

NEW CASES OF VERTEBRATE PREDATION BY THE RING-TAILED LEMUR (*LEMUR CATT*A), WITH REFERENCE TO DIFFERENCES FROM *EULEMUR* SPECIES AND OTHER PRIMATES

Shinichiro ICHINO

Primate Research Institute, Kyoto University and German Primate Center

Hajarimanitra RAMBELOARIVONY

Department of Zoology, University of Fort Hare

ABSTRACT Vertebrate predation by the ring-tailed lemur (*Lemur catta*) has rarely been observed, although this species is one of the most intensively studied lemur species. In this paper, we report four new cases of vertebrate predation by ring-tailed lemurs at Berenty Reserve, Madagascar, and summarize the characteristics of this behavior. In all cases, females preyed on chameleons in the rainy season. They caught the chameleons with their hands, killed them by biting off the heads, and subsequently ate the bodies. While they were consuming their prey, they were approached by other females, one of whom snatched the prey away. In contrast, males were not interested in the prey, except one juvenile. This study showed that vertebrate predation behavior by ring-tailed lemurs seems to be (1) one involving the craniocervical killing bite, (2) female-biased, (3) low in frequency compared to closely related *Eulemur* species, and (4) seasonal.

Key Words: Vertebrate predation; Lemur; Diet; Meat-eating; Killing bite.

INTRODUCTION

Vertebrate predation has been reported in at least 38 species of free-ranging nonhuman primate (Butynski, 1982) and has been discussed from ecological viewpoints, such as diet or predator-prey relationships, and from anthropological perspectives, such as the origins of human hunting (Teleki, 1975; Rose, 1978; Steklis & King, 1978).

Vertebrate predation by non-nocturnal (diurnal and cathemeral) lemurs has rarely been observed, especially in wild populations (Tattersall, 1982; Clarke, 1987; Mittermeier et al., 2006). Recently, however, several cases of vertebrate predation have been reported, and vertebrates have come to be considered a part of non-nocturnal lemur diets, especially in *Eulemur* species (Jolly et al., 2000; Mizuta, 2002; Simmen et al., 2003).

Unlike *Eulemur* species, the ring-tailed lemur (*Lemur catta*) does not appear to prefer vertebrates as a food resource. For example, in experiments performed in captivity, *Eulemur* species showed interest in and consumed vertebrates, whereas ring-tailed lemurs did not (Jolly & Oliver, 1985). Glander et al. (1985) also reported that ring-tailed lemurs in colonies at the Duke University Primate Center showed no interest in dead birds, although *Eulemur fulvus* and *Eulemur macaco* consumed some birds and lizards.

Only one case of vertebrate (chameleon) predation by ring-tailed lemurs has been reported (Oda, 1996). Here, we report four new cases of vertebrate predation by ring-tailed lemurs and summarize the characteristics of this behavior with reference to differences from closely related *Eulemur* species and other primates.

SUBJECTS AND METHODS

These incidents were observed at the Berenty Reserve in southern Madagascar, where ring-tailed lemurs have been studied intensively by many researchers since the 1960s (Jolly et al., 2002; 2006). All except one case (case 4) were observed in the same troop (Troop T1A), which has been studied continuously by Koyama and his colleagues since 1989. Kin relationships among females in this group were thus known (Koyama et al., 2001; 2002). Troop T1A consisted of 11 individuals in November 2001 (case 1), including 4 lactating females, 1 non-lactating adult female, and 3 adult males. In November–December 2005 (cases 2 and 3), it consisted of 15 individuals, including 3 lactating females, 3 non-lactating adult females, and 5 adult males.

Three (cases 1, 3 and 4) of the four incidents were observed by SI and one (case 2) was observed by HR. SI has studied the troop since 1998 and could readily identify all troop members. HR could also identify all adult members of the troop.

