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## Zoology

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### Taxonomy and Evolution of the *Sinica* Group of Macaques: 3. Overview of Natural History

Jack Fooden

A Contribution in Celebration  
of the Distinguished Scholarship of Robert F. Inger  
on the Occasion of His Sixty-Fifth Birthday

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- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*, Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D. C.
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**Jack Fooden**

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Division of Mammals  
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## Table of Contents

ABSTRACT .....	1
INTRODUCTION .....	1
NATURAL HISTORY OF THE <i>SINICA</i> GROUP ...	1
Habitats .....	1
Arboreality/Terrestriality .....	3
Food .....	4
Predators and Parasites .....	4
Seasonal Migration .....	5
Troop Size and Composition .....	5
Home Range .....	7
Male Emigration .....	8
Seasonal Breeding .....	8
Mating Behavior .....	10
Life History .....	11
Geographic and Ecological Relationships with Other Primates .....	14
SUMMARY .....	16
ACKNOWLEDGMENTS .....	17
LITERATURE CITED .....	17
APPENDIX: <i>Macaca assamensis</i> Locality Rec- ord Supplement .....	22

## List of Illustrations

1. Locality records and inferred limits of natural distribution of *sinica* group species ..... 2
2. *Macaca radiata* young adult male following *M. mulatta* adult female, with another *M. mulatta* individual sitting nearby ..... 15

## List of Tables

1. Troop size in forest populations of *sinica* group species ..... 5
2. *Macaca radiata*: troop size in forest troops compared with that in nonforest troops ..... 6
3. *Macaca radiata*: ratio of sexually mature males (subadults and adults) to sexually mature females (adults) in 418 troops .. 6
4. Home range area in *Macaca sinica* and *Macaca radiata* ..... 7



# Taxonomy and Evolution of the *Sinica* Group of Macaques:

## 5. Overview of Natural History

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### Abstract

The *sinica* group of macaques includes four species: *Macaca sinica*, *M. radiata*, *M. assamensis*, and *M. thibetana*. The geographic ranges of these species extend from tropical Sri Lanka (*M. sinica*) to subtropical east-central China (*M. thibetana*). In the present review of the natural history of the *sinica* group, these species are compared with respect to habitat, arboreality/terrestriality, food, predators and parasites, seasonal migration, troop size and composition, home range, male emigration, seasonal breeding, mating behavior, life history, and geographic and ecological relationships with other primates.

### Introduction

The *sinica* group is one of four species groups of macaques defined by the morphology of male and female reproductive organs (Fooden, 1971, p. 72). This group includes four species: *Macaca sinica*, in Sri Lanka; *M. radiata*, in southern peninsular India; *M. assamensis*, in the central and eastern Himalayan foothills and adjacent mountains of Southeast Asia; and *M. thibetana*, in east-central China (fig. 1). Taxonomic accounts of these four species have been published recently (Fooden, 1979, 1981, 1982a, 1983).

This paper is a comparative review of the natural history of *sinica* group species. Information available for these species varies greatly in completeness. In addition to works cited here, those cited in previously published species accounts should also be consulted. A comprehensive review

of other aspects of the systematics and evolutionary biology of these species is in preparation.

In citations of unpublished natural history notes recorded on specimen tags or in collectors' field notebooks in Chinese museums, the following institutional abbreviations are used: IZAS—Institute of Zoology, Academia Sinica, Beijing; KIZ—Kunming Institute of Zoology, Academia Sinica, Kunming. I thank officials of these institutions for generously providing access to specimens and field notebooks in their custody.

I am happy to dedicate this paper to Robert F. Inger, distinguished zoologist and valued colleague, on the occasion of his 65th birthday anniversary.

### Natural History of the *Sinica* Group

#### Habitats

Habitats of species in the *sinica* group differ climatically according to the varying latitudes of the geographic ranges of these species (fig. 1). The latitudinal effect on climate is further accentuated by an altitudinal effect, since the more northern species tend to inhabit higher altitudes. In the range of *M. sinica* (latitude 06°–09°N, altitude 0–2100 m), climate varies from tropical wet to tropical arid; in the range of *M. radiata* (08°–21°N, 0–2100 m), climate also varies from tropical wet to tropical arid, but arid habitats constitute a greater proportion of the total; in the range of *M. assamensis* (15°–30°N, 0–3100 m; see KIZ 780118, 780144, Bilushui Shan, Yunnan, China), climate is subtropical wet; and in the range of *M. thibetana* (25°–

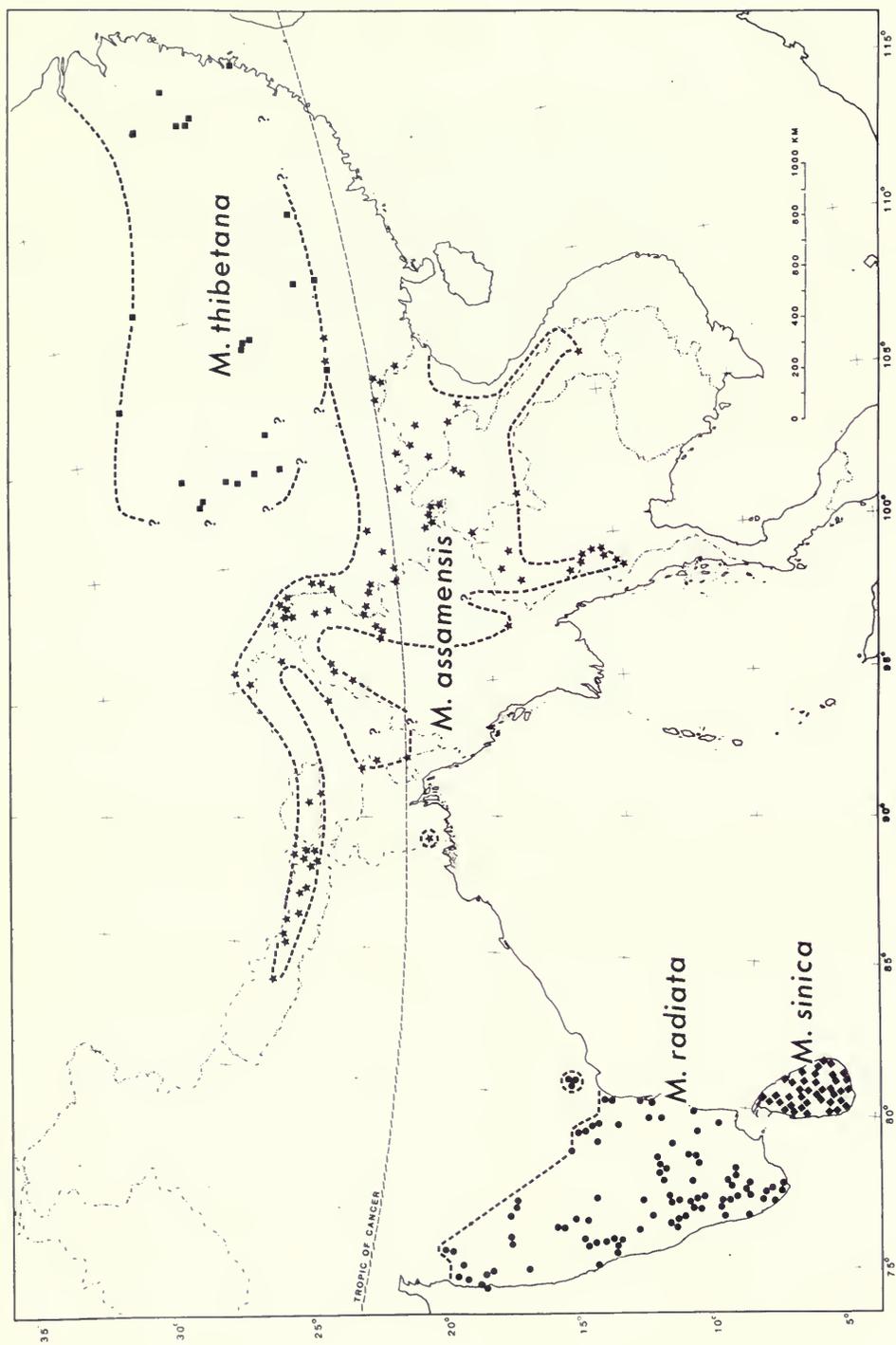


FIG. 1. Locality records (solid map symbols) and inferred limits of natural distribution (dashed lines) of *sinica* group species. References for locality records: *M. sinica* (diamonds)—Fooden, 1979, p. 131; McKay, 1973, p. 34 (Gal Oya region, ca. 7°11'N, 81°46'E); Shotake & Santiapillai, 1982, p. 80 (Kokkavil, 9°16'N, 80°24'E); Vavuniya, 8°45'N, 80°30'E; Trincomalee, 8°34'N, 81°14'E; Ratnapura, 6°41'N, 80°24'E). *M. radiata* (circles)—Fooden, 1981, p. 4; Fooden et al., 1981, p. 464; Karanth, 1982, p. 82 (Bhadra Wildlife Sanctuary, ca. 13°30'N, 75°30'E); Singh et al., 1984, p. 8 (Hassan, 13°00'N, 76°05'E). *M. assamensis* (stars)—Fooden, 1982a, pp. 4, 5; additional references in Appendix. *M. thibetana* (squares)—Fooden, 1983, p. 6; Fooden et al., 1985, p. 14.

33°N, 1000–2500 m), climate varies from subtropical wet to moderate continental moist, with snow in winter.

