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Monandrous Social Organization of Pigtailed Langurs (Simias concolor) in the Pagai Islands, Indonesia

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Between June 1986 and October 1992, in 3 periods totaling 12 months, we studied social organization of pigtailed langurs (Simias concolor) in the Pagai Islands, Indonesia. With one possible exception, all of 20 family groups contained only 1 adult male each. Nine of them contained only 1 adult female, and 11 contained ≥ 2 adult females. Mean group size is 4.1 individuals. Home ranges varied from 7 to 20 ha, and population density averages 21 animals/km². Simias concolor is sexually dimorphic—in a museum sample males average 29% heavier than females, and their canine teeth are on average nearly twice the length of female canines. Combined data from several studies indicate that 60% of S. concolor groups contain an adult pair plus young, and 40% are multifemale groupings. We suggest that any 1-male mating system that comprises a mixture of 1-female and multifemale groups in the same population should be termed monandry.

KEY WORDS: pigtailed langur; *Simias concolor*; one-male groups; one-female groups; multifemale groups; monandry; unmated males; sex ratio; sexual dimorphism; Mentawai Islands; home range; leadership; population density.

INTRODUCTION

We describe social organization of pigtailed langurs (*Simias concolor*). Tenaza studied this species for 5 months in North and South Pagai Islands

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in 1986 and 1987, and Fuentes studied it for 7 months on North Pagai Island in 1992. We determined sexual dimorphism with data from museum specimens and publications.

Simias is endemic to the Mentawai Archipelago, located in the Indian Ocean 85–135 km west of Sumatra, Indonesia. It consists of four main islands and scores of associated islets. From north to south, the four main islands are Siberut, Sipora, North Pagai, and South Pagai. Total area of the archipelago is ca. 7000 km² (World Wildlife Fund, 1980). Simias inhabits all four main islands, and also the islets of Simalegu, Simatapi, and Sinakak, off the east coast of S. Pagai. Simias is the only primate on Simalegu and Simatapi, but everywhere else in its range, Simias is sympatric with Hylobates klossii, Macaca pagensis, and Presbytis potenziani (Tenaza, 1987).

Simias inhabits lowland rain forest, swamp forest, selectively logged forest, and secondary forests by logging roads, lumber camps, and native gardens (Kawamura and Megantara, 1986; Tenaza, 1987; Tilson, 1977; Watanabe, 1981). Simias is the favored prey of Mentawai's native hunters, and has no other serious predators (Mitchell and Tilson, 1986; Tenaza and Tilson, 1985; Tenaza, 1989b). Islanders hunt Simias with bows and poisoned arrows and air rifles (Tenaza, 1987, 1989c).

Miller (1903) established the monotypic genus Simias for the pigtailed langur. Chasen and Kloss (1927) recognized 2 subspecies, Simias concolor siberu from Siberut, and S. c. concolor from Sipora and the Pagai Islands. Although Groves (1970) united Simias with Nasalis, Medway (1970) and Napier (19885) argued that the pigtailed langur and the proboscis monkey are morphologically too different to be congeneric. We follow Medway and Napier.

Simias occurs in two color phases, a common dark brown-to-black morph, and a rare pale-yellowish form (Miller, 1903; Tenaza, 1987; Tilson, 1977; Watanabe, 1981). The pale morph does not occur on North Pagai Island, but is present on Siberut, Sipora, South Pagai, Sinakak, Simalegu, and Simatapi (Tenaza, 1987).

Simias live in groups of 1 adult male and 1–5 or more adult females plus their young. Adult male Simias produce a characteristic call consisting of a series of loud nasal barks audible to about 500 m (Kawamura and Megantara, 1986; Tenaza, 1989b; Tilson, 1977; Watanabe, 1981). Males emit these type-1 long calls (Gautier and Gautier, 1977) spontaneously or in response to calls of other males, mostly in early morning and late afternoon. This exchange of calls is the only frequent interaction between groups (Tenaza, 1989b).

