instantaneous records of hand use (when we were able to record that the animal used either the right or the left hand). The proportion of ad libitum data varies among behaviors because of variability in visibility of different behaviors. As the visibility of the third and the fourth finger use should not vary with the sampling method, the instantaneous and ad libitum data were pooled for analysis. During the field study, we videotaped several bouts of feeding and grooming using a SONY DCR-TRV230E video camera (Sony Comp., Tokyo, Japan) with infrared sensing. To validate qualitatively the ad libitum sampling method, we repeatedly watched the videotaped sequences at normal speed to evaluate whether there was any indication of a systematic bias in recording the third or the fourth finger; i.e., owing to better visibility of the stronger fourth finger or owing to slower movement of one of the two fingers.

Following the procedure commonly used in studies of lateral preferences in primates [Ward, 1995], we applied binomial tests to test for finger preferences during particular acts and with specific objects, the null hypothesis being ambipreference ($P = q = 0.5$). We conducted binomial tests for each individual as well as the pooled data from all four individuals. The effect of individual identity and object being processed on finger preferences in probing was analyzed with a generalized linear model, GLM [Fahrmeir & Tutz, 2002], with the number of records of usage of the third and the fourth fingers 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.

This research was approved by the Ethical Commission of the Faculty of Science of University of South Bohemia for Treatment of Laboratory Animals and it adhered to Madagascar national laws.

RESULTS

Table III presents results of binomial tests that compare the use of the third and the fourth fingers

TABLE III. Number of Records and Results of Binomial Tests for Preference of the Third and the Fourth Fingers in Four Individuals and Four Main Finger-Use Behaviors

	Tap			Probe			Mouth			Groom		
	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*
Lucy	22	0	0.000***	98	86	0.080	8	0	0.008**	12	3	0.028*
Koulic	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***

Significance level indicated by asterisks: ***$P<0.001$, **$P<0.010$, *$P<0.050$.

for tapping, probing, putting in mouth and grooming (Figs. 2–4). 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 probing in the four aye-ayes we have observed:

$$\text{Model}: \text{const.} + \text{individual} + \text{object} + \text{individual} * \text{object}, \quad \log L = -211.324, \quad \text{DF} = 28$$

$$-2\Delta \log L(\text{model} - \text{object}) = 216.011 \sim \chi^2_{24}, \quad P = 0.000$$

$$-2\Delta \log L(\text{model} - \text{individual}) = 130.422 \sim \chi^2_{21}, \quad P = 0.000$$

$$-2\Delta \log L(\text{model} - \text{individual} * \text{object}) = 130.422 \sim \chi^2_{17}, \quad P = 0.000.$$

Tables IV and V present data on probing with the third and the 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 for vegetable foods (Fig. 5). When feeding on jackfruit, the fourth finger was used almost exclusively. When feeding on nectar from 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 *T. 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 (Table V and Fig. 6). 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 third 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. However, the preference for either the third or the fourth finger for probing in soft tissues differed among individuals.

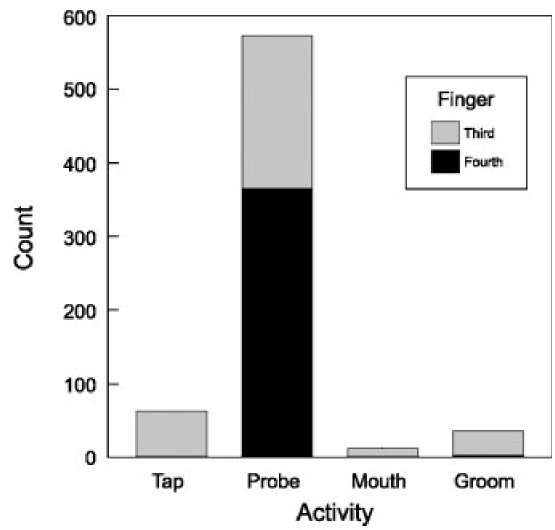

Fig. 2. Number of records of using the third and the fourth fingers in four main finger-use behaviors for all individuals combined.