Species in the *sinica* group differ in the kinds and diversity of forest habitats that they occupy within their geographic ranges. *M. sinica* successfully inhabits all three major forest types—evergreen, semievergreen, and arid—within its range (Dittus, 1977b, p. 256; Fooden, 1979, p. 121). Arid zone forest habitats of *M. sinica* are restricted to the immediate vicinity of streams and ponds. Dittus (1982, p. 276; 1985, p. 4) has documented the important effects of recurrent tropical cyclones on the habitats of *M. sinica*.

Although *M. radiata* also has been observed in all forest types within its geographic range, it is rarely encountered in evergreen forests and instead is much more common in semievergreen, deciduous, and disturbed habitats (Prasad et al., 1979, p. 738; Fooden, 1981, p. 15; Singh et al., 1984, p. 8). The preference of *M. radiata* for disturbed habitats has been reconfirmed by a recent field survey (Pirta et al., 1981, pp. 431, 433):

Most of the bonnet groups were found outside the forest inhabiting roadsides near agricultural areas covered with a thick vegetation of banyan (*Ficus bengalensis*), pipal (*Ficus religiosa*) and imli (*Tamarindus indica*) trees. . . . It was also observed that bonnet monkeys are very rare in the interior forest, and some groups which do live in jungle are found near tribal huts or the forest bungalows.

Although *M. radiata* apparently prefers nonevergreen and disturbed habitats to evergreen forest, in its generally nonevergreen habitats this species intensively exploits scattered or clumped evergreen trees, such as fig trees, for food and roosting places (Singh et al., 1980, p. 102). At Elephanta Island, near Bombay, Kuruvilla (1980, p. 979) reports:

During the dry seasons most of the trees shed their leaves. At this time the macaques [*M. radiata*] select roosts where evergreen trees are numerous.

The preferred habitat of *M. assamensis* evidently is subtropical midelevation mountain broadleaf evergreen rainforest (Fooden, 1982a, p. 17; Li Zhixiang, 1973, unpublished field notes, KIZ: Coll. No. 73231, Satun, Yunnan, China). This species occasionally has been recorded in decid-

uous and bamboo forests and in cultivated fields, but only in the immediate vicinity of mountain broadleaf evergreen forest (Dào, 1978, p. 382; Fooden, 1982a, p. 17). One anomalous, possibly relict, record of this species is in the Sundarbans tidal mangrove swamps at the mouths of the Ganges River (Anderson, 1872, p. 529; Fooden, 1982a, p. 2; Zoological Survey of India, National Zoological Collection, Calcutta, Specimen No. 11999).

The preferred habitat of *M. thibetana* also evidently is midelevation mountain broadleaf evergreen rainforest (Fooden, 1983, p. 11; Xiong, 1984, p. 3; Fooden et al., 1985, p. 24). This species, like *M. assamensis*, occasionally moves opportunistically from evergreen forest into adjacent bamboo groves, natural clearings, and cultivated fields (Mell in Matschie, 1912, p. 309; Xiong, 1984, p. 5; Quan Guoqiang, 1960, unpublished field notes, IZAS 17966–69, Sujiapo, Guizhou).

#### Arboreality/Terrestriality

*Macaca sinica*, *M. radiata*, and *M. assamensis* evidently are much more arboreal than *M. thibetana*. In well-studied troops of *M. sinica*, daytime activity at one locality was 76% arboreal (Dittus, 1977b, pp. 245, 257). In *M. radiata*, daytime activity at various localities is estimated to range from 70% to 90% arboreal (Sugiyama, 1972, p. 251; Rahaman & Parthasarathy, 1979, p. 415; cf. Clarke, 1978, p. 518). Percentage estimates of arboreal activity are not available for *M. assamensis*, but this species is rarely observed on the ground and therefore probably is at least as arboreal as *M. sinica* and *M. radiata* (Fooden, 1982a, p. 17; Quan Guoqiang, 1960, unpublished field notes, IZAS 17942–47, 17955–58, Zhung Shan, Yunnan, China). *M. thibetana*, by contrast, is often observed on the ground and appears to be more terrestrial than arboreal (David, 1874, p. 9; 1875, p. 256; Mell in Matschie, 1912, p. 309; Steward, 1925, p. 80; Fooden et al., 1985, p. 24); this species often leaves marks on the ground where it travels and forages (Xiong, 1984, p. 4; Fooden et al., 1985, p. 24).

Nighttime sleeping is exclusively arboreal in *M. sinica* (Dittus, 1977b, p. 245) and in *M. radiata*, except in treeless urban areas (Kuruvilla, 1980, p. 979; Fooden, 1981, p. 16). Although nighttime sleeping habits have not been reported for *M. assamensis*, this species probably also sleeps in tall trees. *M. thibetana*, however, does not sleep in

trees, but instead sleeps on cliffs or in caves (Xiong, 1984, pp. 3, 8; Fooden et al., 1985, p. 24).

*M. sinica*, *M. radiata*, and *M. thibetana* are known to enter streams freely (Fooden, 1979, p. 122; 1981, p. 16; Xiong, 1984, p. 5). This probably also applies to *M. assamensis*.

## Food

Like other macaques, species in the *sinica* group are predominantly vegetarian, with animal food constituting less than 5% of the total dietary intake. *Macaca sinica*, *M. radiata*, and *M. thibetana* are known to eat fruit, flowers, seeds, shoots, leaves, resin, and other parts of a wide variety of plants in their environment; this probably also is true of *M. assamensis*. *Macaca sinica* is recorded in one area as eating parts of 41 species of trees and 22 or 23 species of shrubs (Dittus, 1977b, p. 247); *M. radiata* is recorded as eating parts of 36 plant species in one area and about 40 plant species in another (Makwana, 1980, p. 10; Kuruvilla, 1980, p. 981); and *M. thibetana* is recorded as eating parts of at least 19 plant species in one area (Xiong, 1984, p. 4). Seasonal changes in plant foods have been carefully documented for *M. sinica* by Dittus (1974, ch. 2, pp. 91–102) and for *M. radiata* by Kuruvilla (1980, pp. 982–985), who also notes age and sex differences in plant feeding patterns. Of all plant parts eaten, fruits generally are the main food of *M. sinica*, *M. radiata*, and *M. assamensis* (Dittus, 1977b, p. 248; Kuruvilla, 1980, p. 981; Fooden, 1981, p. 17; 1982a, p. 17); these three species all eat figs, which constitute more than half the diet in some populations of *M. sinica*. Bamboo shoots are an important food of *M. radiata*, *M. assamensis*, and *M. thibetana* (Fooden, 1981, p. 17; Xiong, 1984, p. 5; Li Zhixiang, 1973, unpublished field notes, KIZ: Coll. No. 73231, *M. assamensis*, Satun, Yunnan, China). Leaves may constitute a major part of the diet of *M. thibetana*; of 17 food plants tabulated for this species, 11 are exploited for their leaves and only 5 for their fruit (Xiong, 1984, p. 4). Leaves also may be important in the diet of some populations of *M. assamensis*; according to Li Zhixiang (1973, unpublished field notes, KIZ: Coll. No. 73231, see above), the diet of one specimen of this species collected in May in Yunnan was 60% leaves and 40% bamboo shoots. All four species in the *sinica* group are notorious raiders of cultivated fields; among other crops pilfered, rice is habitually taken by *M. sinica*

and *M. radiata*, and maize is habitually taken by *M. assamensis* and *M. thibetana*.

Animal food, including both invertebrates and vertebrates, is reported as part of the diet of all four species (*M. sinica*: Dittus, 1977b, p. 248; Fooden, 1979, p. 123; Farook, 1979, p. 76. *M. radiata*: Rahaman & Parthasarathy, 1979, pp. 415, 420–421; Kuruvilla, 1980, pp. 986–987; Fooden, 1981, p. 17. *M. assamensis*: Fooden, 1982a, p. 17. *M. thibetana*: Xiong, 1984, p. 4; Fooden et al., 1985, p. 25). Insects, including larvae and adults, probably are the most important prey of these macaques. Also recorded as prey are spiders and spiders' eggs, snails, small fish, lizards, snakes, birds and birds' eggs, palm squirrels, and tree mice. Although animal food constitutes less than 5% of the diet of these species, it apparently is nutritionally important: *M. sinica* spends about 20% of daily foraging time searching for animal prey (Dittus, 1977b, p. 248); *M. radiata* has been observed to swim across a fast-flowing stream to obtain birds' eggs at a nesting ground (Krishnan, 1972, p. 539); and *M. thibetana* troop members have been observed fighting over the remains of a lizard that one of them had killed (Xiong, 1984, p. 4).

Xiong (1984, p. 5) reports that starvation is a frequent cause of death in *M. thibetana* in winter when food is in short supply for this species. In-troop fights over food also are common in this species.

During the rainy season, *M. sinica* and *M. radiata* obtain adequate water from food and from tree holes and wet surfaces (Dittus, 1977b, p. 247; Fooden, 1979, p. 123; 1981, p. 18; Kuruvilla, 1980, p. 980). During the dry season these species make long daily trips to drink at permanent water sources. No information is available concerning how *M. assamensis* and *M. thibetana* satisfy their water requirements.