BACKGROUND AND METHODS

Study Sites and Habitats

The principal sites for the 1986–1987 portion of this study were Simalegu and Sinakak Islands. Simalegu is about 200 ha; Sinakak is about 600 ha. The exact location of these islets is described elsewhere (Tenaza, 1987). Tenaza observed *Simias* at these sites from June 26 to July 6, 1986, and 19 September 19 to December 16, 1987. *Simias* in the Simalegu and Sinakak study areas are in swamp forest and lowland rain forest (Whitten, 1984). Fuentes studied *Simias* from April 4 to October 15, 1992, in the Betumonga region in southwest North Pagai. His main study area is a 136-ha patch of lowland rain forest, and he made briefer observations of *Simias* in nearby swamp and secondary forests.

Rainfall

Minas Lumber Company provided data from its South Pagai weather station for the 12-year period of 1974–1985. Mean annual rainfall during that period is 4420 mm (SD = 1061, Range: 2655 to 6383).

Trail Systems and Maps

We cleared, marked, and mapped trails as follows: (1) Simalegu Island, 7 km of trails accessing 150 of the island's 200 ha; (2) Sinakak Island, 13 km of trail accessing 300 of the island's 600 ha; and (3) Betumonga, 6 km of trails accessing 136 ha. We marked trails with numbered aluminum tags nailed to trees at 25-m intervals on Sinakak and Simalegu and at 10-m intervals at Betumonga. We determined compass directions for mapping trails and observations via Brunton and similar compasses. Marked trails allowed us to pinpoint observations on field maps.

Observational Techniques

Due to persistent hunting by natives, *Simias* are fearful of humans. Therefore, whenever possible we stalked and watched them from hiding. We used Leitz 10×40 Trinovid binoculars and Sworvski 8×40 binoculars.

Sexing Animals in the Field

We readily sexed *Simias* via their ischial callosities. The black ischial callosities of male *Simias* "...are joined solidly together along the median line, but in the female they are separated by a narrow strip of softer skin"— the female's urogenital triangle (Miller, 1903, p. 68). From infancy onward, this sex skin is glaringly pink against the female's black callosal skin, and it swells conspicuously in adolescent and adult females (Tenaza, 1989c). In frontal view, elongated nipples distinguished females that have borne young. Other criteria useful for sexing males in the field include the adult male's bright pink penis, his long canine teeth, and his larger, stockier body build compared to females. At times the penis was conspicuously erected in males sitting on their haunches watching us from arboreal perches (Watanabe, 1981).

	Adult	Adult		Older	
Location	Males	Females	Infants	Young	Total
Sabeugugung	1	1	0	0	2
Betumonga	2	0	0	0	2 5
Betumonga	1	3	0	1	5
Betumonga	1	1	0	1	3
Betumonga	2	3	2	2	9
Betumonga	1	3	0	1	5
Betumonga	1	3	2	1	7
Betumonga	1	2	0	1	4
Betumonga	1	0	0	0	1
Sinakak	1	0	0	0	1
Sinakak	1	5	3	0	9
Sinakak	1	2	0	0	3
Sinakak	1	2	2	0	5
Sinakak	1	2	0	0	3
Sinakak	1	0	0	0	1
Simalegu	1	0	0	0	1
Simalegu	1	1	0	1	3
Simalegu	1	1	1	0	3
Simalegu	1	1	0	1	3
Simalegu	1	2	0	0	3
Simalegu	1	2	2	0	5
Simalegu	1	1	0	0	2
Simalegu	1	1	0	1	3
Berkat	1	1	0	0	2
Purourougat	1	1	0	0	2

Table I. Composition of 25 Simias concolor Social Units in the Pagai Islands^a

"Six bachelor males are included. Infants are young still carried by their mothers.

