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TAXONOMY AND EVOLUTION
OF THE *SINICA* GROUP OF MACAQUES:
2. SPECIES AND SUBSPECIES ACCOUNTS
OF THE INDIAN BONNET MACAQUE, *MACACA RADIATA*

JACK FOODEN

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ABSTRACT

The present species account of *Macaca radiata* (E. Geoffroy, 1812), the Indian bonnet macaque, is based on study of all known museum specimens (128) and on review of relevant literature. The northern limit of distribution of this species is not the Godavari River, as generally assumed, but instead is 100–250 km south of the Godavari River for most of this river's length. External and cranial characters of *M. radiata* are analyzed, with particular emphasis on geographic, ontogenetic, and seasonal variation of pelage color and on allometry of craniofacial proportions. An extensive review of the natural history of this species focuses on habitats, predators, diet, relations with other primate species, troop size and composition, home range area, intertroop behavior patterns, breeding behavior and seasonality, life-table survivorship probabilities, and mortality factors. Two subspecies are recognized: *M. r. radiata*, which is widely distributed, and *M. r. diluta* Pocock, 1931, which is restricted to a relatively narrow southeastern coastal zone. For each subspecies, basic information is provided on synonyms, types, type-locality, distribution, and diagnostic external characters. A gazetteer of *M. radiata* localities includes information on available museum specimens and on published field notes by collectors or observers.

INTRODUCTION

This account of *Macaca radiata*, the South Indian bonnet macaque, is the second part of a planned comprehensive monographic revision of the four species that constitute the *sinica* group of macaques (*M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*). The first part of this monograph, an account of *M. sinica*, was published elsewhere (Fooden, 1979, pp. 109–140). For the present work, 128 museum specimens of *M. radiata* were examined; about half of these were wild-collected, and the other half were captives (see list of specimens examined). Specimens examined are preserved in the following institutions, which are subsequently cited by means of the indicated abbreviations:

AIUZ	Anthropologisches Institut der Universität Zürich
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BM	British Museum (Natural History), London
BNHS	Bombay Natural History Society, Bombay
FMNH	Field Museum of Natural History, Chicago
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMB	Naturhistorisches Museum, Basel
NHRM	Naturhistoriska Riksmuseet, Stockholm

RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
USNM	U.S. National Museum of Natural History, Washington, D.C.
ZMUZ	Zoologisches Museum der Universität, Zürich
ZSBS	Zoologische Sammlung des Bayerischen Staates, Munich
ZSI	Zoological Survey of India, National Zoological Collection, Calcutta

SPECIES AND SUBSPECIES ACCOUNTS

Macaca radiata (E. Geoffroy, 1812). Synonymies under subspecies headings.

Distribution (fig. 1; Fooden et al., 1981, fig. 1).—Peninsular India from Cape Comorin (8°13'N, 77°34'E) northward to the northern end of the Western Ghats (20°47'N, 73°55'E), the Manjra Plateau (18°17'N, 75°57'E) and the northern end of the Velikonda Range, Eastern Ghats (15°35'N, 79°08'E), with an isolated outlier population in the Vijayawada Hills (16°32'–16°45'N, 80°33'–80°38'E). This demarcation of the northern limit of distribution of *M. radiata*, which also approximately coincides with the southern limit of distribution of *M. mulatta*, is based on results of a recent survey (Fooden et al., 1981, fig. 1) undertaken after the present work had been submitted and accepted for publication. The boundary between *M. radiata* and *M. mulatta* that is specified here is 100–250 km south of the Godavari River, which, following Blyth (1863, p. 9) and Blandford (1889, p. 23), routinely has been cited as the interspecific boundary (Pocock, 1939, p. 38; Prater, 1971, p. 35; Hill, 1974, p. 705; Roonwal & Mohnot, 1977, p. 192). Evidence that the Godavari is not the interspecific boundary previously was provided by Rae (in Southwick et al., 1961, p. 538), Spillett (1968a, p. 8), and Krishnan (1972, p. 540).

E. Geoffroy (1812, p. 98) originally gave the range of this species merely as "l'Inde." The first reasonably precise locality record was provided by F. Cuvier (1820, p. 1), who reported on specimens collected along the Malabar Coast by M. Housard, a French naval officer. Jerdon (1867, p. 12) evidently was the first zoologist specifically to note the allopatric relationship between *M. radiata* and *M. mulatta*.

Macaca radiata was successfully introduced in the Mascarene Islands, east of Madagascar, apparently by sixteenth-century Portuguese mariners (Leguat, [1708] 1891, p. 204; LaCaille, 1763, pp. 216, 230; Newton, 1893, p. 217; de Sornay, 1949, p. 65). During the nineteenth century, museum specimens were collected both in Mauritius (I. Geoffroy, 1851, p. 26) and Réunion (Schlegel, 1876, p. 99), which are the two largest islands in the Mascarene group. Another species of long-tailed macaque, *M. fascicularis*, also was introduced by Europeans in the Mascarene Islands (I. Geoffroy, 1851, p. 29); published reports of monkeys in these islands (all originally introduced) usually are not sufficiently precise to permit unambiguous species determination (cf. Pridham, 1849, p. 226).

An early report of *M. radiata* in "Formosa" (Taiwan) evidently is based on an introduced or captive specimen (ZSI 11826; Blyth, 1860, p. 88; 1863, p. 8; 1875, p. 8). An erroneous report of this species in Nepal (Hodgson, 1834, p. 96) is based on misidentified *M. mulatta* (cf. Hodgson, 1832, p. 339).

External characters (figs. 2, 3, 7; table 1).—Head and body length 455 ± 31 mm in 11 adult females, 527 ± 38 mm in 12 adult males; relative tail length (T/HB) $1.10 \pm .13$ in 10 adult females, $1.07 \pm .09$ in 12 adult males; weight $3.85 \pm .50$ kg in 14 adult females, $6.67 \pm .85$ kg in 13 adult males. Dorsal pelage color

TABLE 1. External measurements and ratios in adult *Macaca radiata*.

Locality No. ¹	Head and body length (mm)	Relative tail length (T/HB)	Relative ear length (E/HB × 100)	Weight (kg)
Adult females, <i>M. r. radiata</i>				
10	480, 515 ²	1.16, 1.10	7.7, 7.4	...
15	470, 470	1.02, 1.05	8.1, 7.7	3.63, 3.63
33	455	0.95	7.7	3.86
38	4.99 ²
45	450	1.13	8.2	...
59	400	0.88	9.3	...
62	445	1.18	7.9	...
71	470	1.16	8.1	...
? ³	375, 430	...	?10.0, 8.4	4.16, 4.16
? ⁴	2.93 - 4.42 (N = 8) ⁵
$\bar{X} \pm S.D. (N)$	458 ± 31 (10)	1.07 ± .10 (9)	8.0 ± .5 (9)	3.85 ± .50 (14)
Adult females, <i>M. r. diluta</i>				
87	?328, 420	?1.60, 1.36	?15.2, 10.7	...
Adult males, <i>M. r. radiata</i>				
7	507 ²	1.26	7.9	7.26
10	570, 570	0.96, 1.09	7.5, 7.9	...
12	590	1.14	8.1	8.85
15	530	1.06	7.7	6.58
26	520	1.08	7.7	5.44
33	495, 508, 530	0.98, 1.13, 0.94	7.7, 7.5, 7.4	..., ..., 5.90
59	450	1.06	8.9	...
63	510	1.10	6.9	...
? ⁴	5.67-7.00 (N = 8) ⁶
$\bar{X} \pm S.D. (N)$	525 ± 40 (11)	1.07 ± .09 (11)	7.7 ± .5 (11)	6.67 ± .85 (13)
Adult male, <i>M. r. diluta</i>				
82	545 ²	1.00	7.3	...

¹For key to locality numbers, see distribution map (fig. 1).

²Skin only; adult status inferred from external measurements.

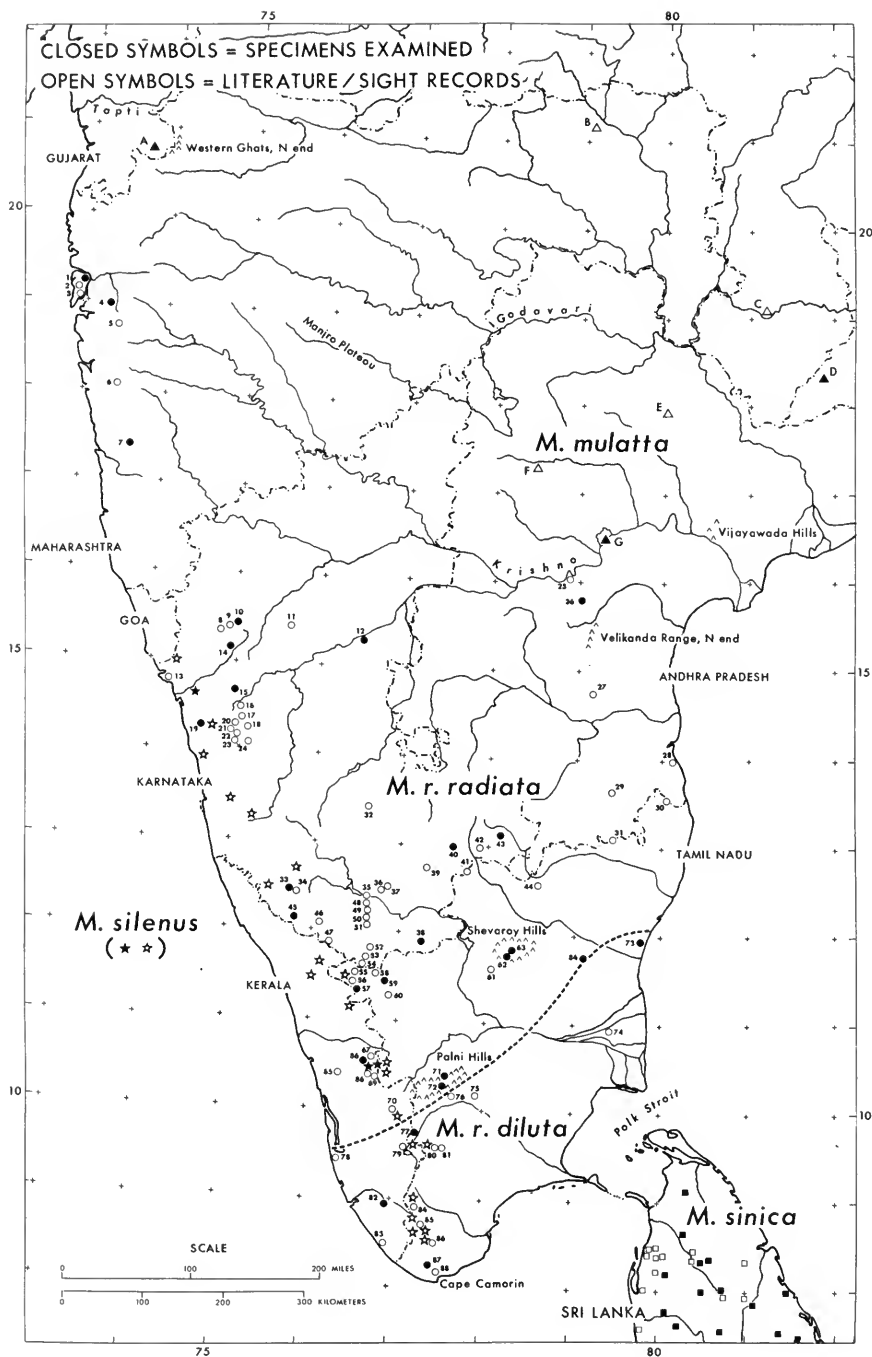
³External measurements from Hill, 1974, p. 708.

⁴Weights from Hartman, 1938, p. 468.

⁵ $\bar{X} = 3.69$, S.D. = 0.45.