RESULTS

Case 1: 2 November 2001

Troop T1A was moving through the forest toward a water basin at the edge of the open area. At 16:47, SI found that a lactating female (KUB-9096♀) had climbed a small *Pithecellobium dulce* tree. At that time, her mother (KUB-90♀) and three juveniles were nearby. KUB-9096♀ suddenly grasped a chameleon sitting on a branch about 2 m from the ground. She tried to bite the chameleon's head, but failed due to the chameleon's efforts to escape. She had descended to the ground while struggling with the chameleon. KUB-9096♀ then climbed another tree (*Cassia* sp.) because her mother (KUB-90♀) had approached her. KUB-9096♀ stopped at a branch that was about 7 to 8 m from the ground. After this, no troop member approached her. KUB-9096♀ then bit the chameleon's head again and the chameleon stopped moving; it had probably died. She then began to feed on the chameleon (Fig. 1).

At 16:50, other troop members moved to the open area and KUB-9096♀ was left alone. At 16:52, she moved to the open area, clutching the dead chameleon in her mouth. At 16:53, her 1-year-old brother (KUB-9000♂) approached her and she attacked him. At 16:54, KUB-9096♀ climbed an *Azadirachta indica* tree in the open area and continued to consume her prey. At 16:56, her aunt, a dominant female (KUB-93♀), approached her three times. KUB-9096♀ fled while emitting a submissive call (the spat call) but did not surrender the prey to her aunt; instead,



Fig. 1. A lactating female lemur (KUB-9096♀) feeding on a chameleon.

she resumed eating it.

At 16:58, KUB-9096♀ suddenly dropped the dead chameleon from her hand. No troop member, including KUB-93♀, approached the remains of the dead chameleon. KUB-9096♀ lost interest in the chameleon and began to eat *Melia azedarach* leaves. She subsequently left the area with the other troop members, leaving the remains of the dead chameleon behind.

The remains of the dead chameleon consisted of the tail, left hind leg, thigh of the right hind leg, and a small part of the intestines. The lengths of the tail, thigh, calf, and foot were 13.3 cm, 3 cm, 2 cm, and 1 cm, respectively. All other parts, including bone and skin, had been completely consumed.

Case 2: 10 November 2005

At 09:00, the members of Troop T1A were resting on the ground and in the trees in the forest. At 09:02, a lactating female (KUB-9001♀) caught a chameleon at a distance of about 20 m from the other group members. She struggled with the chameleon, trying to bite its head; the prey tried to escape by biting her.

At 09:03, the chameleon stopped moving and KUB-9001♀ began to eat it. At 09:33, the second-ranking non-lactating female (KUB-93♀), who was her aunt, approached her. KUB-9001♀ fled from the scene emitting spat calls. At 09:34, KUB-93♀ followed and acted aggressively toward KUB-9001♀. KUB-9001♀ gave up and KUB-93♀ won the rest of the dead chameleon, which was around one-fourth of the total body size. KUB-9001♀ tried to reclaim the dead chameleon by approaching KUB-93♀ with spat calls and trying to groom her. However, KUB-93♀ did not surrender it.

KUB-93♀ left the area at 10:09; only the tail of the dead chameleon remained



Fig. 2. A lactating female lemur (KUB-9001♀) feeding on a spiny chameleon (*Chamaeleo verrucosus*).

behind, and no lemur was interested in it. All other parts of the prey, including bone and skin, had been completely consumed. At 10:10, the troop began to rest. The spines on the chameleon's back indicated clearly that it was a spiny chameleon (*Chamaeleo verrucosus*; Fig. 2).

Case 3: 11 December 2005

At 16:17, the members of Troop T1A were eating cacti near the open area. At 16:30, they began to move into the forest.

At 16:52, SI found that a lactating female (KUB-9001♀) had climbed a branch to a height of approximately 2.5 m from the ground while emitting a spat call, probably due to an approaching dominant female. At that time, KUB-9001♀ had part of a dead chameleon, whose head had already been eaten, in her mouth. She continued to eat it on the branch. At 16:55, she finished eating the chameleon's body and hind legs and continued to chew the tail.