Sexual Dimorphism

Data on sexual dimorphism are from specimens of 8 adult males and 12 adult females in museum collections or published accounts. To determine sexual dimorphism in head and body length and tail length, Tenaza took measurements from labels on specimens of 2 males and 5 females in the Bogor Biological Museum (Bogor, Indonesia); R. T. Thorington, Jr. provided body measurements from 2 male and 3 female specimens in the U. S. National Museum; and we used measurements of 2 males and 4 females published by Chasen and Kloss (1927), 1 male published by Miller (1903), and 1 male and 1 female published by Napier (1985). To determine sexual dimorphism in canine length, Tenaza measured canines on the 2 males and 5 females in the Bogor collection, and R. T. Thorington, Jr., measured canines on 2 males and 3 females in the U.S. National Museum for us. We used measurements of the upper right canine except for one male in the Bogor collection in which the upper right canine is broken. Instead, Tenaza measured its upper left canine. We measured each canine from the occlusal tip to the anterior rim of its maxillary socket. Thorington provided weights for 2 males and 2 females in the U.S. National Museum; the weight of 1 female is from Napier (1985).

RESULTS

Group Structure

Twenty family groups lived in our study areas. Adult members of the 20 groups are as follows: Nine (45%) groups contained 1 adult of each sex; 10 (50%) contained 1 adult male and 2 or more adult females, and 1 (5%) contained 2 adult males and 3 adult females (Table I). Both males in the 2-male family at Betumonga traveled and fed with the group, but Fuentes never saw them interact with one another.

Group Size and Sex Ratio

The adult sex ratio in the 20 family groups (Table I) is 0.6, or 1 male to 1.8 females. Mean size of these family groups is 4.1 (r = 2-9, $SD = \pm$ 2.1). Overall sex ratio for the entire sample of adult *Simias*, including 6 unmated males, is 0.7, or 1 male to 1.4 females. The difference between number of males (N = 27) and number of females (N = 38) in our sample is not significant statistically ($\chi^2 = 1.86$, p > .1).

Unmated Males

Of 6 unmated males, 4 were solitary and 2 were together. Tenaza observed the male dyad during a three-day visit to the Betumonga area in September 1987. They were feeding within 5 m of one another in the same tree. After detecting Tenaza, the males fled together. Tenaza detected no other *Simias* in the vicinity at the time. One unmated male lived in Fuentes' Betumonga study site, 1 lived in the Sinakak site, and another lived in the Simalegu site. Our sightings for each male were clustered at specific locations, indicating that each male was attached to a specific small area.

Leadership and Intragroup Dispersion

Group travel was initiated and led by adults of either sex. There was no fixed leader. When one individual moved from a place and others followed, that individual temporarily was leader. Groups often fragmented while foraging, with members scattering over areas ≤ 90 m in diameter. At other times groups occupied areas only ≤ 5 m in diameter. Group members dispersed individually or as subgroups of 2–4.

Intergroup Conflict

We observed only one intergroup conflict. It occurred during midafternoon on Simalegu Island on July 2, 1986. One group comprised a dark adult male and a pale-phase yellowish adult female, and the other contained a dark adult male, a dark adult female, and a dark half grown juvenile. Tenaza heard them from 100 m away, and approached. The males leapt and brachiated violently through the canopy, one or both of them producing loud, nasal, meowing sounds. The pale female followed the combatants, but the other female and the juvenile remained in a tree crown. Both males descended to the ground ca 20 m from Tenaza, one retreating and the other following. Dense vegetation hid them from his view, but violent rustling of vegetation suggested they were scuffling. The pale female remained in trees just above the males. One of the males uttered a two-bark version of the type-1 long call. After 3-4 min on the ground, both males returned to the forest canopy. The 3-member group departed, and the pair stayed. The male of the pair sat whimpering in a tree for 20 min. Then the pair appeared to detect Tenaza, and they fled rapidly through the canopy together.