⁶ $\bar{X} = 6.60$, S.D. = 0.44.

subspecifically and seasonally variable (see next section), prime pelage drab grayish brown to golden brown, becoming drabber and variably streaked with blackish on the lower back, hair banding variably conspicuous; outer surface of thighs same color as back or drabber, outer surface of arms and shanks somewhat paler, ochraceous gray to pale grayish brown; tail bicolor, dark brown to blackish dorsally (slightly paler distally), pale grayish brown to ochraceous ventrally; pelage of ventral surface of trunk and limbs pale ochraceous buff to whitish, skin of chest and belly pigmented dark bluish gray or mostly unpigmented whitish; crown hairs colored approximately like back (sometimes with blackish tips), radiating from a central whorl to form a conspicuous cap (fig. 2), with posterior crown hairs longer (extending to occiput) than anterior crown hairs (extending to midway between vertex and brow ridges); anterior crown area (between anterior cap hairs and brow ridges) covered with short hairs that diverge laterally to form a median part; facial skin, including that of ears and lips, pinkish buff to tan, occasionally scarlet in females (Anderson, 1879, p. 90; Simonds, 1965, p. 175).



Head and body length in adult males averages about 15% greater than in adult females, and weight in adult males averages about 75% greater than in adult females. Conversely, relative tail length and relative ear length in adult males average about 4%–7% smaller than in adult females.

Geographically, there seems to be a tendency for head and body length to increase from south to north in *M. radiata* (table 1); this tendency is more apparent in female specimens than in male specimens examined. Although external dimensions in *M. radiata* overlap those in Sri Lanka *M. sinica* (Fooden, 1979, table 1), there is a consistent pattern of mean differences between these two species. Head and body length averages about 10%–13% greater in *M. radiata* than in *M. sinica*, weight averages about 9%–26% greater in *M. radiata*, relative tail length

Opposite:

FIG. 1. Locality records of *Macaca radiata* (circles) and neighboring species of macaques (*M. mulatta*, triangles; *M. silenus*, stars; *M. sinica*, squares). Closed symbols indicate specimens examined, open symbols indicate literature or sight records; heavy dashed line indicates inferred border between subspecific ranges of *M. r. radiata* and *M. r. diluta*. For details and references, see Gazetteer. New marginal locality records of *M. radiata* and *M. mulatta* recently have been reported by Fooden et al. (1981, fig. 1).

Macaca r. radiata localities are as follows: 1, Yeur. 2, Salsette Island. 3, Trombay Hills. 4, Matheran. 5, Khandala. 6, Konkan. 7, Ghatmatha. 8, Dharwar, 18.4–29.5 km SW. 9, Dharwar, 4.4–17.5 km SW. 10, Dharwar, 2,300 ft. 11, Gadag. 12, Vijayanagar. 13, Karwar. 14, Devikop. 15, Samasgi. 16, Sorab-Banavasi. 17, Halgalali; Kummuru; Nadhalli; Sorab; Sorab-Shiralkoppa. 18, Karchikoppa; Malalagadde; Shigga. 19, Gersoppa. 20, Avalgodu; Dodder; Haravadike; Hosabale; Kuppe; Kuruvuri; Kyasanur Forest; Nishrani; Tavanandi. 21, Keladi. 22, Marasa. 23, Yalgalali. 24, Sagar-Shimoga. 25, Srisailam. 26, "Malakondapenta." 27, Eastern Ghats. 28, Coromandel Coast. 29, Tirupati. 30, Tada. 31, Sholinghur. 32, Chiknayakanhalli. 33, Haleri. 34, Mysore-Mangalore. 35, Ranganathitoo Sanctuary. 36, Mysore-Bangalore, milestone 28, 30, 32. 37, Mysore-Bangalore, milestone 34, 36. 38, Biligiri Rangan Hills. 39, Mysore-Bangalore, milestone 83.40, Bangalore. 41, Bangalore-Krishnagiri. 42, Malur. 43, Kolar. 44, Jalarpet. 45, Wotekolli. 46, Nagarhole Wildlife Sanctuary. 47, Byrankuppe. 48, Mysore; Ootacamund-Mysore, milestone 117; Ootacamund-Mysore, milestone 121. 49, Ootacamund-Mysore, milestone 114. 50, Ootacamund-Mysore, milestone 107, 108. 51, Ootacamund-Mysore, milestone 92. 52, Gundlupet-Chamrajnagar, milestone 1, 2. 53, Hangala; Somanathapur. 54, Bandipur; Bandipur, 1 mile NE; Bandipur, 1 mile W; Bandipur Wildlife Sanctuary; Kakkenahala; Mangata. 55, Gudalur-Theppakadu; Manali Theppakadu; Mudumalai Wildlife Sanctuary; Padamara; Theppakadu-Kargudi; Veduru Guta. 56, Nilgiri Hills, 5,000–8,600 ft, 7,000 ft; Nilgiri Hills, N; Nilgiri Hills, W. 57, Nilgiri Hills. 58, Sigur Range. 59, Kotagiri; Nilgiri Hills, N and E. 60, Coonoor-Mettupalaiyam, milestone 12; Coonoor-Mettupalaiyam, milestone 17. 61, Siddharkovil. 62, Kurumbapatti. 63, Shevaroy Hills. 64, "Tenmali." 65, Mattathur. 66, Sharnelli Estate. 67, Nelliampathy Hills, N. 68, Nelliampathy Hills, S. 69, Anaimalai Hills. 70, Panniar. 71, Palni Hills, N. 72, Machchur; Palni Hills, 5,500 ft.

Macaca r. diluta localities are as follows: 73, Pondicherry. 74, Kumbakonam. 75, Kodaikanal Road. 76, Kodaikanal Road, milestone 23. 77, Kambam. 78, Alleppey. S. 79, Periyar Lake, N; Periyar Wildlife Sanctuary. 80, Varushnaad Valley. 81, Srivilliputtur-Mudaliar Ootu. 82, Travancore. 83, Trivandrum. 84, Kuttalam. 85, Papanasam. 86, Naraikkadu Estate. 87, Bhutapandi. 88, Aramboli, 5 miles S.

Macaca mulatta localities are as follows: A, Dangs (BM 31.1.11.1–3). B, Nagpur vicinity (Jerdon, 1867, p. 11). C, Orcha (Jay, 1965a, pp. 210, 212). D, Malkangiri (BM 28.3.7.3). E, Pakhal Lake Wildlife Sanctuary (Spillett, 1968a, p. 8). F, Hyderabad vicinity (Rae in Southwick et al., 1961, p. 538). G, Nagarjunakonda Valley, "Siddeldar Hill" (ZSI, uncatalogued); previously, this record was considered anomalous and therefore was thought to be the result of human introduction (Agrawal & Bhattacharyya, 1976, p. 214), but the locality is now known to be within the natural range of *M. mulatta* (Fooden et al., 1981, fig. 1).

Macaca silenus localities are shown here as in Fooden (1975, pp. 79, 168) and Green & Minkowski (1977, p. 305); *M. sinica* localities are shown as in Fooden (1979, p. 131).



FIG. 2. Crown pelage in Indian bonnet macaque, *Macaca radiata* (left, FMNH 82803 ♀, Samasgi), compared with that in Sri Lanka toque macaque, *M. sinica* (right, FMNH 98262 ♂, Maturata). Arrow indicates forehead area left exposed by short anterior cap hairs in *M. radiata*. (Photos by Ron Testa, Division of Photography, FMNH.)

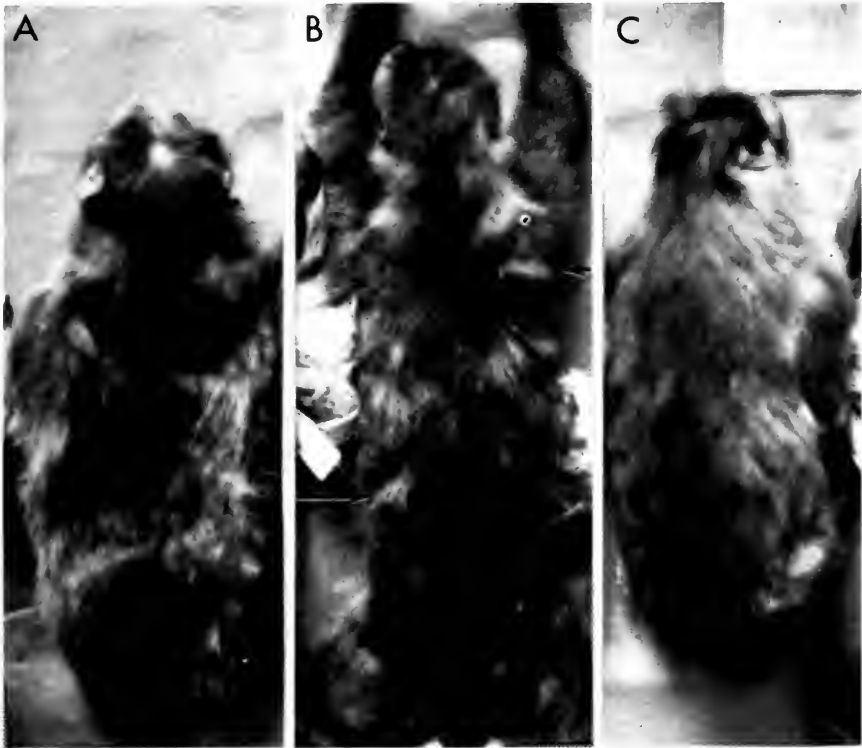


FIG. 3. Seasonal fading and molting of pelage in *Macaca radiata radiata*: A, late dry season, strongly faded specimen with large irregular pale buffy lateral blotches (BNHS 5047 ♀ or 5049 ♀, Samasgi, Loc. No. 15, 12 March 1912); B, early rainy season, newly molted specimen with small scattered tufts of unshed pale fur, two tufts of which are indicated by arrows (BNHS 5052 ♀, Sharnelli Estate, Loc. No. 66, 28 May 1921); C, late rainy season, specimen in prime pelage (BNHS 5048 ♀, Devikop, Loc. No. 14, 21 Nov. 1911).

averages about 13%–14% less in *M. radiata*, and relative ear length in males averages about 16% less in *M. radiata*. All of these mean differences are in accord with Bergmann's and Allen's rules, as noted previously (Fooden, 1971, p. 72).

Pelage color variation: geographic, ontogenetic, seasonal.—Pelage color in *M. radiata* varies geographically (subspecifically), ontogenetically, and seasonally. In *M. r. radiata*, which is the more broadly distributed of the two recognized subspecies, the dorsal fur in adult specimens in prime pelage is drab grayish-brown ("brun-verdâtre," E. Geoffroy, 1812, p. 98) with relatively inconspicuous hair banding, and the ventral fur is pale buffy to whitish; crown hairs in this subspecies frequently are tipped with blackish, the upper back is variably washed with pale yellowish, and the lower back is marked with a variably defined dark brown to blackish median streak. In *M. r. diluta*, which is restricted to a narrow south-eastern coastal zone (fig. 1), the dorsal fur is more brightly colored, pale yellowish brown to golden brown, with hairs conspicuously banded dark brown basally and bright yellowish distally, and the ventral fur is whitish; cap hairs in this subspecies lack blackish tips, and the lower back, although slightly drabber than

the upper back, lacks the blackish median streak that is variably developed in *M. r. radiata*.

Within the range of each of the two recognized subspecies, dorsal pelage color is relatively constant, with little or no tendency toward geographic intergradation between subspecies. For example, a fairly dark grayish brown male specimen of *M. r. radiata* (BM 30.11.1.29) collected at Gathmatha, near the northwestern limit of the subspecific range, closely matches three males (BM 30.11.1.18–20) collected at Haleri (600 km SSE of Gathmatha) and also matches another male (BM 30.11.1.25) collected at Vijayanagar (375 km SE of Gathmatha). A second, slightly paler male (BM 30.11.1.24) collected at Vijayanagar matches a male (BM 21.11.5.2) collected at Sharnelli Estate (525 km S of Vijayanagar) and also matches a female (BM 30.11.1.30) collected at Palni Hills (600 km SSE of Vijayanagar), both localities near the southern limit of distribution of *M. r. radiata*. Similarly, three seasonally faded (see below) specimens of *M. r. radiata* collected at Marlakonda (BM 30.11.1.26–27 ♂♂, BM 51.608 ♀), near the northeastern limit of the subspecific range, match a faded female specimen (BM 30.5.24.2) collected at Kurumbapati (450 km S of Marlakonda), at the southeastern limit of the range. Comparable networks of matching specimens interconnect other collecting localities within the range of *M. r. radiata*.