At 16:56, the tail fell from her hand and she lost interest in it. No other troop member approached the tail. At 16:59, KUB-9001♀ began to travel with the other troop members. Only the tail of the chameleon remained. All other parts, including bone and skin, had been completely consumed. Although we could not estimate the size of the chameleon, it seemed to be a relatively small individual.

Case 4: 8 February 2011

At 18:19, SI found that an adult female of an unknown group (Female A) was eating a chameleon on a tree (about 2 m above the ground) in the Ankoba forest area. She was biting its head while holding it in both hands. The chameleon was not moving and appeared to be dead. One adult female (Female B) was the only other lemur near Female A. Neither female had an infant.

At 18:22, Female B approached Female A and sniffed the chameleon in A's hands. Female A acted aggressively toward Female B and B fled from her. Female A then resumed eating the chameleon. At 18:28, Female B approached Female A again. At 18:29, Female B stood up on the branch and then sat down again in the same place.

At 18:30, Female A approached Female B and B fled from her. Female B moved to Female A's former location and sniffed repeatedly at the branch. She then approached Female A slowly and grabbed the chameleon in A's hands. Female A acted aggressively toward Female B and B fled from her. Female A then resumed eating the chameleon.

At 18:35, Female A approached Female B and B fled from her. Female B moved to the place where Female A was sitting and sniffed at the branch again. Female A resumed eating the chameleon.

At 18:36, Female A moved to another branch about 5 m above the ground with the chameleon in her mouth. At 18:37, she moved again in the tree, and at 18:38, she disappeared into a large *Tamarindus indica* tree. It is unknown whether she consumed all parts of the chameleon or not, as the rest of the chameleon was not found.

Summary of *Lemur* and *Eulemur* Vertebrate Predation

We have summarized all previously reported cases of vertebrate predation by non-nocturnal lemurs, including the cases reported here (Table 1). To the best of our knowledge, vertebrate predation among non-nocturnal lemurs has been reported only in *Lemur* and *Eulemur* species (see also Clarke, 1987). At least 25 cases of vertebrate predation in captivity and in the wild have been reported (Table 1).

DISCUSSION

Vertebrate predation by ring-tailed lemurs is a relatively rare and opportunistic behavior. In the course of long-term study of this species at Berenty for more than 40 years (since 1963; Jolly et al., 2002), only five cases of vertebrate predation, including our four cases, have been recorded. Additionally, there is no report of vertebrate predation in the Beza Mahafaly Special Reserve, another site where long-term studies of ring-tailed lemurs have been conducted (Sauther et al., 1999; Gould et al., 2003; Sussman & Ratsirarson, 2006), although Sauther (1992) reported an attempted bird predation incident.

On the basis of the present cases, we discuss the characteristics of this behavior with respect to the following: (1) the process of predation by ring-tailed lemurs,

Table 1. A summary of the observed cases of vertebrate predation by the *Eulemur* and *Lemur* species.