Range Size and Population Density

Fifteen groups occupied Tenaza's 300 ha study site at Sinakak, for an average of 20 ha per group. On Simalegu, 9–11 groups inhabited 170 ha, ca. 15–19 ha per group. At Betumonga, Fuentes estimated 7–20 ha per group, with larger groups occupying larger portions of the 136-ha study area. Population densities were 26 individuals per km^2 at Betumonga, ca. 20/km² at Sinakak, and ca. 18/km² on Simalegu. Mean density for the three areas combined is ca. 21/km².

Sexual Dimorphism

Adult males in our sample were larger and 29% heavier than females, and their canine teeth averaged 95% longer than the canines of females (Fig. 1 and Table II).

DISCUSSION

Sex Ratio

In Table III, we combined our data on group and population parameters with data from other studies of *Simias*. The family group sex ratio of 0.6 (65 males: 107 females) obtained that way is the same ratio we obtained for family groups in Pagai. When unmated males are included, the adult sex ratio approaches unit (0.9; (101 males: 107 females).

Mateship and Unmated Males

Adult males exhibited three categories of mateship: some lived alone, some accompanied 1 adult female, and some accompanied ≤ 2 or adult females (Fig. 2). The largest known are two groups of 15–20 that Watanabe (1981) saw at Grukna; despite their large size, they contained only 1 adult male and about 4 adult females each. Tilson (1977) saw only 1-female groups in eastern Siberut, but in all other studies multifemale groups outnumber 1-female groups (Table III).

In data from all studies combined, most adult males are in 1-male groups, most adult females are in multifemale groups, and adult males living alone outnumber multiply-mated males (Fig. 3). Adult males lost from family groups are replaced (Tilson, 1977; Watanabe, 1981), presumably from the pool of unmated males. The occurrence of both 1-female and

Fig. 1. Sexual dimorphism in skulls and canine teeth of Simias concolor; adult female 6586 (right) and adult male 6539 (left) in collection of the Bogor Biological Museum, Indonesia.

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		Males			Females		Sampl	Sample Size	Studen	Student t Test
	Mean	Range	. SD	Mean	Mean Range	ß	Male (N)	Female (V)	-	two- tailed p
Head and body length (mm)	531.1	480-571	26.1	476.1	476.1 460-500	13.8	8	12	5.82	- 100: >
Tail length (mm)	160.8	130-190	19.6	136.2	100-165	19.9	ø	12	2.58	<.02
Upper canine length (mm)	16.2	13.8-17.8	1.7	8.3	6.1-10.6	1.5	4	ø	4.53	<.01
Weight (kg)	8.8	8.6-8.9	0.2	6.8	6.8 6.2–7.1	0.5	7	ŝ	4.18	< 05

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Table III.	Table III. Grouping, Sex Ratio, Home Range, and Population Density of Simias concolor ^a	o, Home Range,	and Population D	ensity of Simias co	ncolor ^a	
Parameters	Pagai (N = 20)	Siberut Sarabua (7)	Siberut Grukna (23)	Siberut Sirimuri (15)	Sipora (2)	Sipora (2) Combined (67)
Group size $\widetilde{X} \pm SD$ (range)	4.1 ± 2.1 (2-7)	3.0 ± 1.0 (2-5)	4.1 ± 2.1 (2-7) 3.0 ± 1.0 (2-5) 7.1 ± 6.4 (2-20)	ന	3.0 ± 0.0	4.6 ± 3.1 (2-20)
Adult sex ratio (males per female)	0.6	1.0	0.5	1.0	0.5	0.6 families
Percent of 1-male groups that contained 1 female 2 or more females	55 55 55	0 00	39 61	000	0 100	6,0 0vctan 60 40
Percent of adult males that were unmated	22	14	30	12	88	34
Home range size (ha)	7-20	7-20	35	25-30	i	No reliable estimate
Population density estimate (no./km ²)	21¢	20	220	13	ć	No reliable estimate
"Pagai data are from this study, Sarabua and Grukna data from Watanabe (1981); Sirimuri data from Tilson (1977); and Sipora data from Kawamura and Megantara (1986). Watanabe had one group size entered as 15-20, and another as ca. 20; in calculations for this table, we used 17 and 20 for them. ^b Adult sex ratio for the combined sample is 0.9 if unmated males are included, 0.6 if they are excluded. ^c Twenty-two per square kilometer is the average for the three study sites. Range is 18-26/km ² .	Watanabe had Grukna (Watanabe had one gr ample is 0.9 if unmal the average for the	data from Watar roup size entered ted males are in three study sites	nabe (1981); Sirim I as 15-20, and and cluded, 0.6 if they . Range is 18-26/k	uri data from Tils other as ca. 20; in c are excluded. m ² .	on (1977); an alculations fo	d Sipora data from r this table, we used