Five *M. r. diluta* skins collected at four localities (Travancore, ZSI 8495; Bhutapandi, BM 30.11.1.31, BM 1937.5.26.1; Kambam, BM 30.11.1.28; Pondicherry, RMNH 6f) in extreme southeastern peninsular India are readily distinguishable by their bright color and conspicuous hair banding from all *M. r. radiata* specimens examined. The abrupt geographic transition from *M. r. radiata* coloration to *M. r. diluta* coloration is indicated by the striking difference between a juvenile male (BM 21.11.5.2) of the former subspecies collected at Sharnelli Estate and a juvenile female (BM 30.11.1.28) of the latter subspecies collected at Kambam, which is only about 120 km southeast of Sharnelli Estate. The Sharnelli specimen shares the general drabness of other *M. r. radiata* specimens and, as previously indicated, perfectly matches a specimen (BM 30.11.1.25) of *M. r. radiata* collected at Vijayanagar, which is 525 km north of Sharnelli; the brightly colored Kambam *M. r. diluta* specimen closely matches all four other specimens available of this subspecies. The only specimen examined that shows some evidence of pelage coloration intermediate between that of *M. r. radiata* and *M. r. diluta* is a subadult male (ZSI 12007) collected in South Arcot (probably at "Tenmali"), near the border between the subspecific ranges; the pale yellowish brown South Arcot specimen, which is now somewhat arbitrarily assigned to *M. r. radiata*, tends toward the brightness of *M. r. diluta*, but lacks the conspicuous hair banding characteristic of this latter subspecies.

In addition to differing from each other in dorsal pelage color, *M. r. radiata* and *M. r. diluta* also differ in pigmentation of the ventral skin (not hair), as noted by Pocock (1931b, p. 278). In *M. r. radiata*, the skin of the chest and belly is broadly and deeply pigmented dark bluish gray. By contrast, in four *M. r. diluta* specimens examined (Bhutapandi, BM, 2; Kambam, BM, 1; Travancore, ZSI, 1), the skin of this region is unpigmented whitish with, at most, only small irregularly dispersed blotches of pale bluish pigment; ventral skin pigmentation was not examined in one *M. r. diluta* specimen (Pondicherry, RMNH). Predictably, the geographically intermediate South Arcot specimen (ZSI), which is somewhat intermediate in dorsal pelage color between typical *M. r. radiata* and *M. r. diluta* (see above), also is approximately intermediate in extent and intensity of ventral

skin pigmentation. (I thank Mr. P. K. Das, Zoological Survey of India, Calcutta, for reexamining ventral skin pigmentation in two critical *M. radiata* specimens in the ZSI collection.)

The evolutionary factors responsible for differentiation of *M. r. radiata* and *M. r. diluta* are unclear. Although there is no apparent physiographic barrier between the ranges of these two subspecies, these areas do differ in timing of the annual monsoonal rainy season (fig. 6). In the range of *M. r. radiata*, the months of maximum rainfall are June or July, and the dry season begins in October or November; in the range of *M. r. diluta*, as a result of frontal convergence between the northeast monsoon and the retreating Indian Ocean westerlies (Kendrew, 1953, p. 181), the months of maximum rainfall are October or November, and the dry season begins in January. The adaptive significance, if any, of the relationship between local rainfall patterns and subspecific differentiation in *M. radiata* is not known.

The bright color of the upper back in *M. r. diluta* is similar to the color of the same region in the toque macaque (*M. sinica*), which inhabits Sri Lanka across the Palk Strait from the coastal range of *M. r. diluta*; however, *M. sinica* is readily distinguishable from both subspecies of *M. radiata* by the long anterior crown hairs (fig. 2) and the rufous to tawny color of the outer surface of the thighs in the former species (Fooden, 1979, p. 110). Considered interspecifically, pelage color in subspecies of *M. radiata* and *M. sinica* follows a step cline of increasing brightness with decreasing latitude. In *M. r. radiata*, which is the most northerly subspecies in these two species, the entire dorsal surface is drab, and the cap and lower back are variably washed with blackish; in *M. r. diluta*, which ranges to the southeast of *M. r. radiata*, the upper back is brightly colored, and the cap and lower back lack the blackish wash that is frequently present in *M. radiata*; in *M. s. sinica*, which ranges farther to the southeast in Sri Lanka across the Palk Strait, the upper back, lower back, and outer surface of thighs are all brightly colored; finally, in *M. s. aurifrons*, which is restricted to southwestern Sri Lanka, the cap is marked anteriorly by a patch of bright yellow to golden, and there is a strong tendency to general erythrism (Fooden, 1979, p. 114). Although this unusual clinal pattern that encompasses four subspecies in two species attests to the close relationship between *M. radiata* and *M. sinica*, its evolutionary significance is otherwise obscure.

Neonatal pelage in *M. radiata* is dark (dark brown to near blackish), short, fine, and sparse (Nolte, 1955, p. 83; Simonds, 1965, p. 181; 1974a, p. 155; Rahaman & Parthasarathy, 1969b, p. 150; Krishnan, 1972, p. 545; Hill, 1974, p. 706). At age approximately one month, this dark neonatal pelage is rapidly replaced by a second-stage infantile pelage that is similar in color and pattern to adult pelage but is finer in texture (cf. BM 30.11.1.11, deciduous i 1; Gersoppa). Finally, at age approximately one year, the second-stage infantile pelage is replaced by a juvenile pelage that is essentially indistinguishable from that in adults (cf. BM 30.11.1.28, deciduous m2, permanent M2 erupting; Kambam). Males and females in *M. radiata* appear not to differ appreciably in pelage color or texture.

Conspicuous seasonal pelage variation (molting), which seems to be relatively rare in macaque species, was first noted in bonnet macaques by Pocock (1931b, p. 276). In *M. r. radiata*, molting evidently occurs in late May or early June (table 2), which coincides with the onset of monsoonal rains over most of the range of this subspecies (fig. 6). Judging from specimens examined, molting is preceded by fading of the dorsal pelage, which is first evident in mid-March (Samasgi,

TABLE 2. Seasonal distribution of prime (P) and faded (F) pelage in *Macaca radiata* specimens examined,¹ showing that faded pelage prevails in *M. r. radiata* during March–June (hot dry season preceding season of monsoonal rains).

Lo- cality No. ²	Pelage condition in month collected ³												
	N	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
<i>M. r. radiata</i>													
7	2												2P
10	4												4P
12	2								2P				
14	1												1P
15	6			1P, ⁴ 5F									
19	1					1P(?) ⁵							
26	3					3F							
33	4	4P											
38	1			1F(?)									
40	2			2F									
43	1									1P			
45	1												1P
59	2												
62	1				1F								
63	3					1P, ⁷ 2F							
66	2					1P ⁸	1P						
72 ⁹	2			2F									
72 ¹⁰	1					1P							
Total	39	4P	...	1P,10F	1F	4P, 5F	2P, 1F	...	2P	1P	...	5P	3P
<i>M. r. diluta</i>													
77	1					1P							
82	1											1P	
87	2											2P	

¹These specimens were examined at different times in various museums; under these circumstances, some variation in standards for judging pelage condition is unavoidable. Despite this, the main pattern of seasonal pelage change seems reasonably clear.

²For key to locality numbers, see distribution map (fig. 1).

³Specimens lacking date of collection are not included in this table.

⁴BM 30.11.1.15, adult male, collected 12 March 1912.

⁵BM 30.11.1.12, subadult female with infant (age approximately three months, infantile pelage), collected 29 May 1912.

⁶BM 19.6.2.1, adult male, collected 25 June 1918.

⁷BNHS 5051, adult male, collected 22 May 1929.

⁸BNHS 5052, subadult female, collected 28 May 1921, newly molted (few scattered tufts of faded hair still present; fig. 3).

⁹Palni Hills, 5,500 ft.

¹⁰Machchur.

5 specimens, 12 March)—the fifth month of the seven-month dry season. In faded specimens, the dorsal pelage appears rough-textured and disheveled and is conspicuously blotched with irregular patches of pale buffy hairs (fig. 3), especially anteriorly and laterally. When the rainy season begins, shedding of the faded pelage and concomitant exposure of the prime new pelage evidently occurs fairly rapidly, as indicated by two specimens collected in May–June 1921 at Sharnelli Estate (southwestern peninsular India). In a subadult female (BNHS 5052) collected at this locality on 28 May, the dorsal pelage, which evidently is in the final phase of molting, is mostly prime grayish brown washed with

yellowish, but a few small tufts of longer faded buffy hairs remain unshed laterally on the upper back (fig. 3); in a juvenile male (BM 21.11.5.2) collected nine days later (6 June) at the same locality, the dorsal pelage is entirely prime grayish brown, lacking any trace of faded hairs. The physiological or ecological significance of dry season fading and rainy season molting in *M. r. radiata* is unknown. Fading or molting is not evident in the few specimens available of *M. r. diluta*.

Pigment reduction or absence has been noted rarely in captive *M. radiata*. An albino male with pink irises was observed in 1936 at the Trivandrum Zoo, South India, by Hill (1937, p. 212). A captive male with white fur and skin, but with brown irises, was observed in 1836 in the London Zoo by Ogilby (1838, p. 312). A pale golden brown subadult female museum specimen (USNM 122171) of unknown history also appears to have abnormally reduced pigmentation.

Cranial characters (fig. 4; tables 3, 4).—Skull moderately small, greatest length 104.4 ± 2.4 mm in 10 wild-collected adult females, 120.0 ± 4.0 mm in 12 wild-collected adult males; relative zygomatic breadth (ZB/GL) moderately great, $0.65 \pm .03$ in 10 adult females, $0.67 \pm .02$ in 12 adult males; rostrum moderately projecting, rostral-postrostral ratio $0.46 \pm .02$ in 10 adult females, $0.54 \pm .02$ in 12 adult males; supramaxillary ridges well defined, arching superioposteriorly from canine alveolus to infraorbital rim; supraorbital ridges moderately thick (ca. 6 mm in adult males); temporal lines weakly to moderately defined, usually separate, rarely converging in old males to form a low (ca. 1 mm), posteriorly restricted sagittal crest (FMNH 82802, Dharwar); nuchal crest moderately developed (1–7 mm high) in adult males.

In adult males (table 3), greatest skull length averages significantly larger in six specimens collected north of 14°N lat. (122.9 ± 3.3 mm; extremes, 117.7–127.9 mm) than in six specimens collected south of 13°N lat. (117.2 ± 2.0 mm; 114.6–120.3 mm). In 10 adult female specimens examined, however, there is no indication that greatest skull length increases from south to north. This contrasts with latitudinal increase in head and body length, which is more evident in female specimens than in male specimens examined (table 1).

Ontogenetically, relative zygomatic breadth (ZB/GL) increases slightly from 0.62 in one available infant to 0.67 ± 0.02 in 12 adult males (table 4). By contrast, the ratio of rostral length to postrostral length, which is a measure of relative size of splanchnocranium and neurocranium (Fooden, 1969, p. 41), increases strikingly from 0.22 to 0.54 ± 0.02 in the same specimens (fig. 5). The power function equation for the postnatal allometric relationship between rostral length (y) and postrostral length (x) determined by the method of principal axes is:

$$\log y = 3.395 \log x - 4.860.$$

The 95% confidence limits for the slope are $L_1 = 3.027$ and $L_2 = 3.853$.

Metric and nonmetric cranial characters in *M. radiata* overlap those in *M. sinica*, the Sri Lanka toque macaque, which probably is the closest living relative of *M. radiata*. However, greatest skull length in *M. radiata* specimens examined averages 6%–7% greater than in *M. sinica* (Fooden, 1979, p. 114). Conversely, relative zygomatic breadth averages about 2%–3% less in adult *M. radiata* than in adult *M. sinica*, and rostral-postrostral ratio may also average slightly less in adult *M. radiata* than in adult *M. sinica*. These comparative observations generally agree with those of Pocock (1939, p. 40), who characterizes the skull of *M. radiata* as larger but relatively less robust than that of *M. sinica* (cf. Fooden, 1979, fig. 4).