#	Month, year	Location	Captive/wild	Species of predators	Sex of predators	Prey categories	Prey	References
1	Jan. 1995	Berenty	Wild	<i>Lemur catta</i>	Female (Adult)	Reptilia	Chameleon (<i>Chamaeleo lateralis</i>)	Oda 1996
2	Nov. 2001	Berenty	Wild	<i>Lemur catta</i>	Female (Adult)	Reptilia	Chameleon	This study (Case 1)
3	Nov. 2005	Berenty	Wild	<i>Lemur catta</i>	Female (Adult)	Reptilia	Chameleon (<i>Chamaeleo verrucosus</i>)	This study (Case 2)
4	Dec. 2005	Berenty	Wild	<i>Lemur catta</i>	Female (Adult)	Reptilia	Chameleon	This study (Case 3)
5	Feb. 2011	Berenty	Wild	<i>Lemur catta</i>	Female (Adult)	Reptilia	Chameleon	This study (Case 4)
6	Sept. 1995	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Female (Adult)	Mammalia	<i>Lemur catta</i> (infant)	Pitts 1995
7	Sept. 1998	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Female (Adult)	Mammalia	<i>Lemur catta</i> (infant)	Jolly et al. 2000
8	Oct. 2000	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Female (Adult)	Mammalia	<i>Lemur catta</i> (infant)	Ichino (personal observation)
9	Oct. 1992	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Unknown	Reptilia	Chameleon	Jolly et al. 2000
10	Unknown	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Unknown	Reptilia	Chameleon	Jolly et al. 2000
11	Unknown	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Unknown	Reptilia	Chameleon	Jolly et al. 2000
12	Unknown	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Unknown	Reptilia	Chameleon	Jolly et al. 2000
13	Feb.–Mar. 1999	Berenty	Wild	<i>Eulemur rufus</i> × <i>E. collaris</i>	Unknown	Reptilia	Chameleon	Simmen et al. 2003
14	1996	Manchester (UK)	Captive	<i>Eulemur rufus</i>	Female	Mammalia	Mouse	Jolly et al. 2000
15	May. 1983	Duke (USA)	Captive	<i>Eulemur fulvus</i>	Female	Aves	Brown thrasher	Glander et al. 1985
16	Jun. 1983	Duke (USA)	Captive	<i>Eulemur fulvus</i>	Female	Aves	Brown thrasher	Glander et al. 1985
17	Feb. 1984	Duke (USA)	Captive	<i>Eulemur fulvus</i>	Female (juvenile)	Reptilia	Fence lizard	Glander et al. 1985
18	Dec. 2000	Ampijoroa	Wild	<i>Eulemur fulvus</i>	Unknown	Aves	<i>Terpsiphone mutata</i> (nestlings)	Mizuta 2002
19	Dec. 2000	Ampijoroa	Wild	<i>Eulemur fulvus</i>	Unknown	Aves	<i>Placensis sakalava</i> (egg)	Nakamura 2004
20	Unknown	Ampijoroa	Wild	<i>Eulemur fulvus</i>	Unknown	Aves	Unknown birds and/or eggs	Thalmann (cited in Curtis, 2004)
21	May. 1989	Duke (USA)	Captive	<i>Eulemur collaris</i>	Male (1-year-old)	Aves	Mourning dove (egg)	Shedd 1990
22	1983	Jersey	Captive	<i>Eulemur mayottensis</i>	Male	Aves	Blue tit	Jolly & Oliver 1985
23	Feb. 1983	Duke (USA)	Captive	<i>Eulemur macaco</i>	Female (Pregnant)	Aves	Cardinal	Glander et al. 1985
24	1983	Jersey	Captive	<i>Eulemur mongoz</i>	Male and Female	Aves	Sparrow	Jolly & Oliver 1985
25	Nov. 1994	Anjanena	Wild	<i>Eulemur mongoz</i>	Female	Aves	Unknown bird (fledglings)	Curtis 2004

(2) sex differences in the behavior, (3) differences between *Lemur* and *Eulemur* species in the frequency of the behavior, and (4) seasonality of the behavior.

The process of the observed predation was similar to that of classic predation, including the use of the craniocervical killing bite (Steklis & King, 1978; King & Steklis, 1984). The lemurs caught the chameleons with their hands, killed them by biting off the heads, began eating them at the heads, and left the lower parts of the bodies uneaten. They probably attempted to kill the chameleons first because they tried to escape after they were caught (cases 1 and 2). Thus, our observations are consistent with the widespread descriptions of the use of the craniocervical killing bite in primates (King & Steklis, 1984).