## Predators and Parasites

Known nonhuman predators of *M. sinica* are crocodiles (*Crocodylus palustris*), leopards (*Panthera pardus*), and domestic dogs (*Canis familiaris*) (Dittus, 1977b, p. 251; Fooden, 1979, p. 122; Farook, 1979, p. 76; cf. Seidensticker, 1983, p. 325); probable additional predators of *M. sinica* are pythons (*Python molurus*), cobras (*Naja naja*), Russell's viper (*Vipera russelli*), and large eagles and hawks. The same species and, in addition, tigers (*Panthera tigris*) and smaller felids, probably

also are predatory to *M. radiata* (Rahaman & Parthasarathy, 1979, p. 407; Makwana, 1980, p. 11; Fooden, 1981, p. 16). Although predators of *M. assamensis* and *M. thibetana* have not been specifically reported, *M. thibetana* is habitually vigilant while foraging (Xiong, 1984, p. 2), which suggests that predation, possibly nonhuman, is a substantial threat. *Macaca thibetana* troop members have been observed in a protracted skirmish with an attacking kite (*Milvus korschun*) (Xiong, 1984, p. 2), which, however, is too small to be a serious predator of these macaques.

Parasitological surveys of *sinica* group species have mainly concentrated on *M. sinica* and *M. radiata* (Reardon & Rininger, 1968, p. 578; Fiennes, 1972, symposium; Wong & Conrad, 1978, p. 413; McSwain, 1983, pp. 62, 89, 91). Parasitic organisms reported for these two species include viruses, bacteria, fungi, protozoa, trematodes, cestodes, nematodes, and arthropods. A tickborne virus, the agent of epidemic Kyasanur Forest disease, is often fatal to *M. radiata* in Shimoga District, India (Trapido et al., 1964, p. 763). Parasitic protozoa and nematodes have been reported in wild-collected *M. assamensis* in Vietnam and China (Sandground, 1933, pp. 564, 575; Yin, 1973, p. 355; 1980, p. 23; Long et al., 1979, p. 320).

### Seasonal Migration

In some areas *M. assamensis* and *M. thibetana* are known to migrate seasonally between higher elevations in summer and lower elevations in winter. Crump (in Wroughton, 1916, p. 476) indicates that *M. assamensis* descends to 600–1200 m in winter in the Sikkim-Darjeeling area (cf. Fooden, 1982a, p. 17), and Shou et al. (1964, p. 62) report that this species also habitually descends from the mountains in winter in Guangxi and Yunnan. Xiong (1984, p. 3) provides greater detail concerning the seasonal migration of *M. thibetana* at Huang Shan in southeastern Anhwei: the summer range in this area is at 1300–1700 m; the fall range is at 500–700 m; the winter range is at 400–600 m; and the spring range is at 570–1700 m. In some other areas, *M. thibetana* evidently remains at higher elevations in fall and winter: NE Jiangxi—Qianshan Xian, Jan., 1000–1200 m (IZAS 17970); NE Guizhou—Jiangko, Oct., 1200 m (KIZ 3193); Fanjing Shan, Dec., 1200 m, 2350 m (Fooden et al., 1985, p. 24); central Sichuan—Emei Shan, Oct., ca. 1500 m (Wilson, 1913, p. 224); Baoxing, NNW,

11 March, ca. 2500 m (David, 1874, p. 9). At Huang Shan, north-facing slopes are favored in summer and south-facing slopes are favored in winter; this suggests that the migration of *M. thibetana* in this area probably is an adaptation to seasonal temperature extremes as well as to local availability of plant foods. Although *M. sinica* and *M. radiata* are not known to migrate seasonally, some troops of these two species extend their home ranges considerably during the dry season in order to reach distant permanent sources of drinking water (Koyama, 1973, p. 229; Dittus, 1977b, p. 247). Such seasonal range extension may provide a model for the origin of true seasonal migration, as occurs in *M. assamensis* and *M. thibetana* (see Darlington, 1957, p. 243).

### Troop Size and Composition

Judging from available data, troop size is roughly similar in all four species in the *sinica* group (table 1). In forest populations that are relatively independent of humans, mean troop size in these species is about 20 to 25 individuals and extreme troop sizes are about 7 and 70 individuals. In *M. radiata*, nonforest troops that are more or less closely associated with humans generally tend to be larger than forest troops (table 2; Pirta et al., 1981, p. 433; Singh et al., 1984, p. 10); however,

TABLE 1. Troop size in forest populations of *sinica* group species.\*

Species	Mean troop size**	Extreme troop sizes	No. of troops observed
<i>M. sinica</i>	21.6	8–51	28†
<i>M. radiata</i>	24.9 ± 12.3	7–50	13
<i>M. assamensis</i>	>20	10–50	>25
<i>M. thibetana</i>	>20	10–70	>9

\* References: *M. sinica*—Eisenberg & Lockart, 1972, p. 76; Eisenberg et al., 1972, p. 870; Dittus, 1974, ch. 2, p. 66; 1975, p. 137; 1977b, p. 243; 1980, p. 267; cf. Farook, 1979, p. 74. *M. radiata*—see Table 2. *M. assamensis*—Fooden, 1982a, p. 18; Quan Guoqiang, 1960, unpublished field notes, IZAS 17942–47, 17955–58, Zhung Shan, Yunnan, China, 10 to 20 individuals in each of three troops. *M. thibetana*—David, 1875, p. 256; Xiong, 1984, p. 1; Fooden et al., 1985, p. 26.

\*\* Data inadequate for computation of standard deviations, except in *M. radiata*.

† At least three of these troops are partly dependent on food sources generated by humans (Dittus, 1974, ch. 2, p. 71) and therefore are not typical forest troops.

TABLE 2. *Macaca radiata*: troop size in forest troops compared with that in nonforest troops.

Forest troops			Nonforest troops (urban, rural, roadside, temple)			Reference
Mean ± SD	Ex-tremes	N	Mean ± SD	Ex-tremes	N	
36.0 ± 2.8	34-38	2	...	...	...	Nolte, 1955, p. 78
...	...	...	21.1 ± 8.9	10-43	14	Rahaman & Parthasarathy, 1967, p. 253
33.7 ± 3.5	30-37	3	28.9 ± 7.4	16-44	10	Sugiyama, 1972, p. 255; Koyama, 1973, p. 228
17.0 ± 14.1	7-27	2*	29.5 ± 15.4	15-59	6*	Simonds, 1973, p. 601; 1974a, p. 152
...	...	...	23	...	1	Singh & Sachdeva, 1977, p. 606
...	...	...	39.7 ± 5.5	34-45	3	Rahaman & Parthasarathy, 1979, p. 408
41**	...	1	48.5†	...	1	Kuruvilla, 1980, p. 978
25.5 ± 14.5	12-50	5‡	36.9 ± 26.2	10-100	22‡	Fooden et al., 1981, p. 469
14.6 ± 4.9	11-23	5§	22.7 ± 9.6	7-44	28§	Singh et al., 1984, p. 10
24.9 ± 12.3	7-50	18	28.2 ± 16.8	7-100	85	Summary
...	...	...	17.7 ± 1.40	5-59	308	Kurup, 1984b, p. 59

\* For more recent census data on some of these troops, see Makwana (1980, p. 10).

\*\* Mean size of troop whose membership varied between 38 and 44 individuals, October 1974-September 1975.

† Mean size of troop whose membership varied between 45 and 52 individuals, October 1974-September 1975.

‡ Excludes Elephanta Island troops, which are more accurately reported by Kuruvilla (1980, p. 978) and are tabulated separately.

§ Some of these troops apparently are also included in the population study of Pirta et al., 1981, p. 433.

recently published data on 308 nonforest troops in four Indian states indicate that mean size in such troops probably is smaller than previously inferred (table 2; Kurup, 1984b, p. 59). Provisioned temple troops of *M. radiata* and *M. thibetana* sometimes reach extraordinary sizes of 100 to 300 individuals (Li, 1960, p. 202; Fooden et al., 1981, p. 469; Guo, 1981, p. 65). Solitary males, unknown in *M. sinica*, *M. radiata*, and *M. assa-*

*mensis*, have been reported in *M. thibetana* by three observers (David, 1874, p. 9; Mell in Matschie, 1912, p. 309; Steward, 1925, p. 80).

In an average troop, about 50 to 60% of the members are sexually mature (Fooden, 1979, p. 125; 1981, p. 25; 1982a, p. 18; Xiong, 1984, p. 2; Singh et al., 1984, p. 12; Kurup, 1984b, p. 63). The ratio of sexually mature males (subadults and adults) to sexually mature females (adults) is 0.60

TABLE 3. *Macaca radiata*: ratio of sexually mature males (subadults and adults) to sexually mature females (adults) in 418 troops.

Sexually mature individuals				Reference
Pooled sex ratios (males : females)	Extreme sex ratios in troops observed	No. of individuals observed	No. of troops observed	
0.88	0.12-2.00	330-331	26*	Simonds, 1973, p. 600
0.52	0.50-0.56	64	3	Rahaman & Parthasarathy, 1979, p. 409
0.71	0.71-0.71	47-55	2	Kuruvilla, 1980, p. 978
0.79	0.27-1.67	418	27**	Fooden, 1981, p. 24
0.61	0.36-1.75	92	9	Koyama & Shekar, 1981, p. 248
0.68	0.25-2.00	181	10†	Fooden et al., 1981, p. 470
0.93	...	[425]	33‡	Singh et al., 1984, pp. 10, 11
0.69§	...	[3,028]	308	Kurup, 1984b, p. 59
0.73	0.12-2.00	4,585-4,594	418	Summary

\* Cf. Makwana (1980, p. 10), who reports more recent data for some of the same troops.

\*\* Excludes troops reported by Simonds (1973, p. 600), which are tabulated separately; also excludes troops reported by Nolte (1955, p. 78), for which age-sex categories probably are not coordinate with those in other studies.

† Age-sex data recorded in unpublished field notes on troops reported previously.

‡ Some of these troops apparently are also included in the population study of Pirta et al., 1981, p. 432.

§ Excludes subadults, which are not separated according to sex in this study.