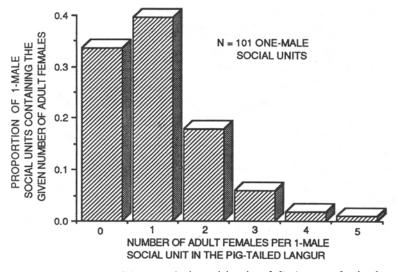


Fig. 2. Variation in adult sex ratio in social units of *Simias concolor* in the Mentawai Islands. The graph combines our data with those from Tilson (1977), Watanabe (1981), and Kawamura and Megantara (1986).

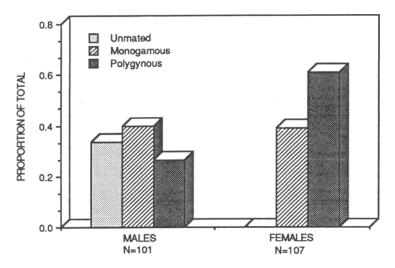


Fig. 3. Comparative mating status of adult male and adult female Simias concolor in the Mentawai Islands. All females were mated, but 34% of males were unmated. The graph combines data with those from Tilson (1977), Watanabe (1981), and Kawamura and Megantara (1986).

multifemale families in monkey populations also occurs in Papio hamadryas (Kummer, 1968), Alouatta seniculus (Izawa, 1976), Cercopithecus neglectus (Wahone et al., 1993), and probably other species.

Monandry in Simias. Although a high proportion of Simias belong to 1-female groupings, 60% of family groups contain only one adult of each sex. Accordingly, it would be incorrect to label Simias as either polygynous or monogamous. A similar definitional problem exists with regard to some traditional human societies in which polygyny was considered the cultural norm, but in which most married individuals were monogamously wedded (Murdock, 1949; Westermarck, 1903). In Simias, Papio hamadryas, Alouatta seniculus, and some human societies, the social system is flexible enough to allow the formation and maintenance of 1-female—monogamous—and multifemale—polygynous—groups in the same population. We suggest that this be called monandry, defined as a mating system in which the breeding group consists of 1 adult male and \geq 1 adult females plus their young, such that the population of breeding groups consists of a mixture of monogamous and polygynous families.

Sexual Dimorphism

On average, males in our sample were significantly longer-bodied than females, but there is overlap between the largest females and the smallest males. However, in canine length and body weight, there is no overlap between males and females in our samples (Table II). The sexual dimorphism in canines is obvious at a glance (Fig. 1). With regard to body size, adult males in the field are conspicuously stockier (Watanabe, 1981). Large males armed with large canine teeth is a feature that *Simias* shares with other primates whose mating systems enable some males to acquire multiple mating partners (Alexander *et al.*, 1979; Clutton-Brock and Harvey, 1976).

Unmated Males

We confirm that unmated male Simias tend to live solitarily (Watanabe, 1981; Kawamura and Megantara, 1986). In other Asian colobines, some unmated males, like most unmated male Simias, live alone and some form groups. In Presbytis entellus (Dolhinow, 1972), Nasalis larvatus (Yeager, 1989), and P. thomasi (Gurmaya, 1986), unmated males group together. In P. aygula (Ruhiyat, 1983), P. cristata (Wolf and Fleagle, 1977), P. femoralis (Megantara, 1989), P. melalophos (Curtin, 1976), and P. rubicunda (Davies, 1987) some unmated males form groups and others live alone. The male

dyad that Tenaza observed briefly at Betumonga is the only indication that unmated male *Simias* may group.