Chameleons seem to be the most common vertebrate prey of ring-tailed lemurs in the wild. In all five cases, including one previously described case (Oda, 1996), ring-tailed lemurs preyed on chameleons. No other vertebrate prey has been reported (Table 1). Only two chameleon species (*Chamaeleo lateralis*, *C. verrucosus*) are known to be present in Berenty (Oda, 1996), and both were preyed upon by ring-tailed lemurs (Table 1). In captivity, *Eulemur* species preyed upon and consumed some birds, lizards, and mice (Glander et al., 1985). However, in the wild, *Eulemur* species have been reported to prey only on chameleons, infant ring-tailed lemurs, and the nestlings/fledglings or eggs of some birds (Table 1). In all cases of *Eulemur* predation on infant ring-tailed lemurs, the infants were very small and probably could not move by themselves (Pitts, 1995; Jolly et al., 2000; Ichino, pers. obs.). Thus, chameleons appear to be the only mobile vertebrate prey of *Lemur* and *Eulemur* species in the wild. Birds and lizards probably move too quickly to be captured by lemurs in the wild.

In all cases, only adult females preyed on chameleons and other females subsequently approached; one succeeded in snatching the prey (case 2). In contrast, no males preyed upon or approached the prey, except one juvenile (case 1). This female-biased predation pattern has also been observed in *Eulemur* species in captivity (Glander et al., 1985). In contrast, male-biased predation patterns have been reported in anubis baboons (Harding, 1973; 1975), chimpanzees (Teleki, 1973; Stanford et al., 1994), and white-faced capuchins (Fedigan, 1990; Rose, 1994).

The lack of sexual dimorphism in body mass among lemurs (Kappeler, 1991) might explain the female-biased predation patterns of *Lemur* and *Eulemur* species. Koyama et al. (2008) found no sex difference in the body mass of adult ring-tailed lemurs at Berenty. Most (92.2%) female ring-tailed lemurs at Berenty give birth every year, and 82.0% of births occur in September (Koyama et al., 2001). It is, therefore, expected that the energy requirements of most adult females may be higher than those of adult males during the lactation period (approximately September–January at Berenty). In three of four cases (cases 1–3), lactating females preyed on the chameleons. Lactation is the most costly reproductive period for female mammals (Clutton-Brock et al., 1989), and some studies of non-human primates (Sauther & Nash, 1987; Tirado Herrera & Heymann, 2004) have suggested that female protein requirements may increase during lactation. The need for protein or other micronutrients, such as vitamin B₁₂ (Hausfater, 1976), may thus underlie the predatory behavior.

The female-biased predation pattern cannot be explained simply by the number

of males in a group. Among group-living lemurs, the number of males is generally nearly equal to that of females in a group (Kappeler, 2000). The sex ratio of Troop T1A (cases 1–3) was not strongly biased toward females (see SUBJECTS AND METHODS).

Female dominance (Jolly, 1966; Kappeler, 1990; Pereira et al., 1990) may affect the female-biased predation pattern. However, our observations suggest that male ring-tailed lemurs have no strong interest in chameleons. Moreover, most *Eulemur* species are not female-dominant (Pereira et al., 1990), although they also showed a female-biased predation pattern (Glander et al., 1985).

Although the predation pattern of ring-tailed lemurs is similar to that of *Eulemur* species, the frequency of predation by ring-tailed lemurs may be lower than that by *Eulemurs*. Vertebrate predation by ring-tailed lemurs has been reported less frequently than that by *Eulemur* species (Table 1), although the ring-tailed lemur is one of the most intensively studied lemur species (Jolly et al., 2002). In contrast to *Eulemur* species, ring-tailed lemurs did not eat vertebrates in captivity (Jolly & Oliver, 1985; Glander et al., 1985). This difference between *Lemur* and *Eulemur* species might be explained by differences in diet and gastrointestinal morphology. Simmen et al. (2003) found that brown lemurs (*Eulemur rufus* × *E. collaris*) were more frugivorous than sympatric ring-tailed lemurs (*Lemur catta*) at Berenty in the middle of the dry season. Morphologically, the ring-tailed lemur has a relatively large and haustrated cecum that is suitable for the microbial breakdown of plant cell walls (Campbell et al., 2000). In contrast, the measurement of gastrointestinal transit time using radio-opaque barium-impregnated polyethylene spheres has suggested that microbial processing is not significant in *Eulemur fulvus* (Campbell et al., 2004). Thus, ring-tailed lemurs appear to be more folivorous than *Eulemur* species and may require little animal matter.