TABLE 4. Home range area in *Macaca sinica* and *Macaca radiata*.

Mean home range area (hectares)	Extremes (hectares)	Habitat	No. of troops observed	Reference
<i>Macaca sinica</i>				
> 100	...	Forest	2	Eisenberg & Lockart, 1972, p. 76; Eisenberg et al., 1972, p. 870
ca. 41.3 ± 26.7	17-115	Various	13	Dittus, 1974, ch. 2, p. 70; 1977b, p. 250
> 200	...	Forest	1	Hladik & Hladik, 1972, p. 205
<i>Macaca radiata</i>				
26	...	Garden	1	Singh & Pirta, 1978, p. 265
ca. 100	...	Plantation	3	Rahaman & Parthasarathy, 1979, p. 415
240	...	Various	2	Kuruvilla, 1980, p. 979
ca. 212	ca. 130-260	Forest	5	Fooden, 1981, p. 22
ca. 195	ca. 40-260	Roadside	4	Fooden, 1981, p. 22
ca. 100	ca. 100	Garden	2	Fooden, 1981, p. 22

in 26 troops of *M. sinica* (276 mature individuals; Dittus, 1975, pp. 133, 137; cf. Farook, 1979, p. 74), 0.73 in 418 troops of *M. radiata* (ca. 4,590 individuals; table 3), and 0.43 in 3 troops of *M. assamensis* (30 individuals; Fooden, 1982a, p. 18). These ratios are not significantly different from 0.72, which is the weighted mean ratio for all three species (chi square, 3.75; df, 2;  $0.20 > P > 0.10$ ); the low ratio in *M. assamensis* suggests possible divergence, but available data for this species are insufficient to establish this. In *M. thibetana*, although no data are available concerning the ratio of sexually mature males to sexually mature females, Xiong (1984, p. 2) reports that the ratio of all males to all females among 115 individuals in 5 troops is 1.80; if confirmed as a general rule in *M. thibetana*, the great excess of males over females in this species would set it apart from all other studied species of macaques.

Two small isolated all-male subgroups have been reported in the vicinity of larger mixed-sex troops. In *M. sinica*, Dittus (1975, p. 139) observed an all-male group of fluctuating size, maximum 9 to 10 (2 adults, 1 subadult, 6 to 7 juveniles), that remained isolated for at least 3.5 years peripheral to a troop of 33 to 34 members; 3 nonpermanent juvenile members of the all-male group are known to have detached from the main troop, and another nonpermanent juvenile member detached from a neighboring troop. In *M. radiata*, Simonds (1973, p. 600) observed a group of 3 males that remained isolated for at least several weeks within the home range of a mixed-sex troop of 28 members; 1 of the males in this isolated group is known to have detached from the main troop, and the other 2 may have also.

### Home Range

Home range area is known from fairly complete data for several troops of *M. sinica* and *M. radiata* (table 4) and from fragmentary data for a few troops of *M. thibetana*; home range area in *M. assamensis* is unknown. In *M. sinica*, home range area varies from 17 to >200 hectares, and, in *M. radiata*, home range area varies from 26 to ca. 260 hectares; available data suggest that home ranges may tend to average somewhat smaller in *M. sinica* than in *M. radiata*. In *M. sinica*, home range area is positively correlated with troop size (Dittus, 1977b, p. 250); this probably also applies to *M. radiata*.

In *M. thibetana*, seasonally migratory troops at Huang Shan, southeastern Anhui, have very large home ranges, each of which encompasses several mountains (Xiong, 1984, p. 5). When adequate food is locally available, a troop at Huang Shan forages within an area less than 2.5 km in diameter (less than 500 hectares). In winter when food is scarce, by contrast, a foraging troop may travel 30 km in one day, at a rate of 6 to 7 km/hr, searching for seeds as it moves. At Fanjing Shan, north-eastern Ghizhou, in late November-early December, a troop of *M. thibetana* remained within an area of less than 200 hectares for four days (Fooden et al., 1985, p. 25).

Troop home ranges are known to be relatively stable over many years in *M. sinica* (3½ years; Dittus, 1974, ch. 2, p. 68), *M. radiata* (16 years; Makwana, 1980, p. 9; Fooden, 1981, p. 22), and *M. thibetana* (4 years; Xiong, 1984, p. 5); this presumably also applies to *M. assamensis*. A troop of *M. radiata* in Mysore City returned to its orig-

inal home range after an unnatural move that lasted 37 days and took the troop 2 km away from its home range (Singh & Pirta, 1978, p. 265).

Home ranges of adjacent troops often overlap, at least in *M. sinica* and *M. radiata* (Dittus, 1977b, p. 250; Rahaman & Parthasarathy, 1979, p. 415; Kuruvilla, 1980, p. 979; Fooden, 1981, p. 22). In overlap areas, intertroop tension is high (Dittus, 1974, ch. 2, p. 68; Rahaman & Parthasarathy, 1979, p. 415; Kuruvilla, 1980, p. 979; Fooden, 1981, p. 23; Xiong, 1984, p. 2). In these areas, larger troops are frequently, but not always, dominant to smaller troops. In *M. radiata* and *M. thibetana*, fierce intertroop fights have been observed in overlap areas. After confrontations in overlap areas, both troops generally withdraw to more remote parts of their respective home ranges.

### Male Emigration

Intertroop transfer of males has been documented by field observations in *M. sinica* and *M. radiata* and is suggested in *M. thibetana*. Although relevant observations are lacking in *M. assamensis*, it seems likely that male transfer is widespread or universal in the *sinica* group. The pattern in *M. sinica*, where male transfer has been most intensively studied (Dittus, 1975, p. 140), may be typical. In *M. sinica*, all males probably leave their natal troop as adolescents, sometime between age 3.5 years and age 7.0 years, before their first breeding season. Adult males also may emigrate, on average about once every 5 years. Emigration usually occurs during the breeding season. Emigrating males, both adolescents and adults, are seldom or never dominant in the troops they leave, but an emigrating adult sometimes becomes dominant in the troop that he enters. The hardships and combats involved in emigration probably are a major cause of mortality in males, particularly in adolescent males, in which the annual mortality rate reaches approximately 30%. An apparent genetic consequence of male emigration in *M. sinica*, as in other macaques, is that the coefficient of relationship within troops, estimated from blood protein polymorphism, is relatively low ( $0.191 \pm 0.054$ ; Aoki & Nozawa, 1984, p. 179) and average heterozygosity of blood protein alleles is relatively high (0.078; Shotake & Santiapillai, 1982, p. 93).

Although early field observations of *M. radiata* suggested that male emigration was rare or absent in this species (Simonds, 1965, p. 186; Rahaman & Parthasarathy, 1969a, p. 275), subsequent stud-

ies revealed that it is fairly common (Simonds, 1973, p. 600; Makwana, 1980, p. 9; Pirta et al., 1981, p. 432; Fooden, 1981, p. 29; Ali, 1984, p. 319; cf. Wade, 1979, p. 363; Small, 1982, p. 3; Caldecott, 1984, p. 12). In *M. radiata*, as in *M. sinica*, none of the emigrants observed was the dominant male in the troop that he left, although one became dominant in the troop that he entered. Further study of emigration in *M. radiata* is required to clarify similarities and differences between male emigration in this species and *M. sinica*. In *M. thibetana*, new arrivals from another troop (number and sex of these individuals not specified) have been identified among troop members of the lowest dominance rank (Xiong, 1984, p. 7).

Female emigration evidently is relatively rare in the *sinica* group. Two instances (of which one is equivocal) are reported in *M. sinica* (Dittus, 1975, p. 139; Farook, 1979, p. 77), and four instances are reported in *M. radiata* (Rahaman & Parthasarathy, 1969a, p. 268; Moore & Ali, 1984, p. 101; Moore, 1984, p. 579).

### Seasonal Breeding

Breeding seasonality is well documented in *M. sinica* and *M. radiata* and less well documented in *M. assamensis* and *M. thibetana* (see references below). In all four species, apparently, a well-defined period of maximum copulations precedes a well-defined birth season by 5 to 6 months, which is the typical gestation length in macaques (Ardito, 1976, p. 215). The frequency of copulations during the peak mating period probably is more than 10 times greater than during the rest of the year (Fooden, 1981, p. 27). Occasional reversed periodicity of annual mating and birth seasons evidently may occur in all four species. Although annual reproductive cycles generally are approximately synchronous within each of these four species, they are only partially synchronous between species.

In 18 troops of *M. sinica* in the Polonnaruwa area, mating frequency peaks in July–September, and birth frequency peaks in December–February (Dittus, 1975, p. 134; 1977a, p. 312); a few births also are reported in September and October, which may indicate reversed periodicity of mating and birth seasons. At Anuradhapura, a locality about 80 km from Polonnaruwa, the birth season in 5 to 6 troops reportedly is in the spring, slightly later than at Polonnaruwa, and the peak mating period

therefore presumably is in the fall; 2 to 3 troops at this locality had reversed periodicity, with the birth season reportedly in the fall and the peak mating period presumably in the spring.

In *M. radiata*, at numerous localities from Bombay to Mysore, the peak mating period is in August–November, although matings at low frequency also have been observed in other months (Parthasarathy, 1977, p. 49; Rahaman & Parthasarathy, 1979, p. 413; Makwana, 1980, p. 11; Kuruvilla, 1980, p. 977; Fooden, 1981, p. 27). In accord with the well-defined mating frequency peak, 86 of 88 recorded births at these same localities occurred during the period December–June, with 81 of these births more narrowly restricted within the period January–April. The two exceptional birth records, one in September (Rahaman & Parthasarathy, 1979, p. 422) and the other in October (Kuruvilla, 1980, p. 979), suggest reversed periodicity.