FIG. 4. Cranial characters in *Macaca radiata radiata*, adult female (above; BM 30.11.1.14, Samasgi, Loc. No. 15) and adult male (below; BM 30.11.1.15), Dharwar, Loc. No. 10; upper left I2 missing, upper left I2 deviated to right). Approximately 0.4 natural size. (Photos by Ron Testa, Division of Photography, FMNH.)

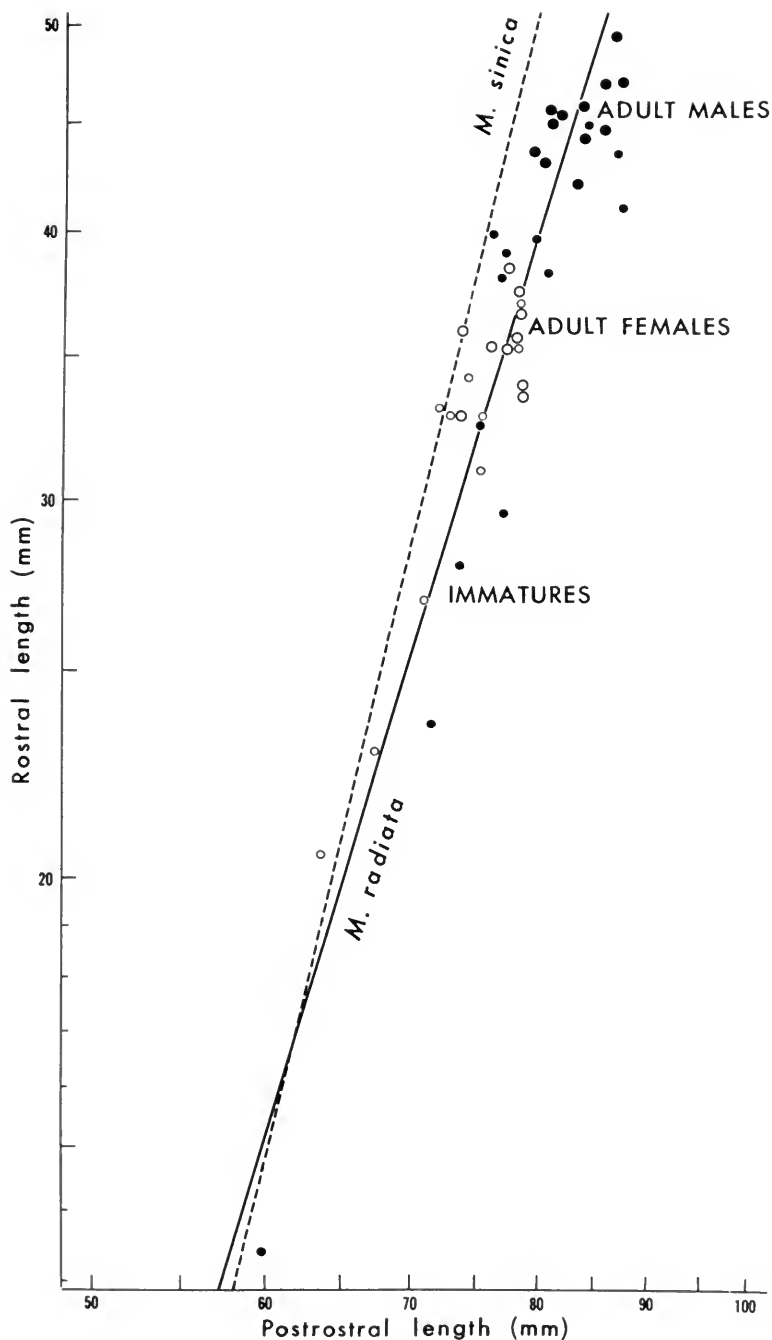


FIG. 5. Allometry of rostral length (y) vs. postrostral length (x) in immature and adult specimens of *Macaca radiata* (open circles = females, closed circles = males; smaller circles = immatures, larger circles = adults; solid line = principal axis) compared with corresponding allometry in *M. sinica* (dashed line = principal axis). *Macaca radiata* principal axis, $\log y = 3.395 \log x - 4.860$; *M. sinica* principal axis, $\log y = 4.317 \log x - 6.507$ (Fooden, 1979, p. 115).

TABLE 3. Latitudinal analysis of greatest skull length in adult specimens of *Macaca radiata*; means and standard deviations indicated for northern (\bar{x}_N) and southern (\bar{x}_S) halves of female and male samples and for total (\bar{x}_{Tot}) of each sample.

Latitude (°N)	Locality No. ¹	Greatest skull length (mm)	
		Adult females	Adult males
18°59'	4	...	123.3
15°48'	26	...	117.7
15°28'	10	104.1	121.5, 127.8
15°19'	12	...	124.0
14°40'	15	99.0, 104.1	123.0
			$\bar{x}_N = 122.9 \pm 3.3$ (n = 6)
12°27'	33	102.6	114.6, 117.1, 118.6
12°08'	45	105.5	...
		$\bar{x}_N = 103.1 \pm 2.5$ (n = 5)	
11°50'	63	...	120.3
11°45'	62	107.2	...
11°26'	59	107.7	116.3
11°20'	57	...	116.1
10°22'	71	104.9	...
8°16'	87	104.0, 105.0	...
		$\bar{x}_S = 105.8 \pm 1.6$ (n = 5)	$\bar{x}_S = 117.2 \pm 2.0$ (n = 6)
		$\bar{x}_{Tot} = 104.4 \pm 2.4$ (n = 10)	$\bar{x}_{Tot} = 120.0 \pm 4.0$ (n = 12)

¹For key to locality numbers, see distribution map (fig. 1).

TABLE 4. Cranial dimensions and ratios ($\bar{x} \pm$ S.D.) in immature and adult specimens of *Macaca radiata*.

Age class	N	Skull, greatest length (mm)	Relative zygomatic breadth (ZB/GL)	Postrostral length (mm)	Rostral- postrostral ratio
Infants	1	71.0	.62	59.8	.22
Juveniles	7	93.0 \pm 10.1	.65 \pm .02	72.2 \pm 5.1	.39 \pm .07
Subadult females	8	99.5 \pm 6.7	.66 \pm .02	74.6 \pm 2.7	.44 \pm .03
Adult females	10	104.4 \pm 2.4	.65 \pm .03	76.9 \pm 2.0	.46 \pm .02
Subadult males	7	113.3 \pm 5.5	.66 \pm .01	81.6 \pm 4.5	.50 \pm .02
Adult males	12	120.0 \pm 4.0	.67 \pm .02	83.1 \pm 2.6	.54 \pm .02

Fifteen adult male *M. radiata* specimens without locality data, most or all of which probably are zoo specimens, average significantly larger (greatest skull length, 123.9 \pm 4.5 mm; extremes 113.6–129.7 mm) than wild-collected specimens reported above (table 3). This difference presumably is a result of artificial conditions of captivity. Because of this difference, measurements of specimens without locality data have not been included in the present analysis of cranial characters in *M. radiata*; in previous revisions of macaque species, I have included (injudiciously, it now appears) some measurements of known or probable zoo specimens.

Natural history.—*Macaca radiata* inhabits monsoonal peninsular India (fig. 6), where it occupies a broad range of wooded and partly wooded habitats from sea level to 2,100 m (table 5). Above 2,100 m, sheltered upland forest (shola) gradually yields to open grassland, and monkeys are absent; the highest peak in peninsular India is 2,695 m. Forest types in which troops of *M. radiata* have been encountered include deciduous (Sugiyama, 1968, p. 289; Kurup, 1971, p. 17), bamboo (Kinloch, 1923, p. 552; Nolte, 1955, p. 84), evergreen (Webb-Peploe,

1947, p. 630; Hutton, 1949, p. 689; Sugiyama, 1972, p. 247), and shola (McCann in Lindsay, 1926, p. 592; Khan, 1977, p. 517). Sightings of this species seem to be more common in lowland deciduous and bamboo forests than in upland evergreen and shola forests (J. R. O'Brien, specimen tag, BNHS 5052, Sharnelli Estate; Kinloch, 1923, p. 552; Hutton, 1949, p. 689; Krishnan, 1972, p. 536). Troops of *M. radiata* often occur in heavily disturbed or manmade habitats, including cultivated areas where roadside trees are nearby (Simonds, 1965, p. 175); village outskirts (Nolte, 1955, p. 79); temple compounds (Shortridge in Wroughton & Ryley, 1913, p. 60); and suburbs, urban parks, and urban market areas (W. Elliot, 1839, p. 95; Rahaman & Parthasarathy, 1967, p. 253).

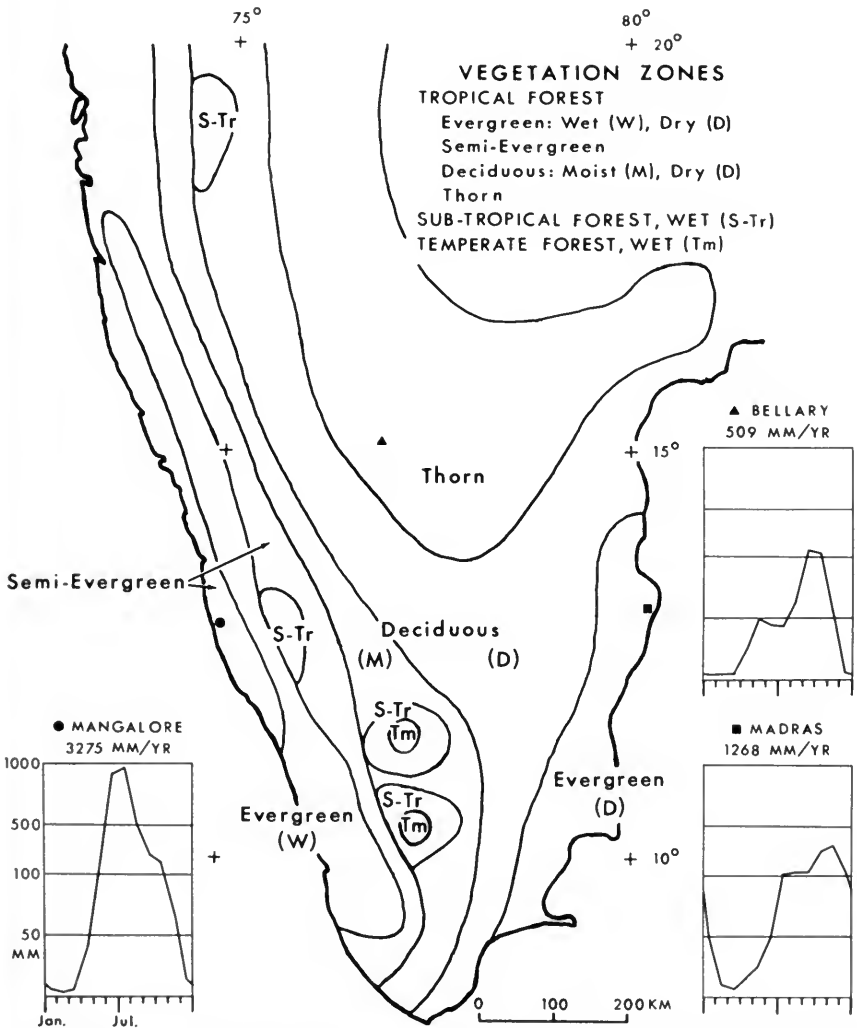


FIG. 6. Vegetation zones (Roonwal & Mohnot, 1977, p. 27) and typical annual rainfall curves (Walter et al., 1975, map 5) in peninsular Indian habitat of *Macaca radiata*.

TABLE 5. Altitudinal distribution of accurately known *Macaca radiata* localities; for details see Figure 1 and Gazetteer.