Interestingly, the frequency of predation may differ among troops. In three cases involving Troop T1A (cases 1–3), the predating females and those who approached them or snatched the prey were part of a kin group (KUB-kin group) within the troop. The predating females were sisters (KUB-9096♀ and KUB-9001♀), and one of them preyed on chameleons twice (cases 2 and 3). The approaching females were their mother (KUB-90♀) and aunt (KUB-93♀), respectively. Females in the kin group may recognize chameleons as food resources. In contrast, Simmen et al. (2003) reported that ring-tailed lemurs in another troop at Berenty mobbed and avoided the chameleons. Thus, different troops at Berenty may respond differently to chameleons.

Predation by ring-tailed lemurs may be a seasonal behavior. All cases, including that reported in a previous study (Oda, 1996), were observed at the beginning or in the middle of the rainy season (November–February). In contrast, vertebrate predation by *Eulemur* species has been observed at the end of the dry season and in the early rainy season (Table 1).

Seasonality in predation has also been reported for other primates (e.g., Takahata et al., 1984; Stanford et al., 1994 for chimpanzees; Hausfater, 1976 for yellow baboons; Rose, 1997 for white-faced capuchins) and considerable temporal variation has been found in the frequency of predation (Mitani & Watts, 2005). Hypotheses to explain this seasonality can be categorized into three types of causal factors:

ecological conditions, prey characteristics, and predator characteristics (Mitani & Watts, 2005).

Our observations suggest that prey (chameleon) and predator (lemur) characteristics may be causal factors for seasonal predation by ring-tailed lemurs. First, chameleons are active during the rainy season and their skin colors become brighter, enabling other animals to identify them easily (Oda, 1996). Thus, chameleons may become more readily available and easier to capture for lemurs in this season. Second, the seasons of predation also mark the end of the lactating and weaning seasons of ring-tailed lemurs at Berenty (Gould, 1990; Koyama et al., 2001). As discussed above, female ring-tailed lemurs may supplement their protein requirements by eating meat in these seasons.

ACKNOWLEDGEMENTS We are grateful to Mr. Jean de Heaulme and his family for their kind permission to carry out our studies and their hospitality at Berenty Reserve; A. Randrianjafy and H. Andriamialison, former directors of the Botanical and Zoological Park of Tsimbazaza, and the Government of the Republic of Madagascar, for their kind permission to perform our research in Madagascar; and N. Koyama and two anonymous reviewers for their invaluable advice. This work was supported by Grants-in-Aid for Scientific Research from the Ministry of Education, Culture, Sports Science and Technology of Japan to S. Kobayashi (No. 16252004), and Y. Tahakata (No. 21405015); Grant-in-Aid for JSPS Fellows (No. 06J0271) the Canon Foundation in Europe, the Kyoto University Foundation to S. Ichino; and the Young Researcher Overseas Visits Program for Vitalizing Brain Circulation of JSPS. This work was also supported by a grant from the Zoological Society of St. Louis to H. Rambeloarivony.

REFERENCES

- Butynski, T.M. 1982. Vertebrate predation by primates: A review of hunting patterns and prey. *Journal of Human Evolution*, 11: 421-430.
- Campbell, J.L., J.H. Eisemann, C.V. Williams & K.M. Glenn 2000. Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Haplemur griseus*, and *Lemur catta*. *American Journal of Primatology*, 52: 133-142.
- Campbell, J.L., C.V. Williams & J.H. Eisemann 2004. Characterizing gastrointestinal transit time in four lemur species using barium-impregnated polyethylene spheres (BIPS). *American Journal of Primatology*, 64: 309-321.
- Clarke, A.S. 1987. Animal foods in the diets of prosimian and New World primates. In (G. Mitchell & J. Erwin, eds.) *Comparative Primate Biology, Vol. 2, Part B: Behavior, Cognition, and Motivation*, pp. 133-165. Alan R. Liss, New York.
- Clutton-Brock, T.H., S.D. Albon & F.E. Guinness 1989. Fitness costs of gestation and lactation in wild mammals. *Nature*, 337: 260-262.
- Curtis, D.J. 2004. Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology*, 124: 234-247.
- Fedigan, L.M. 1990. Vertebrate predation in *Cebus capucinus*: Meat eating in a neotropical monkey. *Folia Primatologica*, 54: 196-205.