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 appears to specialize in tasks requiring high mobility, sensitivity and preci-

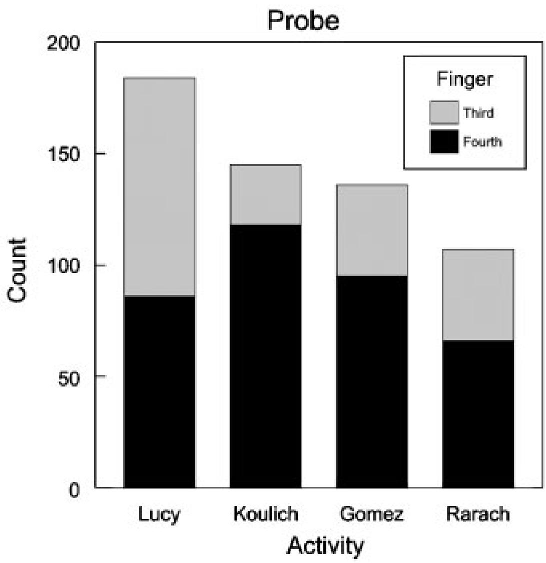

Fig. 3. Number of records of using the third and the fourth fingers for probing by four individuals.

sion, whereas the fourth finger appears to specialize in tasks requiring strength, scooping action or deep access.

The third finger was used for a broader range of tasks compared with 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 [Ancrenaz et al., 1994; Andriamasimanana, 1994; Erickson, 1995; Milliken et al., 1991; Petter & Petter, 1967; Sterling, 1994]. Although we did record a single instance of tapping with the fourth finger, it is probably either an exception or possibly the finger was misidentified. Tapping was very common and the relatively low frequency of recorded cases in this study does not reflect its low incidence but rather the difficulties posed in identifying the rapidly moving finger in the field.

We recorded only the use of the third finger when inserting a finger into the mouth. We suggest that this act was actually composed of two different behaviors that we were unable to reliably discrimi-

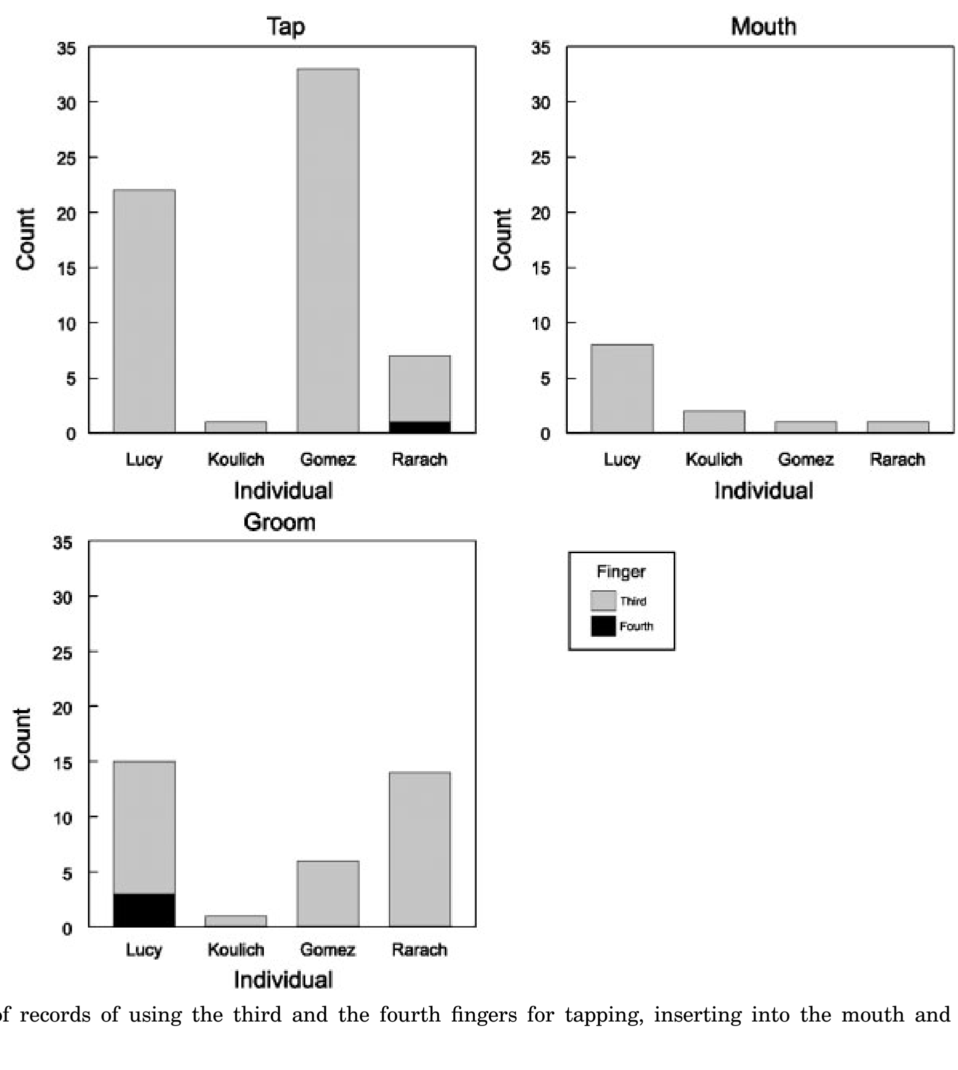

Fig. 4. Number of records of using the third and the fourth fingers for tapping, inserting into the mouth and grooming by four individuals.