The peak mating period (August–November) and birth season (January–April) in *M. radiata* approximately coincide with the corresponding reproductive seasons in most troops of *M. sinica* at Anuradhapura (peak mating period, fall; birth season, spring) and are only one or two months later than the corresponding seasons in *M. sinica* at Polonnaruwa (peak mating period, July–September; birth season, December–February). Although known annual reproductive cycles are approximately synchronous in these two species, these cycles are inversely correlated with local wet and dry seasons. In most parts of the range of *M. radiata*, the peak mating period is at the end of the rainy season, and the birth season is at the end of the dry season (Fooden, 1981, p. 27); in *M. sinica*, however, matings at Polonnaruwa and Anuradhapura peak at the end of the dry season, and births peak at the end of the rainy season (Lancaster & Lee, 1965, p. 509; Dittus, 1977c, p. 269). The significance of synchronism with respect to the calendar and of divergence with respect to local wet–dry seasons in the annual reproductive cycles of these two species is unclear.

In *M. assamensis*, 8 of 10 records available from eastern India to northern Vietnam (Fooden, 1982a, p. 20) indicate that births probably peak in the summer (rainy season) and that matings therefore probably peak in the winter (dry season). The remaining two records from natural populations of this species indicate births in winter, which suggests reversed periodicity. In a zoo in Germany, four infants that were produced in nine years by a captive female *M. assamensis* were all born in

the spring—successively in May, March, May, and April (Dathe, 1983, p. 126). In a laboratory population of 10 *M. assamensis* females, reproductive seasonality was individually variable, and response to experimental changes in photoperiod also was individually variable (Wehrenberg & Dyrrenfurth, 1983, p. 120).

Evidence concerning breeding seasonality in *M. thibetana* is ambiguous. Reports from three widely separated localities, one in the western part of the range, one in the central part, and one in the eastern part, suggest that matings in this species peak in the spring and that births peak in the fall (Fooden et al., 1985, p. 26). However, data from two additional localities in the eastern part of the range, one of them particularly well studied, indicate reversed periodicity, with matings reportedly most frequent during the fall (late September–early November; Xiong, 1984, p. 6) and one birth record apparently in the spring (Fooden, 1983, p. 13; C. Pope, 1926, unpublished field note, American Museum of Natural History, N.Y., Specimen No. 84475, Chong'an Xian, Fujian).

Numerous observations are available concerning breeding seasonality in captive *M. radiata*. A colony of this species kept outdoors at Davis, Calif., has maintained annual reproductive seasonality for more than 10 years (Judge & Rodman, 1976, p. 535; Glick, 1979, p. 272; Silk et al., 1981, p. 1109). The mating season in this colony starts in August and peaks in October and November, as in India; matings in the Davis colony then continue at a moderately high level for another three months, December–February, which are not included in the peak mating season in India (Fooden, 1981, p. 27). As an apparent consequence of the more protracted mating season, the peak birth season in the Davis colony (March–June) is two months later than the peak birth season in India (January–April; Fooden, 1981, p. 27). Glick (1979, p. 272) notes that the mating season of *M. radiata* at Davis generally coincides with months of high humidity and precipitation, and the birth season coincides with months of low humidity and precipitation; the same relationship between reproductive seasons and wet–dry seasons also applies to *M. radiata* in India (see above).

Captives in two other *M. radiata* colonies also maintain breeding seasonality, approximately as in natural populations. An indoor colony kept at Lucknow, India, apparently has a peak mating period in September–October (Kamboj et al., 1984, p. 493), and an outdoor colony of *M. radiata* at Lawrenceville, Ga., has a birth season in April–

August, with a strong peak in April (Hadidian & Bernstein, 1979, p. 433), approximately as in the Davis colony. In two indoor colonies, one in Virginia and one in California, however, conceptions and births evidently occur through most of the year (Valerio et al., 1969, p. 291; Redman & Schneider, 1979, p. 7); the Virginia colony apparently exhibited breeding seasonality during the first year of captivity, but lost seasonality in the second year.

In the outdoor Davis colony and the indoor Lucknow colony, serum testosterone level, measured in the morning, reaches an annual peak during the mating season; this peak is approximately double the nonmating season minimum (Glick, 1979, p. 277; Kamboj et al., 1984, p. 492). Serum testosterone level in *M. radiata* also exhibits a daily cycle, with a nighttime maximum that is 6 to 11 times greater than the daytime minimum (Mukku et al., 1976, p. 779; Kholkute et al., 1981, p. 428; Kamboj et al., 1984, p. 492); the nighttime increase has been experimentally abolished by exposure to constant light (Mukku et al., 1976, p. 779). Correlated with the mating season testosterone peak in the Davis colony is a seasonal increase in testis size (length and width increase by about 30%) and a seasonal increase in male body weight (about 5% increase) (Glick, 1979, pp. 271, 274). Seasonal testosterone cycles apparently disappear in some indoor colonies of *M. radiata* (Murty et al., 1979, p. 158; Munshi, 1980, p. 13; Murty et al., 1980, p. 52); this may be related to different conditions of captivity. Semen volume and sperm number, studied by electroejaculation, show no seasonal change in one indoor colony of *M. radiata* (Sharma et al., 1984, p. 235).

Captive females of *M. radiata* kept in two indoor colonies in India are reported to become anovulatory and exhibit amenorrhea from April to July in Bangalore (Murty et al., 1979, p. 153; Srinath, 1980, p. 19) and from July to September in Bombay (Munshi, 1980, p. 11); most of these months are outside of the peak mating period in natural populations (Fooden, 1981, p. 27). In the Bangalore colony, ovarian and menstrual cycles resume during the period September–December, which approximately corresponds to the peak mating period in natural populations; no information is available concerning the date of cycle resumption in the Bombay colony. In Bangalore, newly captured females, obtained at any time of year, were found to exhibit amenorrhea for six or more months after introduction into the colony; these females began to cycle regularly when they

were kept for two or three months within sight of a separately caged mature male in the same room (Madhwa et al., 1975, p. 394; Srinath, 1980, p. 17). In a colony of *M. radiata* in Bombay, Jayaraman et al. (1979, p. 683) report that newly introduced females began to cycle regularly after alfalfa was added to their diet.

### Mating Behavior

Several accounts, partly divergent, are available concerning mating behavior in natural populations of *M. radiata* (Simonds, 1965, p. 193; 1977, p. 161; Rajagopal, 1965, p. 232; Rahaman & Parthasarathy, 1969a, p. 275; 1969b, p. 154; 1971, p. 99; 1979, p. 422; Sugiyama, 1972, p. 252; Parthasarathy, 1977, p. 49; Ali, 1984, p. 319); differences between these accounts may indicate individual or local differences in the behavior of this species. Although observers agree that subordinate males in *M. radiata* are not excluded from access to estrous females during the peak mating period, most reports suggest that dominant males engage in proportionally more copulations than subordinate males. Some studies indicate that dominant males may form relatively stable consort relationships with dominant females, whereas subordinate males and females tend to be more promiscuous in their matings. Intra-troop social tensions apparently increase during the peak mating period. Dominant males sometimes interfere with copulations of subordinate males (4 of 308 attempted copulations in one study), but peaceful serial mountings of one female by two or three males, including dominant and subordinate males, also have been reported. Subordinate males and estrous females sometimes withdraw 500 m from other troop members before copulation.

Most copulations in *M. radiata* are initiated by males (55 of 59 attempted copulations in one study; 241 of 308 attempted copulations in another). Sexual skin is relatively inconspicuous in females of *M. radiata*, and, unlike females in some other macaque species, they rarely solicit copulation by approaching males and presenting their hindquarters. Males apparently recognize estrous females by olfactory cues, probably associated with cyclical changes in cervical mucus (Ovadia et al., 1971, p. 132; McArthur et al., 1972, p. 109; Sheth et al., 1975, p. 134; Nasir-ud-Din et al., 1979, p. 397). Before mounting, a male often examines a female's perineum, frequently with digital probing of the vagina, and smells or tastes the vaginal contents,

which probably consists primarily of cervical mucus. During the peak mating season, some males examine the perineum of most or all sexually mature females every day. Copulation apparently is completed in less than one minute and usually is accomplished in a single mounting (26 of 28 copulations in one study; 294 of 308 in another), with 5 to 30 pelvic thrusts to ejaculation. Following copulation, excess ejaculate on the female's perineum is sometimes eaten by one or both partners or by another male. Copulations may occur either on the ground (197 of 362 observed copulations in one study; 54%) or in trees (46%). Males may attempt to copulate with unreceptive females, who express their unwillingness by vocalizing and fleeing (31 of 308 attempted copulations in one study). Homosexual mountings, not consistently correlated with social dominance, have often been observed in *M. radiata*.

Mating behavior in a long-established captive colony of *M. radiata* is generally within the range of variation observed in natural populations (Glick, 1980, p. 350; Shively et al., 1982, p. 375; Samuels et al., 1984, p. 998), despite the unnatural preclusion of male emigration in the captive colony. In this colony, Small (1983, p. 127) reports that females without infants enter estrus earlier and begin copulations earlier than females with infants. In an experimental group of males and ovariectomized females, sexual behavior was reduced relative to that in a control group of males and intact females (Rasmussen, 1984, p. 353).