- Glander, K.E., B.Z. Freed & J.U. Ganzhorn 1985. Meat-eating and predation in captive-born semi-free-ranging *Lemur fulvus* and caged *Lemur macaco*. *Zoo Biology*, 4: 361-365.
- Gould, L. 1990. The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology*, 11: 297-318.
- Gould, L., R.W. Sussman & M.L. Sauther 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, 120: 182-194.
- Harding, R.S.O. 1973. Predation by a troop of olive baboons (*Papio anubis*). *American Journal of Physical Anthropology*, 38: 587-591.
- 1975. Meat-eating and hunting in baboons. In (R. H. Tuttle, ed.) *Socioecology and Psychology of Primates*, pp. 245-257. Mouton Publishers, The Hague.
- Hausfater, G. 1976. Predatory behavior of yellow baboons. *Behaviour*, 56: 44-68.
- Jolly, A. 1966. *Lemur Behavior*. University of Chicago Press, Chicago.
- Jolly, A., S. Caless, S. Cavigelli, L. Gould, M.E. Pereira, A. Pitts, R.E. Pride, H.D. Rabenandrasana, J.D. Walker & T. Zafison 2000. Infant killing, wounding and predation in *Eulemur* and *Lemur*. *International Journal of Primatology*, 21: 21-40.
- Jolly, A., A. Dobson, H.M. Rasamimanana, J. Walker, S. O'Connor, M. Solberg & V. Perel 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *International Journal of Primatology*, 23: 327-353.
- Jolly, A., N. Koyama, H. Rasamimanana, H. Crowley & G. Williams 2006. Berenty Reserve: A research site in southern Madagascar. In (A. Jolly, R.W. Sussman, N. Koyama & H. Rasamimanana, eds.) *Ringtailed Lemur Biology: Lemur catta in Madagascar*, pp. 32-42. Springer, New York.
- Jolly, A. & W.L.R. Oliver 1985. Predatory behavior in captive lemur spp. *Zoo Biology*, 4: 139-145.
- Kappeler, P.M. 1990. Female dominance in *Lemur catta*: More than just female feeding priority? *Folia Primatologica*, 55: 92-95.
- 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*, 57: 132-146.
- 2000. Causes and consequences of unusual sex ratios among lemurs. In (P.M. Kappeler, ed.) *Primate Males: Causes and Consequences of Variation In Group Composition*, pp. 55-63. Cambridge University Press, Cambridge.
- King, G.E. & H.D. Steklis 1984. New evidence for the craniocervical killing bite in primates. *Journal of Human Evolution*, 13: 469-481.
- Koyama, N., M. Aimi, Y. Kawamoto, H. Hirai, Y. Go, S. Ichino & Y. Takahata 2008. Body mass of wild ring-tailed lemurs in Berenty Reserve, Madagascar, with reference to tick infestation: A preliminary analysis. *Primates*, 49: 9-15.
- Koyama, N., M. Nakamichi, S. Ichino & Y. Takahata 2002. Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989-1999. *Primates*, 43: 291-314.
- Koyama, N., M. Nakamichi, R. Oda, N. Miyamoto, S. Ichino & Y. Takahata 2001. A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates*, 42: 1-14.
- Mitani, J.C. & D.P. Watts 2005. Seasonality in hunting by non-human primates. In (D.K. Brockman & C.P. van Schaik, eds.) *Seasonality in Primates: Studies of Living and Extinct Human Primates*, pp. 215-241. Cambridge University Press, New York.
- Mittermeier, R.A., W.R. Konstant, F. Hawkins, E.E. Louis, O. Langrand, J. Ratsimbazafy, R. Rasoloarison, J.U. Ganzhorn, S. Rajaobelina, I. Tattersal & D.M. Meyers 2006. *Lemurs of Madagascar (2nd edition)*. Conservation International, Washington, D.C.
- Mizuta, T. 2002. Predation by *Eulemur fulvus fulvus* on a nestling of *Terpsiphone mutata*