TABLE IV. Number of Records and Results of Binomial Tests for Preference of the Third and Fourth Fingers for Probing in Four Individuals and Three Different Sources of Vegetable Food

	Coconut			Kernels			Jackfruit			Nectar		
	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*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**

Significance level indicated by asterisks: $^{***}P<0.001$, $^{**}P<0.010$, $^{*}P<0.050$.

TABLE V. Number of Records and Results of Binomial Tests for Preference of the Third and the Fourth Fingers for Probing in Four Individuals and Four Different Sources of Animal Food

	Soft tissues			Dead wood			Live wood			Bamboo			Twigs		
	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*	Third	Fourth	*P*
Lucy	10	0	0.002**	3	4	0.547	22	0	0.000***	2	0	0.500	12	1	0.003**
Koulic	1	37	0.000***	4	2	0.469	0	0	–	6	0	0.031*	0	0	–
Gomez	3	8	0.035*	12	6	0.142	2	2	0.750	12	0	0.000***	1	0	1.000
Rarach	1	0	1.000	3	1	0.500	5	0	0.063	1	0	1.000	2	0	0.500
Total	15	45	0.000***	22	13	0.043*	29	2	0.000***	21	0	0.000***	15	1	0.001**

Significance level indicated by asterisks: $^{***}P<0.001$, $^{**}P<0.010$, $^{*}P<0.050$.

nate in the field. Following feeding with their digit, especially on coconuts, aye-ayes may put their finger into the mouth to lick the remaining contents. However, the fact, that this behavior also frequently occurs outside the feeding context, suggests that aye-ayes may 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 among primates.

According to our data, aye-ayes also preferred the third finger for grooming fur. However, 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. However, 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, if the exact finger was not identified, the act was not 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 (no similar systematic bias was found between recording of movements of the third and the fourth fingers for other recorded behaviors). 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. Iwano [1991] reports grooming with both the third and the fourth fingers. 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. However, the most important seasonal source of nectar for aye-ayes, flowers of *Ravenala madagascariensis*, is 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 is eating eggs by captive aye-ayes [Iwano 1991] or eating ants and probably also other insects from hollow twigs as observed in our study. 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