Limited information is available concerning mating behavior in natural populations of *M. sinica* and *M. thibetana* (Jay, 1965, p. 570; Dittus, 1974, ch. 2, p. 109, ch. 3, p. 35; 1977a, p. 311; Xiong, 1984, pp. 5, 7), and none is available for *M. assamensis*. Mating behavior in captive *M. sinica* has been reported by Hill (1939, pp. 25, 31; 1974, p. 717). In *M. sinica* and *M. thibetana*, threats and fighting between males over access to estrous females may be more frequent and violent than in *M. radiata* (but see Singh et al., 1984, p. 15); serious injuries reportedly are inflicted in such fights in *M. sinica* and *M. thibetana*. In *M. sinica*, a consort pair typically withdraws up to 300 m away from its troop, apparently to reduce contact with competing males; somewhat similar behavior also has been reported in *M. radiata* (see above). In *M. thibetana*, high-ranking males reportedly intimidate lower-ranking males and thereby monopolize most of the estrous females. In *M. sinica*, as in *M. radiata*, sexual skin in females is inconspicuous, and copulation apparently is usually initiated by

males (Hill, 1974, p. 717—captive); in *M. thibetana*, by contrast, sexual skin is reported to swell conspicuously during estrus, and females have been observed to initiate copulations by approaching and presenting to males. In both *M. sinica* and *M. thibetana*, a profuse vaginal discharge—presumably cervical mucus—has been noted during estrus. As in *M. radiata*, males in *M. sinica* and *M. thibetana* have been observed to inspect the female perineum before copulation; this includes digital examination and smelling or tasting the vaginal discharge. Copulation in *M. thibetana* reportedly is completed in 40 to 60 seconds, which presumably indicates that ejaculation is accomplished in a single mount. Attempts by males to force copulation on unreceptive females have been observed in *M. thibetana*, as in *M. radiata*.

### Life History

Available life history information is relatively good for *M. sinica* and *M. radiata* and relatively poor for *M. assamensis* and *M. thibetana*. Length of the gestation period is best known in *M. radiata*. Valerio et al. (1969, p. 295) report that the gestation period in a captive colony of this species is  $159 \pm 6$  days (mean  $\pm$  SD) for 5 female births,  $163 \pm 3$  days for 11 male births, and  $162 \pm 4$  days for both sexes combined. Similar gestation periods in *M. radiata* also are reported by Hartman (1938, p. 470)—166 days for one female and 169 days for one male (cf. 153 days for one stillborn male); Souri and Swani (1962, p. 83)—ca. 165 days for one birth, sex unspecified; Stabenfeldt and Hendrickx (1972, p. 619)—ca. 167 days for four births, sex unspecified; Jayaraman et al. (1979)— $179 \pm 4$  days for four males; and Srinath (1980, p. 20)—166 days for 27 births, sex unspecified. In *M. sinica*, Hill (1966, p. 138) reports a gestation period of 180 days, without specifying the number or sex of births observed; the mean gestation period in this species probably is less than 180 days, judging from known mean gestation periods for small macaques (cf. Ardito, 1976, p. 215). In *M. thibetana*, Xiong (1984, p. 6) reports that the gestation period for two captive births (sex unspecified) was about eight months; if confirmed as typical for this species, this would be about as long as the gestation period in mandrills (Ardito, 1976, p. 216).

Prenatal mortality information is available for captive *M. radiata* maintained at Davis, Calif. (Hendrickx & Nelson, 1971, p. 414; Hendrickx &

Binkerd, 1980, p. 48). In an indoor group of this species, the prenatal mortality rate was 26.0% of 227 pregnancies during nine years; 16.8% of these pregnancies resulted in spontaneous abortions, and 9.2% resulted in stillbirths. In an outdoor group, the prenatal mortality rate was markedly higher, 41.0% during a two-year period (number of pregnancies unspecified).

The sex ratio at birth in a few sampled natural populations of *M. sinica* and *M. radiata* is close to 1:1. In two local populations of *M. sinica*, this ratio is 57 males: 54 females (1.06), which is not significantly different from 1.00 (Dittus, 1975, p. 132). In a smaller sample of three local populations of *M. radiata*, the sex ratio at birth is 17 males: 15 females (1.13) (Fooden, 1981, p. 31). In captive populations of *M. radiata*, the sex ratio at birth appears to be highly variable. In a colony of this species maintained in Virginia, Valerio et al. (1969, p. 295) report that the sex ratio at birth during a two-year period was 11 males: 5 females (2.20), and, in a colony maintained in California, Redman and Schneider (1979, p. 7) report that this ratio during a seven-year period was 118 males: 140 females (0.84). In a subsequent study of a separately confined part of the California colony, Silk et al. (1981, p. 1113) report that the sex ratio at birth during a 10-year period was 110 males: 71 females (1.55). This ratio fluctuated annually from a low of 0.72 to a high of 3.60; annual fluctuations in the sex ratio at birth of this captive group were found to be correlated with differential survival of male and female infants during the preceding year and with dominance rank-order of mothers. No information is available concerning sex ratio at birth in *M. assamensis* and *M. thibetana*.

Birth weight in captive *M. radiata* reported by Valerio et al. (1969, p. 295) is  $388 \pm 34$  g (mean  $\pm$  SD) for 5 females and  $411 \pm 56$  g for 11 males. Similar captive birth weights in this species also have been reported by Hartman (1938, p. 470), 330 g for one female and 370 g for one male, and by Leutenegger (1977, p. 154), mean 368 g for four newborn, sex unspecified. Jayaraman et al. (1979, p. 683) note that weight in four captive-born male infants ( $361 \pm 40$  g) averages greater than in one wild-born male infant (316 g). Composite mean birth weights in captivity are 378 g for females ( $N = 6$ ) and 396 g for males ( $N = 16$ ). The ratio of mean birth weight to mean adult weight in captive *M. radiata* is 0.10 for females and 0.038 for males. These ratios are based on mean adult weights of

3.753 kg for 10 captive females (Leutenegger, 1977, p. 154) and 10.550 kg for 5 captive males (Glick, 1979, p. 271; cf. Rosenblum & Smiley, 1980, p. 250); captive adult males apparently weigh about 50% more than adult males in natural populations (see Fooden, 1981, p. 3). In *M. thibetana*, weight of one newborn or young infant (sex unspecified) recorded by Xiong (1984, p. 6) is 550 g; the ratio of this infant's weight to mean adult weight ( $14.8 \pm 4.22$  kg, both sexes combined; Xiong, 1984, p. 2) is 0.037.

Infant mortality, from birth to age one year, apparently averages about 45% in natural populations of *M. sinica* (Dittus, 1980, p. 268) and about 50% in natural populations of *M. radiata* (Fooden, 1981, p. 32). In *M. sinica*, Dittus (1975, pp. 135, 137) reports that the mortality rate of female infants significantly exceeds that of male infants at one locality and vice versa at another locality; in *M. radiata*, Singh et al. (1984, p. 12) report that the mortality of female infants exceeds that of male infants in nonurban habitats and vice versa in urban habitats. In a captive population of *M. radiata*, Redman and Schneider (1979, p. 6) report that infant mortality during the first six months of life varied from 11.8% in indoor individual cages to 41% in an outdoor group enclosure. In a subsequent 10-year study of the same outdoor group, Silk et al. (1981, p. 1111) report that infant mortality during the first six months of life was 48% (61 deaths/126 infants) and was particularly intense during the first month of life (57/61 deaths). In this study, infant mortality was highest in female offspring of low-ranking mothers and also tended to be high in offspring of young mothers (less than age six years). Spontaneous abortions, stillbirths, and neonatal deaths in this colony were not correlated with either primagravidity or gravidity order (Small & Rodman, 1981, p. 165).

Weaning in natural and captive populations of *M. radiata* occurs at approximately age six months (Kaufman & Rosenblum, 1966, p. 240; 1969, p. 51; Rahaman & Parthasarathy, 1969b, p. 156; Singh et al., 1980, p. 105; Cantwell & Reite, 1984, p. 429; cf. Simonds, 1965, p. 193); the weaning period generally coincides with the beginning of the next mating season for the mother. Weaning in *M. thibetana* also occurs about age six months (Xiong, 1984, p. 6).

In captive *M. sinica*, menstruation apparently begins about age 2.5 to 3.0 years, and length of the normal menstrual cycle is estimated to be 29

days (Hill, 1939, pp. 23, 34). In *M. radiata*, mean length of the menstrual cycle is  $28 \pm 4.3$  days (SD; 1,262 cycles, 130 females), modal length is 28 days (ca. 650 of 1,260 cycles), and extreme cycle lengths are 15 and 42 days (Srinath, 1980, p. 20); similar cycle lengths are reported for smaller samples of *M. radiata* by Hartman (1938, p. 468), Valerio et al. (1969, p. 287), McArthur et al. (1972, p. 108), Stabenfeldt and Hendrickx (1972, p. 614), Madhwa Raj et al. (1975, p. 395), Jayaraman et al. (1979, p. 683), and Munshi (1980, p. 11). The mean duration of menstrual flow in captive *M. radiata* is reported as 3.8 days (N = 17 females) by Valerio et al. (1969, p. 286) and as  $4 \pm 1.05$  days (SD; N = 1,262 cycles) by Srinath (1980, p. 20; cf. Madhwa Raj et al., 1975, p. 395). During the peak mating season, females in natural populations of *M. radiata* probably are in estrus for four or five days during each cycle (Rahaman & Parthasarathy, 1971, p. 100). In *M. assamensis*, Wehrenberg et al. (1980, p. 523) report that length of the menstrual cycle is  $32 \pm 2$  days (mean  $\pm$  SD; 14 captive females).