- (Aves: Monarchidae) in dry forest in north-western Madagascar. *Folia Primatologica*, 73: 217-219.
- Nakamura, M. 2004. Predation by *Eulemur fulvus fulvus* on eggs of *Ploceus sakalava sakalava* (Aves: Ploceidae) in Ankarafantsika, Madagascar. *Folia Primatologica*, 75: 376-378.
- Oda, R. 1996. Predation on a chameleon by a ring-tailed lemur (*Lemur catta*) in the Berenty Reserve, Madagascar. *Folia Primatologica*, 67: 40-43.
- Pereira, M.E., R. Kaufman, P.M. Kappeler & D.J. Overdorff 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatologica*, 55: 96-103.
- Pitts, A. 1995. Predation by *Eulemur fulvus rufus* on an infant *Lemur catta* at Berenty, Madagascar. *Folia Primatologica*, 65: 169-171.
- Rose, L.M. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, 15: 95-114.
- 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology*, 18: 727-765.
- Rose, M.D. 1978. The roots of primate predatory behavior. *Journal of Human Evolution*, 7: 179-189.
- Sauther, M.L. 1992. The effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar. Ph.D. dissertation, Washington University, St. Louis.
- Sauther, M.L. & L.T. Nash 1987. Effect of reproductive state and body size on food consumption in captive *Galago senegalensis braccatus*. *American Journal of Physical Anthropology*, 73: 81-88.
- Sauther, M.L., R.W. Sussman & L. Gould 1999. The socioecology of the ringtailed lemur: Thirty-five years of research. *Evolutionary Anthropology*, 8: 120-132.
- Shedd, D.H. 1990. Avian nest predation by a semi-captive collared lemur (*Lemur fulvus collaris*). *Primates*, 31: 607-609.
- Simmen, B., A. Hladik & P. Ramasiarisoa 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. *International Journal of Primatology*, 24: 949-968.
- Stanford, C.B., J. Wallis, H. Matama & J. Goodall 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. *American Journal of Physical Anthropology*, 94: 213-228.
- Steklis, H.D. & G. E. King 1978. The craniocervical killing bite: Toward an ethology of primate predatory behavior. *Journal of Human Evolution*, 7: 567-581.
- Sussman, R.W. & J. Ratsirarson 2006. Beza Mahafaly Special Reserve: A research site in southwestern Madagascar. In (A. Jolly, R.W. Sussman, N. Koyama & H. Rasamimanana, eds.) *Ringtailed Lemur Biology: Lemur catta in Madagascar*, pp. 43-51. Springer, New York.
- Takahata, Y., T. Hasegawa & T. Nishida 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *International Journal of Primatology*, 5: 213-233.
- Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.
- Teleki, G. 1973. *The Predatory Behavior of Wild Chimpanzees*. Bucknell University Press, Lewisburg, Pennsylvania.
- 1975. Primate subsistence patterns: Collector-predators and gatherer-hunters. *Journal of Human Evolution*, 4: 125-184.
- Tirado Herrera, E.R. & E.W. Heymann 2004. Does mom need more protein? Preliminary observations on differences in diet composition in a pair of red titi monkeys (*Callicebus cupreus*). *Folia Primatologica*, 75: 150-153.

————— Accepted May 18, 2011

Correspondence Author's Name and Address: Shinichiro ICHINO, *Unit of Behavioral Ecology and Sociobiology, German Primate Center, Kellnerweg 4, D- 37077 Göttingen, GERMANY.*

E-mail: shinichiro.ichino [at] gmail.com