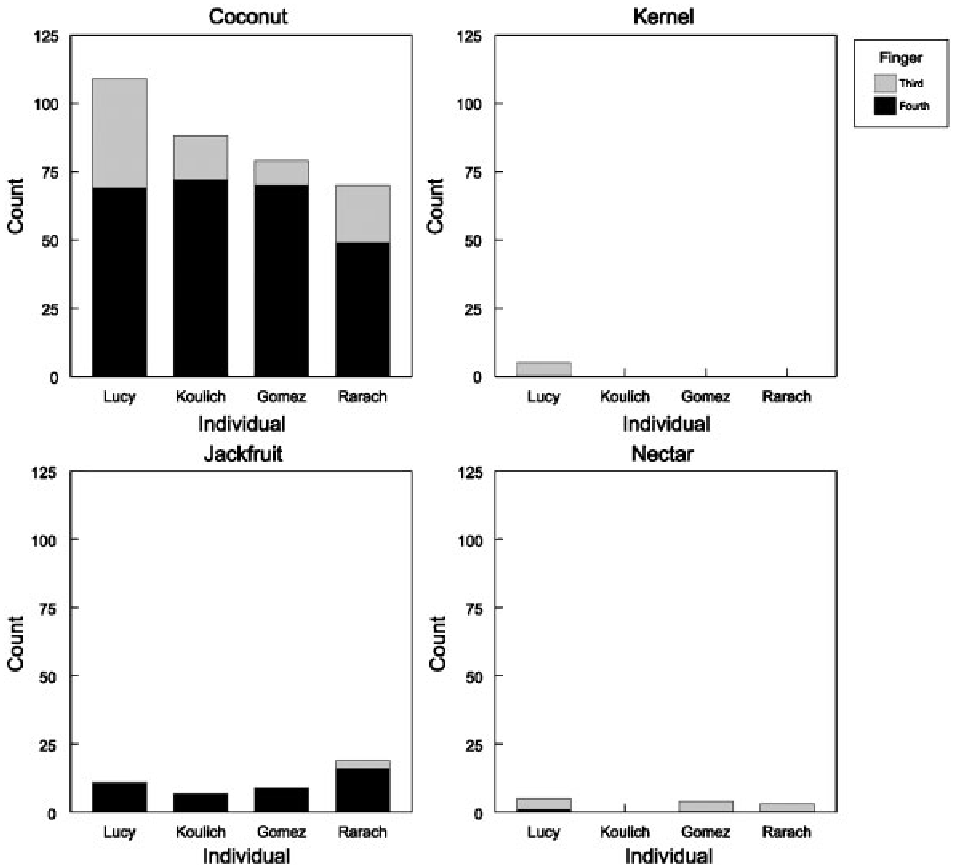

Fig. 5. Number of records of using the third and the fourth fingers for probing by four individuals in four different sources of vegetable food, i.e., coconut, kernel, jackfruit and nectar.

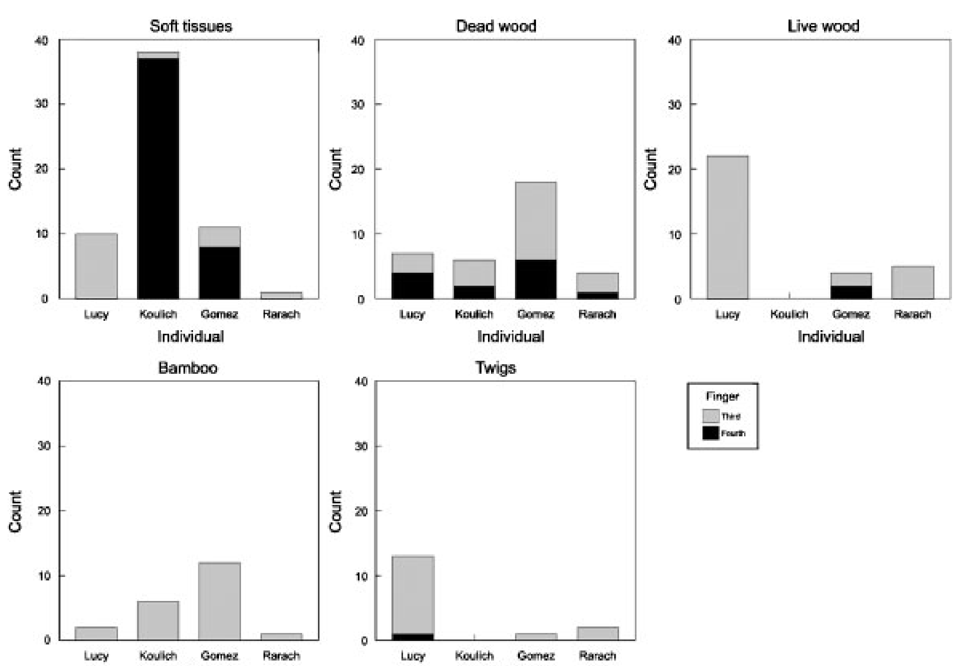

Fig. 6. Number of records of using the third and the fourth fingers for probing by four individuals in five different sources of animal food, i.e., soft tissues, dead wood, live wood, bamboo and twigs.

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, *T. 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 detail. 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 that wild aye-ayes using the third finger while eating fruits but does not specify 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 the video sequence recorded by Nicolas Gabriel (St. Thomas Productions) using an endoscope camera placed inside a coconut, which was presented to a captive subadult male in the Jersey Zoo. In this video one can see the fourth finger acting as a scoop, scratching the coconut flesh with rapid movements that are audible to human observers in the field. The shavings piled inside the nut are then collected, primarily using the 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 is 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 [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. However, 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 the fourth fingers as reported by Milliken [1995]. However, even in Milliken's study, the combined use of two fingers sometimes occurred 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 the fourth finger morphology [Milliken et al., 1991; Soligo, 2005]. The third finger is highly mobile, especially in the metacarpophalangeal joint; it is very thin and, supposedly, very sensitive. Compared with the fourth finger, the third finger makes a better probe to access narrow cavities in hard wood or bamboo, including irregular mines of insects such as termites, where it can hook and extract an invertebrate prey. The third finger is also well suited for collecting nectar from flowers, but it may be too fragile to resist strong bending 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 suitable for penetrating into or enlarging holes in fruit pulp, rotten wood or other relatively soft materials. It is also suitable as a scratching tool to scrape the 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 possible that the fourth finger providing these important functions allowed the aye-aye to evolve divergent morphological specializations of the third finger.

In conclusion, the hand of aye-ayes is unique in possessing two fingers that are specialized for behaviors unparalleled in 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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