Altitude (m)	Locality Nos.
0-499	12, 19, 66
500-999	10, 14, 15, 20, ¹ 45, 53, 54, ² 69, 71
1,000-1,499	33, 40, 43, 55, ³ 56, ⁴ 63, ⁵ 70, 72 ⁶
1,500-1,999	56, ⁷ 59, ⁸ 63 ⁹ 72, ¹⁰ 80
2,000-2,499	56 ¹¹

¹Kyasanur Forest.

²Bandipur, 1 mile NE; Bandipur, 1 mile W; Mangata.

³Mudumalai Wildlife Sanctuary.

⁴Nilgiri Hills, N; Nilgiri Hills, W.

⁵Shevaroy Hills, 4,500 ft.

⁶Machchur.

⁷Nilgiri Hills, N & E.

⁸Kotagiri.

⁹Shevaroy Hills, 5,400 ft.

¹⁰Palni Hills, 5,500 ft.

¹¹Nilgiri Hills, 7,000 ft.

Daytime activity (0600-1800 hr) in *M. radiata* probably is about 90% arboreal (10% terrestrial) in forest troops and about 70% arboreal in troops in cultivated areas (Sugiyama, 1972, p. 251). Nighttime sleeping is exclusively arboreal, except in treeless urban areas where *M. radiata* sleeps on roofs or ledges of buildings (R. S. N. Pillay, specimen tag, BM 1937, 5.26.1, Bhutapandi; Rahaman & Parthasarathy, 1967, p. 254). Forest troops probably change sleeping trees nearly every night (Nolte, 1955, p. 79). When moving through trees, *M. radiata* runs nimbly along the upper surface of branches, like other macaques, but it does not bound, as do sympatric langurs (*Presbytis entellus*) (Krishnan, 1972, p. 539). *Macaca radiata* also is adept at scaling cliffs. On the ground, these macaques often stop and stand bipedally to survey their surroundings (Sugiyama, 1972, p. 250). When frightened on the ground, they usually flee into the canopy (Simonds, 1965, p. 196; Rajagopal, 1965, p. 229), but they also have been observed to flee on the ground in bamboo forest (Nolte, 1955, p. 84). Strong sunlight is avoided when possible (Rahaman & Parthasarathy, 1969a, p. 273). These monkeys swim well and appear to enjoy water (Stonor, 1944, p. 591); near a temple at Sholinghur, northeastern Tamil Nadu, a mother bonnet macaque was observed swimming with her infant on her back (Krishnan, 1972, pl. 3).

Judging from alarm and flight reactions observed in *M. radiata*, probable natural predators are tigers, leopards, smaller wild felids, and large predatory birds (Sugiyama, 1972, p. 261). Crocodiles and large snakes are other possible natural predators. Domestic dogs are greatly feared by *M. radiata* (Nolte, 1955, p. 84) and have been observed to kill an infant monkey (Simonds, 1965, p. 179). However, a jackal did not provoke a flight response, but instead was mobbed and driven off by a troop of bonnet macaques (Nolte, 1955, p. 84).

The natural diet of *M. radiata*, like that of other macaques, is predominantly vegetarian and probably consists mostly of fruit (table 6); however, flowers, young leaves, shoots, plant pith, and sap also are eaten. Judging from the known sample of diverse plant species that have been observed to provide food for *M. radiata*, it seems likely that parts of most plant species in the environment are eaten at least occasionally; however, strychnine fruit and cultivated castor beans are said to be avoided (Dixon, 1894, p. 104; Simonds, 1965, p. 175). Wild figs

TABLE 6. Food plants (wild or semi-wild) reported for *Macaca radiata*.

Food plant: family/species ¹	Part consumed	Preference level	Reference (footnote No.)
ANACARDIACEAE			
[<i>Mangifera indica</i>] (mango)	Fruit, flowers, leaves	Favored	2, 3
APOCYNACEAE			
<i>Carissa conject</i> (karwanda)	Fruit, young leaves	Main food (seasonal)	4
CANNACEAE			
[<i>Canna</i> sp.]	Pith	. . .	5
ELAEOCARPACEAE			
[<i>Elaeocarpus</i>] <i>tuberculatus</i>	Fruit	Relished	6
GRAMINAE			
<i>Bambusa arundinacea</i> (bamboo)	Seeds, shoots	Major food	7
<i>Dendrocalamus strictus</i> (bamboo)	Seeds, shoots	Major food	7
giant bamboo	Leaf buds	. . .	8
bamboo spp.	Shoots	Preferred	2, 5
grasses	Seeds, blades	Main food	4, 5, 8
LEGUMINOSAE			
[<i>Acacia</i> spp.]	Fruit, young leaves	Main food	4
<i>Butea frondosa</i>	Flowers	. . .	9
<i>Dalbergia sisoo</i>	Fruit, shoots	. . .	9
<i>Pongamia glabra</i> (pongam)	Fruit, young leaves	Main food (seasonal)	4
<i>Tamarindus indica</i> (tamarind)	Fruit, young leaves	Main food	4, 5, 7, 8
MELIACEAE			
<i>Azadirachta indica</i> (nihm)	Fruit, young leaves	Main food	4
MORACEAE			
<i>Ficus bengalensis</i> (banyan)	Fruit	Major food	7
<i>F. benjamina</i> (banyan)	Fruit	Major food	7
[<i>Ficus</i> spp.] (figs)	Fruit, young leaves	Main food	2, 4, 5
[<i>Morus</i> sp.] (mulberry)	Fruit	Preferred	5
ROSACEAE			
[<i>Pygeum</i>] <i>gardneri</i>	Fruit	Relished	6
VERBENACEAE			
<i>Lantana aculeata</i>	Fruit, flowers, young leaves	Main food	2, 4

¹Names cited as in original source, except where bracketed.

²Nolte, 1955, p. 79.

³Rahaman & Parthasarathy, 1967, p. 253.

⁴Sugiyama, 1972, pp. 249, 252.

⁵Rahaman & Parthasarathy, 1969b, p. 152.

⁶McCann in Lindsay, 1926, p. 592.

⁷Simonds, 1965, p. 177.

⁸Krishnan, 1972, p. 538.

⁹McCann, 1933, p. 810.

may constitute the most important natural food for *M. radiata* (cf. Simonds, 1965, p. 179), as apparently is true for *M. sinica* (Fooden, 1979, p. 123). Animal food items known to be eaten by *M. radiata* include adult and immature insects (notably flies and grasshoppers), spiders, lizards (one observation), and birds' eggs (Hutton, 1949, p. 689; Nolte, 1955, p. 79; Rahaman & Parthasarathy, 1969b, p. 152; Sugiyama, 1972, p. 252; Krishnan, 1972, p. 539). Much of the terrestrial foraging of *M. radiata* apparently is in search of arthropod prey. This species also

expends considerable effort in obtaining birds' eggs and has been observed swimming across a fast-flowing stream to raid a nesting ground. Troops that inhabit agricultural areas probably obtain about 40% of their food by raiding cultivated crops (Simonds in Lancaster & Lee, 1965, p. 493); because this species is regarded as semi-sacred, its crop raiding engenders a tense, ambivalent relationship between bonnet monkeys and local farmers (Buchanan, 1807, p. 55; Baker in Blyth, 1859, p. 283; Shortridge in Ryley, 1913b, p. 492; Rajagopal, 1965, p. 234). Troops in temple and market areas often are deliberately provisioned, or they may obtain their food by raiding houses, shops, and refuse heaps (Rahaman & Parthasarathy, 1967, p. 254; Singh & Sachdeva, 1977, p. 606).

Depending on seasonal abundance, feeding occupies about 40% of daylight hours (Rahaman & Parthasarathy, 1969b, p. 154). Particularly intense feeding periods occur in the morning shortly after awakening and in late afternoon before retiring (Nolte, 1955, p. 80). Like other macaques, *M. radiata* habitually feeds by first stuffing food in the cheek pouches and later chewing and swallowing it (Ogilby, 1838, p. 310; Giebel, 1859, p. 66; Rajagopal, 1965, p. 229). The moisture content of foods evidently is not sufficient to supply the metabolic needs of *M. radiata*, at least during the dry season, and these macaques therefore drink daily at streams or other open water (Nolte, 1955, p. 80). Drinking typically occurs in late afternoon but may also occur at other times; water is gulped directly by mouth. At the height of the dry season, long daily excursions may be necessary to find water (Koyama, 1973, p. 229).

Macaca radiata is partly sympatric with one other species of macaque, *M. silenus*, and with two species of langurs, *Presbytis entellus* and *P. johnii*. However, ecological preferences apparently are not identical in *M. radiata* and the other three sympatric monkey species. *Macaca silenus* and *P. johnii* are restricted to upland evergreen forest (Poirier, 1970, p. 257; Fooden, 1975, p. 81; Khan, 1977, p. 517; Green & Minkowski, 1977, p. 290; Prasad et al., 1979, p. 738), whereas *M. radiata* is more common in deciduous forest (see above). *Presbytis entellus* ranges farther into dry scrubby areas than does *M. radiata* (Simonds, 1965, p. 176). The diet of *M. radiata* is very similar to that of *M. silenus* (Fooden, 1975, p. 82; Green & Minkowski, 1977, p. 295); the diets of *P. johnii* and *P. entellus* include more leaves and less fruit and insects than that of *M. radiata* (Sugiyama, 1967, p. 223; Poirier, 1970, p. 270).

Interspecific encounters between *M. radiata* and *M. silenus* occasionally have been observed in the upland evergreen habitat of the latter species. Judging from the few available published reports (table 7), *M. radiata* is dominant in some of these encounters, *M. silenus* is dominant in some, and neither species is dominant in some. Relative to the distribution of *M. radiata*, however, the distribution of *M. silenus* obviously is highly restricted (fig. 1). This, together with the broad discontinuity that exists between the range of *M. silenus* and that of its nearest relative, *M. nemestrina leonina* (Fooden, 1975, p. 69), suggests that expansion of the range of *M. radiata* has been correlated with reduction of the range of *M. silenus* (Fooden, 1976, p. 228). Regardless of which of these two macaque species is dominant in direct interspecific contacts, it seems clear that, in the long-term zoogeographic view, *M. radiata* generally has gained territory at the expense of *M. silenus*; this probably is a secondary result of changes in climate and vegetation. Recently observed interspecific encounters between *M. radiata* and neighboring *M. mulatta* were not overtly antagonistic (Fooden et al., 1981, in press).

Intergeneric encounters between *M. radiata* and *Presbytis entellus* have been frequently observed. In these encounters, *M. radiata* tends to be dominant and, as an initial response, *P. entellus* tends to withdraw from contact (Simonds, 1965, p. 195; Sugiyama, 1968, p. 289, and 1972, p. 253; Poirier, 1970, p. 261; Makwana & Majumdar, 1980, p. 126). Later, however, once the dominant status of *M. radiata* has been established, these two species may coexist peacefully in close proximity or even in temporarily intermixed troops (fig. 7; Shortridge in Wroughton, 1912, p. 1176; Jay, 1965b, p. 541; Sugiyama, 1967, p. 226; Krishnan, 1972, p. 550; Koyama, 1973, p. 227). Intergeneric encounters between *M. radiata* and *P. johnii* are relatively poorly reported; Hutton (1949, p. 689) indicates that *P. johnii* is dominant in these encounters, whereas Webb-Peploe (1947, p. 629), Simonds (1965, p. 195), and Poirier (1970, p. 261) indicate that these encounters are peaceful or that *M. radiata* is slightly dominant.