Leadership and Intragroup Dispersion

Tilson (1977) found that among *Simias* at Sirimuri, males led, females followed, and group members rarely were >5 m apart. What we observed in Pagai is quite different. First, both sexes led group progression. Second, group perimeters were highly elastic, with group members occupying areas anywhere from 5 to 90 m in diameter while feeding or resting during the day. Struhsaker (1975) found similar variability in *Colobus badius*, with spatial diameter of social groups in the forest canopy ranging from 20 to >100 m.

Home Range

Simias in our study are faithful to particular places—their home ranges. Home range sizes in our study areas are similar to those at Sarabua, smaller than those at Sirumuri, and larger than those at Grukna (Table III). Tilson (1977) observed that home ranges of *Simias* at Sirimuri overlapped peripherally, and Watanabe (1981) estimated 8% overlap in his study sites. Home ranges overlap in Pagai, but we cannot reliably estimate the extent of overlap. The extent to which home ranges are defended still is unknown.

Population Density

Population densities that we observed in Pagai are higher than densities at Sirimuri and Sarabua, but they are only 8-12% as dense as those that Watanabe observed at Grukna (Table III). While Watanabe studied *Simias* at Grukna, commercial loggers were felling trees around his study site. An influx of animals fleeing the logging operation may have caused the high density of *Simias* at Grukna. Or the high density at Grukna may have been natural.

Epilogue on the Threat of Extinction

In January 1990, Tenaza visited Watanabe's former study area at Grukna. Logging had stopped because the trees were gone. Dense scrub stood where the rain forest had been. Where Watanabe estimated 220 Simias per km^2 in 1978, Tenaza found none in 1990. Local people said that it had been easy to hunt for a while after logging stopped because the monkeys had few places to hide. Then, *Simias* vanished from Grukna. Since Tenaza first visited Mentawai in 1970, he has recorded the disappearance of *Simias* from several other places in Pagai and Siberut. If habitat destruction and overhunting are not curtailed, *Simias c. concolor* in the southern Mentawai and *S. c. siberu* in Siberut will continue to decline toward extinction.

MAIN CONCLUSIONS

The typical breeding group of *Simias concolor* consists of 1 adult male and ≥ 1 adult females plus their young. Since there are high proportions of both 1-female and multifemale groups, it would be incorrect to categorize *Simias concolor* as either monogamous or polygynous. Instead, *Simias concolor* and other primates in which both monogamous and polygynous groups occur should be termed monandrous.

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REFERENCES

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Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., and Sherman, P. W. (1979). Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In Chagnon, N. A., and Irons, W. (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, Duxbury Press, North Scituate, MA, pp. 402-435.