Sexual activity begins prior to completion of physical development (Phillips, 1926, p. 267). In natural populations of *M. sinica*, Dittus (1977a, pp. 283, 308) reports that late juvenile females and late juvenile males (age ca. 3.5 years) engage in sexual approaches and consortships with adults; at this age, males begin to emigrate from their natal troops and suffer a concomitant high rate of mortality (Dittus, 1975, p. 136). In natural populations of *M. radiata*, the youngest females and males that were observed to participate in copulations were age ca. 4.5 years (Rahaman & Parthasarathy, 1969b, p. 155; Sugiyama, 1972, pp. 252, 259); Simonds (1974b, p. 91) indicates that both sexes in this species may be capable of copulation at age ca. 3.5 years. In captive *M. radiata*, females engage in copulation as early as age 2.5 to 3.0 years (Silk et al., 1981, p. 1110) and males, as early as age 2 years (Nadler & Rosenblum, 1971, p. 101; Glick, 1980, p. 350). Sperm production in captive *M. radiata* begins about age 3 years (Nadler & Rosenblum, 1971, p. 101). In captive *M. thibetana*, infertile copulations occur as early as age 2 to 3 years (Xiong, 1984, p. 5).

The age at first pregnancy in natural populations of *M. sinica* is estimated by Dittus (1975, p. 129) to be 4.5 to 5.5 years. This probably also is the age at first pregnancy in natural populations of *M. radiata* (Sugiyama, 1972, p. 253; Koyama, 1973, p. 228) and *M. thibetana* (Xiong, 1984, p. 5). In

captivity, *M. radiata* females may become pregnant as early as age 2.8 years, and viable infants have been produced by females as young as age 4 years (Silk et al., 1981, p. 1110).

The mean fertility rate in a natural population of *M. sinica* studied for four years is 0.688 infants/adult female/year (Dittus, 1975, p. 131). In five natural populations of *M. radiata* studied for 1 to 2 years, the corresponding composite mean is 0.794 infants/adult female/year (Kuruvilla, 1980, pp. 978, 979; Fooden, 1981, p. 31); this agrees fairly well with a preliminary report by Kurup (1984b, p. 61), who indicates that the mean fertility rate in an unspecified number of troops of *M. radiata* is 0.73 infants/adult female/year. In captive populations of *M. radiata*, the reported mean fertility rate varies from 0.630 to 0.734 (Valerio et al., 1969, p. 293; Silk et al., 1981, p. 1108).

Adult size in *M. sinica* in natural populations is achieved at age 4.5 to 5.0 years in females and at age 7.0 to 8.0 years in males (Dittus, 1975, p. 129). During growth in this species, females are almost the same size as males until age ca. 5 years when growth in females ceases; males subsequently grow (as subadults) for an additional 2 to 3 years and ultimately achieve an adult weight (5.72 kg) that is about 60% more than adult weight in females (3.59 kg) (Dittus, 1974, ch. 1, p. 36). Adult size in *M. radiata* females and males in natural populations apparently is attained about the same age as in *M. sinica* (Simonds, 1974b, p. 91), and this evidently also is true in captive populations of *M. radiata* (Glick, 1979, p. 271; Rosenblum & Smiley, 1980, p. 250). The same growth pattern probably also applies to *M. thibetana* (Xiong, 1984, p. 2) and, inferentially, to *M. assamensis*.

Menopause in natural populations of *M. sinica* is estimated to occur at age 25 to 30 years (Dittus, 1975, p. 132); fertility apparently is unimpaired until menopause. Postmenopausal females were estimated to constitute about 6% of adult females in this population of *M. sinica*. Postmenopausal females also have been reported in natural populations of *M. thibetana* (Xiong, 1984, p. 7).

In captive groups of *M. radiata*, copulations have been reported in females at age 16.5 years, and a viable infant was born to a female about age 16 years (Jensen et al., 1980, p. 400; Jensen & Blanton, 1981, p. 190). In another captive population of this species, females became pregnant until at least age 16 years, but no female older than age 13 years produced an infant that survived 6 months (Silk et al., 1981, pp. 1110, 1112). An experimen-

tal comparative study of older (age ca. 16.5 years) and younger (age ca. 10 years) mature *M. radiata* females indicates that older females evoke fewer copulations, that their mating behavior is less correlated with estrous cycle phase, and that during estrus their peak plasma estradiol level is diminished (Jensen et al., 1982, p. 451); a 19-year-old *M. radiata* male used in this study apparently had unimpaired virility. A captive female *M. assamensis* that lived to age ca. 28 years conceived until age ca. 18 years; this female produced her last viable infant when she was age ca. 14 years, and she produced two stillbirths at ages ca. 17 years and ca. 18 years (Dathe, 1983, p. 126).

Assuming that a female's first pregnancy occurs about age 5 years and that her last successful pregnancy occurs sometime between age 15 years and age 27 years and assuming a fertility rate of 0.70, an average female that reaches sexual maturity would be expected to produce 8 to 16 infants during her reproductive lifetime. If infant mortality rate is 0.50, 4 to 8 of these offspring may survive to age 1 year.

Longevity records in captivity are 33 to 35 years for *M. sinica* (Hill, 1937, p. 255), ca. 30 years for *M. radiata* (Prater, 1980, p. 36), and ca. 28 years for *M. assamensis* (Dathe, 1983, p. 129). Although aged individuals have been observed in natural populations of all four species in the *sinica* group (Simonds, 1965, p. 180; Dittus, 1975, p. 130; Fooden, 1982a, p. 19; Xiong, 1984, p. 2), estimated average life expectancy at birth is only about 15% of the maximum potential life-span, ca. 4.7 years in natural populations of *M. sinica* (Dittus, 1975, p. 135) and ca. 5.0 years in *M. radiata* (Fooden, 1981, p. 33).

### Geographic and Ecological Relationships with Other Primates

Four levels of geographic and ecological relationships of *sinica* group macaques are discussed in the following paragraphs. These are: (1) allopatry and parapatry between species in the *sinica* group; (2) broad sympatry between *sinica* group macaques and non-*sinica* group macaques; (3) marginal sympatry and parapatry between *sinica* group macaques and non-*sinica* group macaques; (4) sympatry between *sinica* group macaques and gibbons, leaf monkeys, and lorises.

Within the *sinica* group, only *M. assamensis* and *M. thibetana* are in geographic contact (fig. 1). *Macaca sinica* in Sri Lanka is separated from *M.*

*radiata* in peninsular India by the Palk Strait, and *M. radiata* is separated from *M. assamensis* in the Himalayan foothills by a 1,200-km gap in central India. *Macaca assamensis* and *M. thibetana*, by contrast, are parapatric in southeastern China. The latitudinal relationship between the ranges of *M. assamensis* and *M. thibetana* suggests that these two species probably are differentially adapted to warmer and cooler climates, respectively. No information is available concerning ecological or behavioral relationships between *M. assamensis* and *M. thibetana* in the interspecific contact zone.

Although three *sinica* group species—*M. radiata*, *M. assamensis*, and *M. thibetana*—are broadly sympatric with macaques in other species groups, the *sinica* group macaques and sympatric non-*sinica* group macaques are segregated ecologically (Fooden, 1982b, p. 574). In peninsular India, where *M. radiata* is sympatric with *M. silenus*, *M. radiata* typically inhabits deciduous forests or disturbed habitats, whereas *M. silenus* is restricted to upland broadleaf evergreen rainforest (Fooden, 1981, p. 18); these two species sometimes meet in transitional habitat areas (Groombridge, 1984, p. 146), but the pattern of interspecific interaction in such meetings remains unclear. In the Indochinese Peninsula, *M. assamensis* is sympatric with both *M. mulatta* (see Dào, 1978, p. 382) and *M. arctoides*; *M. assamensis*, however, inhabits broadleaf evergreen forest and is mainly arboreal and, therefore, is segregated by habitat from *M. mulatta*, which inhabits secondary and deciduous forests, and by ecological niche from *M. arctoides*, which inhabits broadleaf evergreen forest but is mainly terrestrial (Fooden, 1982a, p. 21). *Macaca thibetana* is sympatric with *M. mulatta* in east-central China, where *M. thibetana* apparently inhabits broadleaf evergreen forest, and *M. mulatta* inhabits secondary and disturbed habitats (Fooden, 1983, p. 14; Fooden et al., 1985, p. 24).

*Macaca radiata*, *M. assamensis*, and *M. thibetana* are marginally sympatric or parapatric with other non-*sinica* group species of macaques. In peninsular India, *M. radiata* is marginally sympatric with the ecologically similar species *M. mulatta* along the 1,000-km border between their ranges (Fooden et al., 1981, p. 465; Saha, 1984, p. 163). At the southeastern end of this border area, a small population of *M. radiata* is isolated ca. 150 km within the range of *M. mulatta*. At a few localities where *M. radiata* and *M. mulatta* have been observed in contact, there is no overt aggression between these species, and, in fact, harmonious mixed-species troops have been recorded



FIG. 2. *Macaca radiata* young adult male (right, long tail) following *M. mulatta* adult female (left, short tail), with another *M. mulatta* individual sitting nearby; these monkeys are part of a mixed-species troop (1 to 3 *M. radiata* members, ca. 25 *M. mulatta* members) that was observed at Kondra Mutla (16°08'N, 79°46'E), Andhra Pradesh, India, 30 April 1980 (Fooden et al., 1981, p. 465).