Troop member counts are available for 38 troops of *M. r. radiata* studied in two areas in western Karnataka (table 8; NW Karnataka, Dharwar-Haliyal, 13 troops; SW Karnataka, all other localities listed, 25 troops). Forest and roadside troops studied in this subspecies average about 29 individuals per troop (range

TABLE 7. Interspecific dominance and subordination in reported natural encounters between bonnet macaques (*Macaca radiata*) and liontail macaques (*Macaca silenus*).

a. *M. radiata* dominant

1. Sugiyama (1968, p. 289), Panniar (ca. 10°00'N, 77°00'E):

In the [evergreen forest] study area bonnet macaques (*Macaca radiata*) lived within the range of lion-tailed macaque troops. Smaller in size but with a larger troop size (about 30 head) the bonnet macaque is more terrestrial and is commoner in dry deciduous forests and in the vicinity of the villages in drier areas. In the study area it was as arboreal as the lion-tailed macaques. Troops of both species were not overtly antagonistic. A troop of bonnet macaques moved among lion-tailed macaques and sometimes even travelled following the latter. Lion-tailed macaques usually did not react to the appearance of bonnet macaques but sometimes moved away slowly from them. Although smaller, bonnet macaques were dominant.

b. Interspecific tolerance, or dominance not observed

2. Poirier (1970, p. 261), Nilgiri Hills, W (ca. 11°25'N, 76°30'E):

At the border of tracts 2 [moist evergreen] and 3 [sholas] . . . overlapped two species of Indian macaques, *M. radiata* and *M. silenus*.

3. Green and Minkowski (1977, p. 300), locality unspecified:

Bonnet macaques (*M. radiata*) typically occur in the drier deciduous forests and scrub jungles at much lower elevations, but sometimes seasonally move up into the wet forests inhabited by lion-tailed monkeys. The few times we saw bonnets with *M. silenus*, no antagonism occurred. . . . However, resource competition with *M. radiata* may have prevented *M. silenus* from successfully occupying the lower elevation forests in which *M. radiata* is so well established.

c. *M. silenus* dominant

4. Vincent Marie in Buffon & Daubenton (1766, p. 171), Malabar district (ca. 11°15'N, 76°00'E):

. . . the other [three species of] monkeys [presumably including *M. radiata*] have so much respect for [*M. silenus*] that they humble themselves in its presence, as if they were able to recognize its [*M. silenus*] superiority. (translated from French)

5. Webb-Peploe (1947, pp. 629-630), Naraikkadu Estate (ca. 8°30'N, 77°30'E):

. . . in evergreen forest . . . [*M. radiata*] will keep out of the way when the Lion-tailed Monkey is about. . . . Occasionally [they] meet on the [arboreal] bridge. The Bonnet Monkey . . . disappears when the Lion-tailed Monkey is in the vicinity.



FIG. 7. Troop of *Macaca radiata radiata* near Dharwar (Loc. No. 9), Feb. 1963, feeding on ground in close association with Indian langur, *Presbytis entellus* (left rear). (Photo courtesy Dr. Phyllis Dolhinow, University of California, Berkeley.)

TABLE 8. Troop size in *Macaca radiata radiata*.

Sample area (Loc. No.) ¹	No. of troops	Individuals per troop		Reference
		$\bar{x} \pm \text{S.D.}$	Extremes	
Forest troops				
Dharwar-Haliyal (8)	3	33.7 \pm 3.5	30-37	Sugiyama, 1972, p.255
Byrankuppe (47)	2	36.0 \pm 2.83	34, 38 ²	Nolte, 1955, p. 78
Moyar R.-Theppakadu (54)	2 ³	17.0 \pm 14.1	7, 27	Simonds, 1974a, p. 152
Subtotal	7	29.6 \pm 10.7	7-37	
Roadside troops				
Dharwar-Haliyal (9)	10	28.9 \pm 7.4	16-44	Sugiyama, 1972, p. 255; Koyama, ⁴ 1973, p. 228
Mysore vicinity-Somanathapur (36, 48, 50, 51, 53)	6	29.5 \pm 15.4	15-59	Simonds, 1973, p. 601; 1974a, p. 152
Subtotal	16	29.1 \pm 10.6	15-59	
Urban troops				
Bangalore (40)	14	21.1 \pm 8.9	10-43	Rahaman & Parthasarathy, 1967, p. 253
Mysore (48)	1	23	23	Singh & Sachdeva, 1977, p. 606
Subtotal	15	21.3 \pm 8.6	10-43	
All troops ⁵	38	26.1 \pm 10.4	7-59	

¹For key to locality numbers, see distribution map (fig. 1).

²Including, respectively, two and five infants in arms.

³These two troops had been recently formed as a result of fission of a larger troop.

⁴Troop E, 30 individuals, including seven infants.

⁵Cf. estimated troop size recently recorded in 29 additional troops, $\bar{x} = 33.2 \pm 24.5$, extremes 10-100 (Fooden et al., 1981, table 1).

7-59). Urban troops of the same subspecies studied in Bangalore and Mysore average about 21 individuals per troop (range 10-43) and therefore generally seem to be somewhat smaller than forest and roadside troops (cf. Krishnan, 1972, p. 538). In the subspecies *M. r. diluta*, in extreme southeastern peninsular India, troop size may average larger than in *M. r. radiata*, judging from a few rough troop census estimates published by Hill (1937, p. 212) and Hutton (1949, p. 689); the former reports that two temple troops of *M. r. diluta* each included at least 50 individuals, and the latter indicates that an unspecified number of forest troops of the same subspecies also each included more than 50 individuals.

Solitary individuals, living independently of any troop, have never been observed in *M. radiata* (Rahaman & Parthasarathy, 1967, p. 254; Sugiyama, 1972, p. 262; Simonds, 1973, p. 600), although such solitary individuals are well known in other species of macaques (Fooden, 1975, p. 51). One small detached all-male group (two adults, one subadult) has been recorded; this group lived within the home range of a troop of 28 members and evidently was composed of troop outcasts (Simonds, 1973, p. 600).

Home range area in *M. r. radiata* averages about 200 hectares in nine forest and roadside troops and about 100 hectares per troop in two urban botanical garden troops (table 9). Daily foraging range is highly variable but may average about 50% of the total home range (Nolte, 1955, p. 79; Rahaman & Parthasarathy, 1969a, p. 274; Sugiyama, 1972, p. 249). Population density averages about one monkey per five hectares. Assuming that an average troop member weighs

TABLE 9. Home range area and population density in troops of *Macaca radiata radiata*.

Locality ¹	No. of troop members	Home range area (hectares)	Density (ind./hectare)	Reference (footnote No.)
Forest troops				
Byrankuppe (47)	34	150	0.23	2
Bandipur A, 1 mile NE (54)	...	±260	...	3
Bandipur B, 1 mile W (54)	...	±260	...	3
Kakkenahala (54)	6	±130	±0.05	3
Mangata (54)	28+	±260	±0.11	3
Means		±212	±0.13	
Roadside troops				
Dharwar D (9)	32	40	0.80	4
Dharwar E (9)	30	220	0.14	5
Hangala (53)	46	±260	±0.18	3
Somanathapur (54)	58	±260 ⁶	±0.22	3
Means		±195	±0.33	
Urban troops (in botanical garden)				
Bangalore 1 (40)	22	±100	±0.22	7
Bangalore 2 (40)	20	±100	±0.20	7
Means		±100	±0.21	

¹Locality numbers (in parentheses) as in distribution map, Figure 1.

²Nolte, 1955, p. 78.

³Simonds, 1965, pp. 178, 180.

⁴Sugiyama, 1972, p. 250.

⁵Koyama, 1973, pp. 225, 228.

⁶Area estimated from map of home range (Simonds, 1965, p. 178, fig. 6-2); this estimate differs from home range area of 2 miles² (520 hectares) specified in text (*ibid.*, p. 177).

⁷Rahaman & Parthasarathy, 1969a, p. 269.

about 3 kg (cf. *M. sinica*, studied by Dittus, 1975, p. 144), the estimated average biomass density in *M. radiata* is approximately 0.6 kg per hectare. One exceptional troop that occupies an unusually small home range (table 9, Dharwar Troop D, 40 hectares) has a population density of nearly one monkey per hectare. Long-term studies indicate that, despite occasionally observed fissions and migrations (Rajagopal, 1965, p. 231; Kawamura in Sugiyama, 1972, p. 263; Simonds, 1974a, p. 153; Singh & Pirta, 1978, p. 265), troops generally tend to remain relatively stable in their home range and total number of members (Sugiyama, 1972, p. 247, two years' observation; Rahaman & Parthasarathy, 1969a, p. 268, three years' observation; Simonds, 1965, p. 176, and 1974a, p. 153, nine years' observation).

In suitable habitats, troops of *M. radiata* generally are closely packed, with about 5%–25% overlap between home ranges of adjacent troops (Simonds, 1965, p. 178; Rahaman & Parthasarathy, 1969a, p. 270; Sugiyama, 1972, p. 248; Koyama, 1973, p. 229). Two of 38 troops studied (table 8) have home ranges that lie completely within the home ranges of two other troops (Simonds, 1974a, p. 153; Koyama, 1974, p. 227); such ranges that overlap completely may be characteristic of newly formed sister troops that have recently developed by fission of a single large ancestral troop (cf. Simonds, *loc. cit.*). By contrast, some areas of apparently suitable habitat are only sparsely occupied by *M. radiata*, and home ranges of

neighboring troops may be separated by up to 4 km of unoccupied territory (Simonds, 1965, p. 178).

The long-term stability of home ranges in *M. radiata* probably is a result, at least in part, of competitive social interactions between adjacent troops. These interactions are known to include intertroop fights, vocal and visual threat behaviors, and mutual avoidance (see below). It seems likely that the wide range of observed intertroop behaviors may represent successive stages in development of a relationship of peaceful coexistence along intertroop borders. At a presumed early stage in development of an intertroop relationship, incursions of one troop into the home range of an adjacent troop are known frequently to result in violent arboreal battles with serious injuries inflicted on some of the combatants (Rajagopal, 1965, p. 230; Rahaman & Parthasarathy, 1969a, p. 271; Yoshida in Sugiyama, 1972, p. 263). In subsequent encounters, threatening vocalizations may replace direct physical conflict, as observed by Rahaman & Parthasarathy (loc. cit.):

. . . on three occasions we noticed troupe 1 trying to invade the core area of troupe 2 . . . , which resulted in serious fights on the first two occasions and in just an aggressive exchange of overtones on the third.

Aggressive staring may represent a later stage in ritualization of intertroop conflict behavior, as suggested by the following observation of Simonds (1965, p. 195):

When the two [adjacent] groups met the subadult and adult males would move toward the other group, and then sit and look at each other with approximately 20 feet between them. Then the males in one of the groups would begin to drift back in the opposite direction and the groups would separate.

Ultimately, in the presumed final stage of intertroop accommodation, one troop may immediately and automatically withdraw in response to advance into its range of an adjacent, more dominant troop (Rahaman & Parthasarathy, 1969b, p. 151; Sugiyama, 1972, p. 263; Kawamura in Koyama, 1973, p. 229; Singh & Sachdeva, 1977, p. 605). In all reported instances of automatic withdrawal, the troop that withdrew contained fewer members than the troop that advanced. Occasionally a small subordinate troop may move temporarily into the home range of a larger dominant troop, but only when the larger troop is absent from that part of its range (Sugiyama, 1972, p. 263). Adjacent troops, however, apparently never commingle (cf. Nolte, 1955, p. 79), and even large dominant troops that have advanced into the range of an adjacent subordinate troop apparently usually return to their own home range (Sugiyama, 1972, p. 263).

Age-sex composition data are available for 35 troops of *M. r. radiata*, and sex ratio data only are available for 18 additional troops (table 10, fig. 8). Observers have distinguished four age-sex classes in these troops: (1) infants, (2) juveniles, (3) subadult and adult females, and (4) subadult and adult males. Because of the annual birth peak in *M. radiata* (fig. 9), age cohorts of immatures are reasonably discrete. Infants are less than one year old and usually are still nursing or are otherwise closely dependent on their mothers. Juveniles, one year old to less than four years old, are more or less independent of their mothers but have not entered the breeding population; although laboratory studies have shown that juvenile males as young as age two and one-half years are physiologically capable of copulation and ejaculation (Rosenblum & Nadler, 1971, p. 394), such sexual behavior by juveniles has not been observed in free-ranging natural troops (see below). Subadults and adults, age four years and older, are actual or potential breeders (reproductives); sexual maturity in males and females usually

TABLE 10. Age-sex composition in observed troops of *Macaca radiata radiata*.