- Chasen, F. N., and Kloss, C. B. (1927). Spolia Mentawiensis-Mammals. Proc. Zool. Soc. Lond. 1: 797-840.
- Clutton-Brock, T. H., and Harvey, P. H. (1976). Evolutionary rules and primate societies. In Bateson, P. P. G., and Hinde, R. A. (eds.), *Growing Points in Ethology*, Cambridge University Press, London, pp. 195-237.
- Curtin, S. H. (1976). Niche Differentiation and Social Organization in Sympatric Malaysian Colobines, Unpublished Ph.D. dissertation, University of California, Berkeley.
- Davies, G. (1987). Adult male replacement and group formation in Presbytis rubicunda. Folia Primatol. 49: 111-114.
- Dolhinow, P. J. (1972). The north Indian langur. In Dolhinow, P. (ed.), *Primate Patterns*, Holt, Reinhart and Winston, New York, pp.
- Gautier, J.-P. and Gautier, A. (1977). Communication in Old World monkeys. In Sebeok, T. A. (ed.), How Animals Communicate, Indiana University Press, Bloomington, pp. 890-964.
- Groves, C. P. (1970). The forgotten leaf-eaters and the phylogeny of the Colobinae. In Napier, J. R., and Napier, P. H. (eds.), Old World Monkeys: Ecology, Systematics, and Behavior, Academic Press, New York, pp. 555-587.
- Gurmaya, K. J. (1986). Ecology and behavior of *Presbytis thomasi* in northern Sumatra. *Primates* 27: 151-172.
- Izawa, K. (1976). Group sizes and compositions of monkeys in the upper Amazon basin. Primates 17: 367-399.
- Kawamura, S., and Megantara, E. N. (1986). Observation of primates in logged forest on Sipora Island, Mentawai. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates 5: 1-12.
- Kummer, H. (1968). Social Organization of Hamadryas Baboons, University of Chicago Press, Chicago.
- Medway, Lord (1970). The monkeys of Sundaland: Ecology and systematics of the cercopithecids of a humid equatorial environment. In Napier, J. R., and Napier, P. H. (eds.), Old World Monkeys; Ecology, Systematics, and Behavior, Academic Press, New York, pp. 513-533.
- Megantara, E. N. (1989). Ecology, behavior and sociality of Presbytis femoralis in East Central Sumatra. Comp. Primatol. Monogr. 2: 171-301.
- Miller, G. S., Jr. (1903). Seventy new Malayan mammals. Smithsonian Misc. Coll. 45: 1-73.
- Mitchell, A. H., and Tilson, R. L. (1986). Restoring the balance: Traditional hunting and primate conservation in the Mentawai Islands, Indonesia. Proc. Tenth Int. Primatol. Congr. 2: 249-260.
- Murdock, G. P. (1949). Social Structure, The Macmillan Company, New York.
- Napier, P. H. (1985). Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles, Part III: Family Cercopithecidae, Subfamily Colobinae, British Museum (Natural History), London.
- Ruhiyat, Y. (1983). Socio-ecological study of *Presbytis aygula* in West Java. *Primates* 24: 344-359.
- Struhsaker, T. T. (1975). The Red Colobus Monkey, University of Chicago Press, Chicago.
- Tenaza, R. R. (1987). The status of primates and their habitats in the Pagai Islands, Indonesia. Primate Conserv. 8: 104-110.
- Tenaza, R. R. (1989a). Female sexual swellings in the Asian colobine Simias concolor. Am. J. Primatol. 17: 81-86.
- Tenaza, R. R. (1989b). Male intergroup vocalizations of the pig-tailed langur (Simias concolor). Primates 30: 199-206.
- Tenaza, R. R. (1989c). Primates on a precarious limb. Anim. Kingdom 92: 26-37.
- Tenaza, R. R., and Tilson, R. L. (1985). Human predation and Kloss's gibbon (Hylobates klossii) sleeping trees. Am. J. Primatol. 8: 299-308.
- Tilson, R. L. (1977). Social organization of simakobu monkeys (Nasalis concolor). J. Mammal. 58: 202-212.
- Wahone, J. M., Rowell, T. E., and Tsingala, H. M. (1993). The natural history of de Brazza's monkey in Kenya. Int. J. Primatol. 14: 445-466.

Watanabe, K. (1981). Variations in group composition and population density of the 2 sympatric Mentawaian leaf-monkeys. Primates 22: 145-160.

Westermarck, E. (1903). The History of Human Marriage, Macmillan and Co., London.

Whitten, A. J. (1984). The Ecology of Sumatra, Gadjah Mada University Press, Yogyakarta.
Wolf, K. E., and Fleagle, J. G. (1977). Adult male replacement in a group of Silvered leaf monkeys (Presbytis cristata) at Kuala Selangor, Malaysia. Primates 18: 949-955.

- World Wildlife Fund. (1980). Saving Siberut: A Conservation Master Plan, World Wildlife Fund,
- Bogor, Indonesia. Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (Nasalis larvatus). Int. J. Primatol. 10: 497-530.