(fig. 2). In the Indochinese Peninsula, *M. assamensis* is parapatric or marginally sympatric with *M. nemestrina* and *M. fascicularis* (Fooden, 1982a, p. 23); *M. nemestrina*, like *M. assamensis*, inhabits broadleaf evergreen rainforest, whereas *M. fascicularis* inhabits secondary, deciduous, and disturbed habitats. The latitudinal replacement of *M. radiata* by *M. mulatta* in the Indian Peninsula and the corresponding replacement of *M. assamensis* by *M. nemestrina* at approximately the same latitude in the Indochinese Peninsula suggest parallel climatic differentiation in these otherwise ecologically similar pairs of species. The relationship between *M. assamensis pelops* and *M. mulatta* in the central and eastern Himalayan foothills also seems to be one of marginal sympatry or parapatry (Fooden, 1982a, p. 24); this probably is a consequence of the relatively sharp altitudinal zonation in this area of midaltitude broadleaf evergreen forest, which is the habitat of *M. assamensis*, and

lower altitude deciduous forest, which is the habitat of *M. mulatta*.

Other genera of primates with which *sinica* group species are sympatric are *Hylobates* (gibbons), *Presbytis* and *Pygathrix* (leaf monkeys), and *Loris* and *Nycticebus* (lorises); the taxonomy used here for nonmacaque genera and species follows Honacki et al. (1982, p. 238). *Macaca assamensis* is sympatric with *Hylobates* spp. in the Indochinese Peninsula, where *M. assamensis* and gibbons inhabit the same broadleaf evergreen forests and have similar, mainly frugivorous diets (Fooden, 1982a, p. 21). *Macaca assamensis* and sympatric gibbons differ, however, in their techniques and efficiency of harvesting arboreal fruit.

Dietary differences separate *sinica* group species, which are primarily frugivorous, from sympatric leaf monkeys (*Presbytis* spp. and *Pygathrix* spp.). In Sri Lanka and peninsular India, *M. sinica* and *M. radiata* are sympatric with *Presbytis* spp.

(Fooden, 1979, p. 123; 1981, p. 19; Herzog & Hohmann, 1984, p. 195). *Macaca radiata* and *Presbytis entellus* are often closely associated, sometimes in mixed-species bands. In interspecific encounters, *M. radiata* generally appears to be dominant to *P. entellus*. In southern peninsular India, south of ca. 15°N, *M. radiata* apparently is more widely distributed in disturbed areas than is *P. entellus*, which tends to be restricted to forested tracts in this region (Kurup, 1984a, p. 253); farther north, however, in northern Karnataka and central Maharashtra, *P. entellus* is widely distributed in disturbed areas (Fooden et al., 1981, p. 465; Kurup, 1984a, p. 253; cf. Prasad et al., 1979, p. 726). In the Indochinese Peninsula, *M. assamensis assamensis* is sympatric with other species of *Presbytis*, sometimes occurring together in the same tree (Fooden, 1982a, p. 21). Sub-Himalayan *M. assamensis pelops* is sympatric with *P. entellus* in the western part of its range (west of the Tista River and Ch'u-mu-pi Shan-ku) and with *P. geei* and *P. pileata* in the eastern part (east of the San-kosh River) (see Fooden, 1975, p. 109).

In China and northern Vietnam, *M. assamensis* and *M. thibetana* evidently are partly sympatric with *Pygathrix* spp. (subgenus *Rhinopithecus*). In southwestern China, *Pygathrix roxellanae* (including subspecies *roxellanae* and *bieti*) probably inhabits higher elevations than *M. assamensis* and *M. thibetana* (Li et al., 1981, p. 9; Fooden, 1983, p. 13). In northern Guizhou, *P. brelichi* apparently occurs within the range of *M. thibetana*, and, in northern Vietnam, *P. avunculus* apparently occurs within the range of *M. assamensis*, but little is known of the natural history of these latter two species of *Pygathrix* (Groves, 1970, p. 569; Quan & Xie, 1981, p. 113; Happel, 1982, p. 292).

In Sri Lanka and peninsular India, *M. sinica* and *M. radiata* are sympatric with *Loris tardigradus* (Pocock, 1939, pp. 38, 177; Fooden, 1979, p. 123), and, in the Indochinese Peninsula, *M. assamensis* is sympatric with *Nycticebus* spp. (Fooden, 1982a, p. 21). Because both genera of lorises are nocturnal and mainly insectivorous, there probably is little direct ecological interaction between sympatric macaques and lorises.

## Summary

1. In the ranges of *M. sinica* and *M. radiata*, climate varies from tropical wet to tropical arid; in the range of *M. assamensis*, climate is subtrop-

ical moist; and in the range of *M. thibetana*, climate is subtropical moist to moderate continental moist.

2. *Macaca sinica* inhabits deciduous forests and broadleaf evergreen forests, *M. radiata* prefers deciduous forests and disturbed habitats, and *M. assamensis* and *M. thibetana* are mainly restricted to broadleaf evergreen forests.

3. *Macaca sinica*, *M. radiata*, and *M. assamensis* are predominantly arboreal, whereas *M. thibetana* apparently is predominantly terrestrial.

4. All four species are mainly vegetarian, consuming various parts of a wide variety of plants, but they also all eat invertebrates and small vertebrates. The diet of *M. thibetana* may include a greater proportion of leaves than that of the other three species.

5. Nonhuman predators of these monkeys include large reptiles, raptorial birds, and carnivorous mammals. Known parasites include viruses, bacteria, fungi, protozoa, trematodes, cestodes, nematodes, and arthropods.

6. At some localities, the two northern species, *M. assamensis* and *M. thibetana*, migrate seasonally between higher altitudes in summer and lower altitudes in winter.

7. Troop size in forest populations of all four species generally averages about 20 to 25 individuals and varies from about 7 to 70 individuals, but troops provisioned by humans may be larger. Solitary males are known only in *M. thibetana*.

8. The weighted mean ratio of sexually mature males to sexually mature females is 0.72 in troops of *M. sinica*, *M. radiata*, and *M. assamensis*; males may outnumber females in troops of *M. thibetana*.

9. Troop home range area in *M. sinica* and *M. radiata* varies from 17 to >200 hectares.

10. Males in *M. sinica* and *M. radiata* are known to emigrate from their natal troop before their first reproductive season.

11. Matings and births exhibit well-defined annual peaks in all four species; breeding seasonality sometimes disappears in captive populations.

12. In all four species, extruded cervical mucus probably serves as an important signal of estrus, and all four species probably are single-mount ejaculators. Species in this group apparently differ in intensity of overt male competition for mates and in precopulatory behavior of estrous females.

13. Available life history information indicates that gestation period and birth weight are greater in male infants than in female infants; sex ratio at birth is near unity in natural populations, but is highly variable in captive populations; infant mor-

tality during the first year of life is about 50%; weaning occurs at about age 6 months; males and females in natural populations begin mating at about age 3.5 to 4.5 years; the age of first pregnancy in females in natural populations is about 4.5 to 5.5 years; mean fertility rate is about 0.70 infants/adult female/year; physical growth ceases at about age 4.5 to 5.0 years in females and at about age 7.0 to 8.0 years in males; maximum longevity in captivity averages about 30 years.

14. Species in this group are segregated from each other geographically, and they are segregated from macaques in other species groups ecologically or geographically.

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## Appendix

### *Macaca assamensis* Locality Record Supplement

In addition to localities shown in previously published distribution maps (Fooden, 1982a, pp. 4, 5), Figure 1 includes the following supplementary records of *M. assamensis*. All coordinates are approximate.

**NEPAL:** Bhargu vicinity, 28°08'N, 85°18'E; Manigaon-Ramche, 28°02'N, 85°13'E (Green, 1981, p. 80).

**BANGLADESH:** Sylhet Forest, N, 25°10'N, 92°00'E; Sylhet Forest, SE, 24°35'N, 92°10'E; Chittagong Hill Tracts Forest Division, N, 23°35'N, 92°15'E (Khan, 1981, pp. 13, 14).

**CHINA:** Xizang, Nyalam vicinity, 28°12'N,

85°58'E (IZAS; Feng Zuojian, 1983, personal communication). **Yunnan**, Santun/Shuanglawu/Qiqing, 27°45'N, 98°35'E (KIZ); Gongshan vicinity, 27°41'N, 98°37'E (IZAS); Bijiang Xian, NE, 26°40'N, 99°05'E (KIZ); Bilushui Shan, 26°35'N, 99°05'E (KIZ); Yao Jia Ping, 26°00'N, 98°50'E (KIZ); Xima Nabang, 24°45'N, 97°45'E (KIZ); Yingjiang, 24°45'N, 98°00'E (IZAS); Xiaoheshan, 24°30'N, 98°35'E (KIZ); Zhung Shan 24°30'N, 98°40'E (IZAS); Jingdong Xian, 24°25'N, 100°50'E (KIZ); Linchang Xian, 23°50'N, 100°05'E (KIZ); Dahongshan, 23°00'N, 102°20'E (KIZ); Dawei Shan, 22°55'N, 103°40'E (KIZ); Menglun, 21°55'N, 101°15'E (KIZ); Menghan, 21°50'N, 100°55'E (KIZ); Xiangming, 21°45'N, 101°25'E (KIZ); Manpa (IZAS)/Mengla Xian (KIZ), 21°30'N, 101°35'E. **Guangxi**, Tian'e, 25°00'N, 107°10'E; Huanjiang, 24°50'N, 108°15'E; Napo, 23°23'N, 105°48'E; Debao, 23°20'N, 106°37'E; Jiangxi, 23°08'N, 106°25'E (Wu, 1983, p. 16).

**VIETNAM:** Luc-yên, 22°05'N, 104°43'E (Dào, 1967, p. 117); Chieng ve, 20°46'N, 104°34'E (Dào, 1978, p. 382).





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