Total troop members	Age-sex composition ¹	Reference (footnote No.)	Total troop members	Age-sex composition ¹	Reference (footnote No.)
7	2:1:3:1	2	27	9:9:5:4	5
10	4:3:1:2	3	27	9:6:6:6	2
11	4:5:1:1	3	28	12:7:5:4	3
14	5:2:5:2	3	28	9:8:7:4	5
14	5:5:4:0	3	28	8:9:6:5	4
15	5:1:4:5	4	30	10:10:6:4	5
16	7:6:1:2	3	30	8:11:4:7	4
16	5:5:4:2	5	30	11:4:8:7	6
17	7:3:6:1	3	31	16:10:3:2	3
20	6:3:5:6	3	32	9:7:8:8	5
20	6:5:5:4	3	32	9:7:10:6	5
20	6:6:3:5	4	33	11:8:8:6	5
22	11:3:5:3	3	34	5:3:17:9 ⁷	8
23	5:4:7:7	3	34	13:8:8:5	5
23	7:5:6:5	5	37	13:11:9:4	5
24	8:7:6:3	5	38	8:5:12:13 ⁷	8
25	8-9:1:7:8-9	4	43	12:20:4:7	3
27	7:8:5:7	3	44	13:11:13:7	5
			59	17:18:10:14	2

¹First entry = No. of adult or subadult females (age ≥ 4 yr.); second entry = No. of adult or subadult males (age ≥ 4 yr.); third entry = No. of juveniles (age 1-3 yr.); fourth entry = No. of infants (age < 1 yr.).

²Simonds, 1974a, p. 152.

³Rahaman & Parthasarathy, 1967, p. 253.

⁴Simonds, 1973, p. 601.

⁵Sugiyama, 1972, p. 255.

⁶Koyama, 1973, p. 228.

⁷Age-sex categories probably not coordinate with those in other studies cited (Simonds, 1965, p. 181); data not included in Figure 8.

⁸Nolte, 1955, p. 78.

is achieved during the breeding season following the fourth birthday, which is about age four and one-half years. At the onset of sexual maturity, females are close to their adult size (head and body length ca. 450 mm, weight 4 kg), and males the same age are only slightly larger than females; however, males continue to grow at least two or three more years after achieving sexual maturity, and they ultimately reach an adult head and body length that is 10%-15% greater than in adult females (weight more than 50% greater than in females).

In troops for which data are available (fig. 8), infants and juveniles (nonreproductives) generally are outnumbered by subadults and adults (reproductives). The mean ratio of infants and juveniles to subadults and adults in 35 troops is 0.75 (S.D. = 0.36, extremes 0.19-1.63); this ratio seems to be somewhat lower in urban troops in Bangalore than in roadside troops in the Dharwar and Mysore areas. Among reproductives, the mean sex ratio of subadult and adult males to subadult and adult females in 53 troops is 0.84 (S.D. = 0.34, extremes 0.12-2.00); in only 10 of these 53 troops does the number of breeding males exceed the number of breeding females (fig. 8). The number of infants generally averages about 80% of the number of juveniles. Mean composition in an average size troop of 26 individuals would be eight subadult or adult females, seven subadult or adult males, six juveniles, and five infants. Part of the observed high

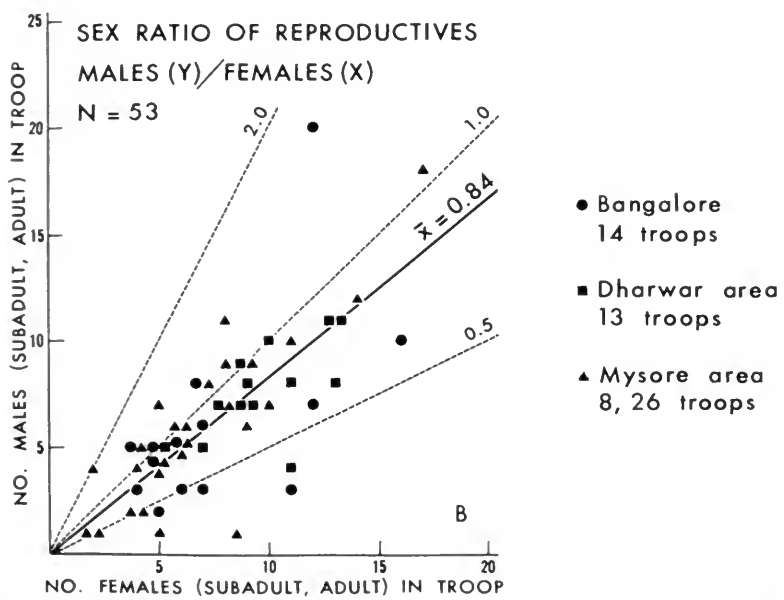
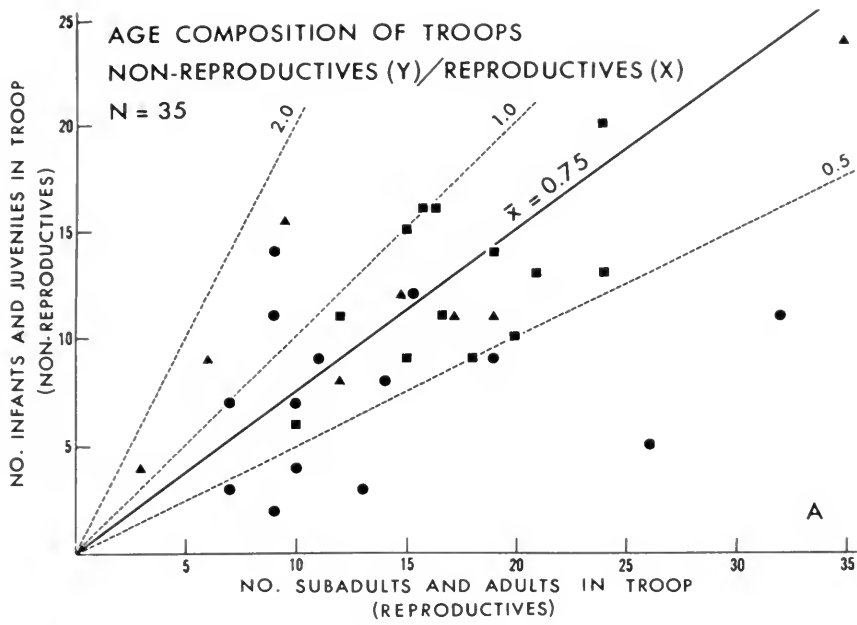


FIG. 8. Bivariate plots of age-sex composition in troops of *Macaca radiata radiata*: **A**, non-reproductives vs. reproductives in 35 troops (table 10); **B**, male reproductives vs. female reproductives in 53 troops (table 10; Simonds, 1973, p. 600).

variability of troop composition may be attributable to variation in the season of observation, which fails to control for seasonal birth and death peaks.

Social relations within troops of *M. radiata* generally conform to the sex-age dominance system that is usual in macaques (Nolte, 1955, p. 78; Simonds, 1965, p. 182; Rahaman & Parthasarathy, 1969b, p. 151; Sugiyama, 1972, p. 255; Koyama, 1973, p. 228). Adult males play a key role in leading the troop during movement, in controlling fighting between troop members, in giving alarm calls, and in defending the troop against external dangers. Among adult males, dominance rank is closely related to body size and, especially, to canine size (Gee, 1964, p. 20; Simonds, 1965; p. 185). Dominance shifts in one carefully studied troop usually span only one or two ranks per year, but three adult males in this troop shifted three or four ranks within one year (table 11). Dominance rank is manifested in the feeding and drinking order of individuals in a troop (Sugiyama, 1972, p. 256; Koyama, 1973, p. 228) and therefore presumably is related to survival when food or water is scarce.

Although the dominance hierarchy in *M. radiata* is generally similar to that in other macaques, observers agree that display of dominance and subordination behaviors in *M. radiata* appears to be somewhat more flexible than in other species, particularly *M. mulatta* and *M. fuscata* (Simonds, 1965, p. 186; Sugiyama, 1972, p. 264). Observers also indicate that social relations in troops of *M. radiata* are characterized by an unusually high incidence of certain social behaviors: namely, intense grooming; clasped resting and sleeping, often in clusters (cf. Kaufman & Rosenblum, 1966, p. 219); mixed-age playing; and homosexual mounting. Individual relations in all of these high-incidence social behaviors frequently fail to conform to expected patterns of dominance and subordination.

Breeding is strongly seasonal in *M. radiata* (fig. 9). More than 80% of 308 copulations observed in two carefully studied troops in Bangalore occurred during September, October, and November (Rahaman & Parthasarathy, 1969b, p. 156), which approximately coincides with the postmonsoon (northeast monsoon) season. These same three months also constitute the peak mating season observed in two other carefully studied troops, one near Mysore and the second near Dharwar (Simonds in Lancaster & Lee, 1965, p. 494; Sugiyama, 1972, p. 252). In the troop studied near Dharwar, most of the relatively few copulations that occurred outside of the September–November mating season involved the alpha male (nine of 14 copulations) and his favorite female partner; of the re-

TABLE 11. Dominance shifts of 10 adult males in Somanathapur troop of *Macaca radiata radiata* (Simonds, 1965, p. 191; 1974a, p. 158).

Male	Estimated age in 1961–1962	Dominance rank on date			
		Oct. 1961	June 1962	July–Sept. 1963	Jan.–May 1970
Dan	Prime	1	4	?	High ranking
Zeb	Prime	2	1	?	Absent
Pim	Late prime	3	5	1	Absent
Hala	Early prime	4	3	4	Rank unclear
One-Eye	Early prime	5	2	?	Absent
Kink	Prime	6	6	?	Absent
Andy	Very old	7	Deceased	Deceased	Deceased
Rock	Late prime	8	7	?	?
Butch	Old	9	8	?	?
Shorty	Old	10	9	?	?

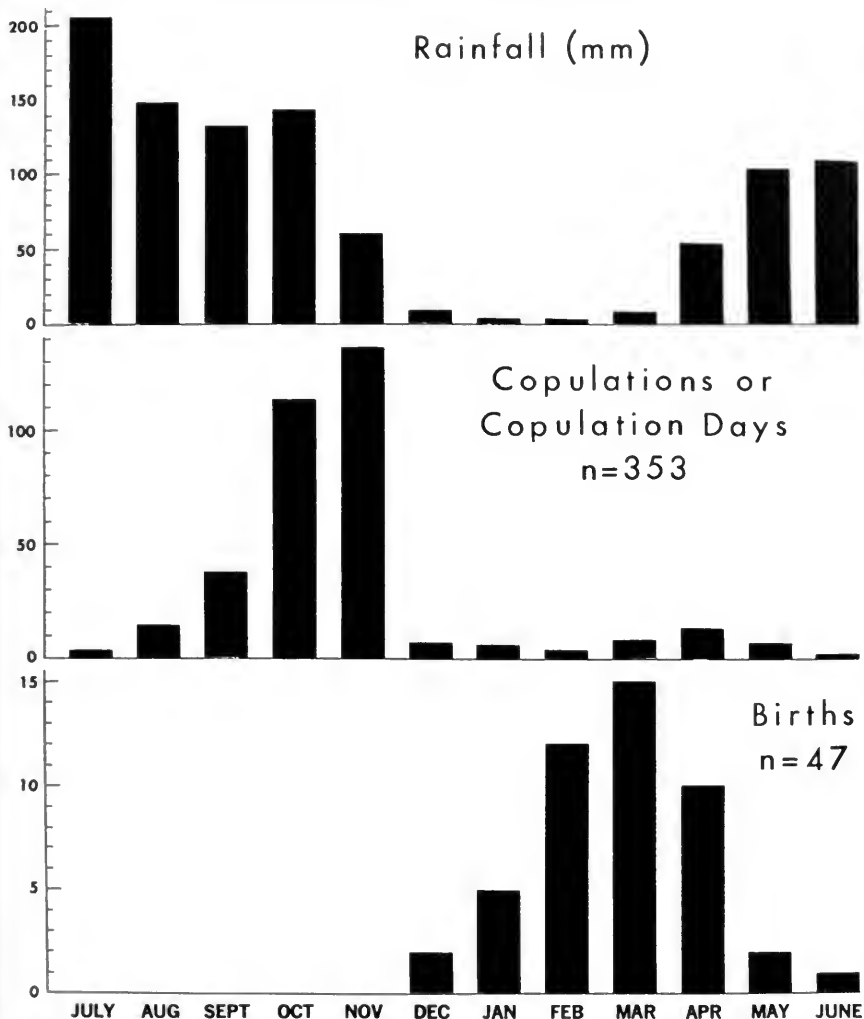


FIG. 9. Reproductive seasonality in *Macaca radiata radiata*. References: Rainfall—Walter et al., 1975, map 5 (monthly means for Belgaum, Mysore, and Bangalore, which are weather stations near or at localities where reproduction observations were made). Copulation activity—Rahaman & Parthasarathy, 1969b, p. 156 (copulations); and Sugiyama, 1972, p. 253 (copulation days). Births—Rahaman & Parthasarathy, 1969b, p. 156; Sugiyama, 1972, p. 253; Koyama, 1973, p. 228; Simonds, 1974a, p. 154; for five additional births observed on unspecified dates between 1 Dec. 1974 and 15 May 1975, see Singh & Sachdeva (1977, p. 606); and for two more births recorded in March–May 1977, see Singh & Pirta (1978, p. 267).

maining five copulations observed outside of the regular mating season in this troop, four involved a young subadult that was not seen to copulate during the regular mating season; the other copulation outside of the regular mating season involved another subadult male; three adult males in this troop were never observed to copulate outside of the regular mating season.

All births ($N = 54$) that have been recorded in wild troops of *M. radiata* are restricted to the period December–June (fig. 9; 47 births in specified months, seven births in unspecified months within the December–May interval). This broadly overlaps the dry season in most of peninsular India. Significantly, it is the mating season (see above), not the birth season, that is timed to occur during the rainy months when food and water are most abundant. About 80% of the accurately dated births occurred during February, March, and April, which is approximately five months after the peak mating period; this is as expected because the gestation period in *M. radiata* is five to six months. The complete absence of births during the period July–November suggests that the relatively few copulations that occur five months earlier (February–June) are inherently infertile.

The timing of natural breeding seasonality in *M. radiata* apparently depends on environmental cues, presumably correlated with rainfall. In a laboratory colony of this species that was maintained for about three years in Davis, California, the annual birth peak shifted to April–July (Judge & Rodman, 1976, p. 535), which is about three months later than in wild troops in India.

Males and females apparently enter the breeding population about age four and one-half years (Sugiyama, 1972, pp. 253, 259). Each breeding female probably is in estrus about four or five days of each approximately 30-day menstrual cycle (cf. Hartman, 1938, p. 470). Because cycles of different females in the same troop usually are not in phase, normally only one or two females are in estrus on any given day during the mating season (Rahaman & Parthasarathy, 1971, p. 100). While in estrus, each female copulates eight to 12 times (total) with two to four male partners. Females usually copulate with more than one male on each day of their estrus period; one female was observed to copulate successively with three different males within a four-minute time span (Simonds, 1965, p. 194).

Subordinate males are not excluded from access to estrous females, but dominant males probably engage in significantly more copulations. In one troop that included six sexually mature males and nine sexually mature females, the alpha male and beta male each copulated on eight days during 30 days of observation during the mating season, two less dominant adult males copulated on six and five days, a lower ranking subadult male copulated on five days, and the lowest ranking subadult male did not copulate at all (Sugiyama, 1972, p. 252). In a troop that included three sexually mature males and six sexually mature females, one male (presumably the alpha male) copulated 26 times during the observation period, whereas the other two males copulated 17 times and 13 times (Rahaman & Parthasarathy, 1971, p. 100). The correlation between dominance status and sexual activity in male *M. radiata* also has been demonstrated in laboratory experiments (Coe, 1977, p. 4208). Although exclusive consort relationships are not maintained, there apparently is a tendency for most copulations to occur between preferred partner pairs.

Social tensions are high during the mating season (Simonds, 1977, p. 161). Although dominant males usually tolerate copulations between estrous females and lower ranking males, dominant males occasionally have been observed to interrupt such matings by an attack on the lower ranking male (Rahaman & Parthasarathy, 1969b, p. 155; Sugiyama, 1972, p. 258). Perhaps to avoid such attacks, a lower ranking male accompanied by an estrous female sometimes

moves more than 500 m away from other troop members before copulating (Sugiyama, loc. cit.).

Copulatory behavior in *M. radiata* usually is initiated by the male partner (93% of 59 copulations observed by Simonds, 1965, p. 194; 78% of 308 copulations observed by Rahaman & Parthasarathy, 1969b, p. 155). Experimental evidence indicates that males recognize estrous females at a distance by an unidentified olfactory cue or pheromone (Rahaman & Parthasarathy, 1971, p. 98); this pheromone presumably is a component of secretions produced by the specially enlarged cervix that characterizes *M. radiata* and other members of the *M. sinica* species group (Hill, 1932, p. 314; Fooden, 1971, p. 71; Kanagawa et al., 1973, p. 211). Having perceived this olfactory signal, a male typically approaches the posterior end of an estrous female, pushes the tail aside, visually inspects the perineal area, smells or tastes secretions in the vagina, and proceeds to mount and copulate. Close examination of the perineum seems to be a ritual, because practically all females that are approached are subsequently mounted (Rahaman & Parthasarathy, 1969b, p. 155); the pheromone that is perceived at a distance and that induces the male to approach probably is the main effective stimulus in male sexual arousal and copulatory behavior. *Macaca radiata* typically is a single mount ejaculator, with five to 30 intromissive thrusts to ejaculation and a total intromissive mount interval of six to 23 seconds (Simonds, 1965, p. 194; Rajagopal, 1965, p. 232; Nadler & Rosenblum, 1969, p. 484).

Occasional transfer of individuals between troops of *M. radiata* is an obvious requisite for maintenance of genetic continuity within the species. Such transfers are not often observed, however, and hence, are only poorly documented (table 12). The rarity or absence of solitary individuals in *M. radiata* (see above) indicates that a bonnet macaque that leaves one troop normally either rapidly joins another troop or fails to survive. Five of six individuals observed in intertroop shifts were males, all either subadult or adult; of these, two were high-ranking (beta, gamma), but none was an alpha male. All four shifts that are reasonably accurately dated occurred during the rainy season (fig. 9); only one of these certainly occurred during the mating season. Based on these skimpy data, the following series of provisional hypotheses may be proposed for future investigation: (1) Under natural conditions, all males of *M. radiata* probably leave their natal troop before reaching their first breeding season, most likely as late juveniles or early subadults; Koyama (1973, p. 228) provides evidence that a male may remain in his natal troop with his mother as late as age four years (cf. Simonds, 1974a, p. 157). (2) Most males probably switch troops at least once more during their life, but not as an alpha male. (3) Most intertroop shifts probably occur during the rainy season, often during the first three months of the rainy season and therefore before onset of the peak mating season. It should be noted that intertroop shifts may be geographically impossible in some widely separated urban troops (Rahaman & Parthasarathy, 1967, p. 251).

Troop reproductive success, measured as the average number of live births per year per sexually mature female is 0.88 in eight *M. radiata* troops that were observed through a complete breeding season (table 13). (Although single births are the rule in *M. radiata* and other macaques, twinning may occasionally occur [Webb-Peploe, 1947, p. 630].) High reproductive success in *M. radiata* also is indicated by incomplete data on 19 additional troops that may not have been observed through a complete breeding season (Rahaman & Parthasarathy, 1967,

TABLE 12. Intertroop movements reported in *Macaca radiata*.

Date	Intertroop mover			Intertroop movement observed	Reference (footnote No.)
	Sex	Age	Original dominance rank		
?	♀	?	?	Shift from Troop 2 to Troop 1 (Bangalore)	1
29-30 May 1962	♂	14-17 yr.	2	Permanent disappearance from Troop D (near Dharwar)	2
1-7 June 1962	♂	6-7 yr.	5	{ Temporary disappearance from Troop D Reentry into Troop D Shift from Troop E to Troop C after death of leader of Troop C (near Dharwar); repeated shifting between troops; finally, permanent entry into Troop C as new leader	2
4 Sept. 1962					2
1962					♂
Summer 1963	♂	ad.	6-10	Shift from Somanathapur troop to Hangala South troop; shift completed in one afternoon, rank unchanged	4
July-Sept. 1963 or Jan.-May 1970	♂	subad.	4-7	Shift from Moyar R. troop to detached group of two isolated males	5

¹Rahaman & Parthasarathy, 1969a, p. 268.

²Sugiyama, 1972, p. 262.

³Kawamura in Koyama, 1973, p. 229.

⁴Simonds, 1974a, p. 158; cf. Simonds, 1965, p. 185.

⁵Simonds, 1973, p. 600.

p. 253; Simonds, 1973, p. 601); of these, four include as many infants as sexually mature females (reproductive success 1.00), and one reportedly includes two more infants than sexually mature females (reproductive success 1.40). The neonatal sex ratio in four carefully studied troops averages 1.1 male infant to 1.0 female infant (table 13), which is not significantly different from 1:1 ($X^2 = 0.125$; $0.9 > P > 0.5$). Obviously, there is no indication in these data that the sex ratio at birth directly determines the sex ratio among sexually mature adults, where females generally outnumber males (fig. 8; cf. Rahaman & Parthasarathy, 1967, p. 254).

Available cross-sectional census data on age structure in two carefully studied troops of *M. radiata* permit a first-approximation life-table analysis of survivorship probability in this species (table 14). Assuming that the two troops studied are reasonably typical of the species and are relatively stable in composition, it may be inferred that there probably are three peaks in the age-specific mortality curve. Not surprisingly, these three inferred mortality peaks are (1) during the first year of life; (2) during the period between age four and six years, when individuals enter the breeding population; and (3) during the period of old age, starting about age 15 years.

TABLE 13. Reproductive success and neonatal sex ratio in troops of *Macaca radiata* observed during birth season.

Locality No. ¹	Birth year of neonate	Reproductive success			Neonatal sex ratio			Reference (footnote No.)
		Sexually mature females	Infants born	Ratio	Female infants	Male infants	Ratio	
9	1962	8	6	0.75	4	2	0.50	2
9	1963	8	7	0.88	3	4	1.33	3
40 (Troop 1)	1965	11	11	1.00	4
40 (Troop 1)	1966	11	9	0.82	4
40 (Troop 2)	1965	6	4	0.67	4
40 (Troop 2)	1966	6	5	0.83	4
48	1975	5	5	1.00	5
53	1961	14	14	1.00	6	8	1.33	6
54	1970	(9) ⁷	(5) ⁷	...	2	3	1.50	8
Totals/means		69	61	0.88	15	17	1.13	

¹For key to locality numbers, see distribution map (fig. 1).

²Sugiyama, 1972, p. 253.

³Koyama, 1973, p. 228.

⁴Rahaman & Parthasarathy, 1969b, p. 156.

⁵Singh & Sachdeva, 1977, p. 606.

⁶Simonds, 1965, p. 179.

⁷Data incomplete; troop not observed during entire birth season.

⁸Simonds, 1974a, p. 155.

TABLE 14. Age distribution in two troops of *Macaca radiata radiata* studied near Dharwar (Loc. No. 9), northwestern Karnataka.

Age ¹ (yr.)	No. of troop members in each age class		
	Troop D ²	Troop E ³	Total
Neonate	6 (2♂♂/4♀♀)	7 (4♂♂/3♀♀)	13 (6♂♂/7♀♀)
1	3 (3/0)	3 (2/1)	6 (5/1)
2	4 (1/3)	4 (2/2)	8 (3/5)
3	3 (3/0)	1 (0/1)	4 (3/1)
4	3 (2/1)	4 (1/3)	7 (3/4)
0-4	19 (11/8)	19 (1/10)	38 (20/18)
5-9	5 (1/4)	11 (3/8)	24 (8/16)
10-14	4 (2/2)		
15-(19)	4 (2/2)		
Total	32 (16/16)	30 (12/18)	62 (28/34)

¹Estimated during birth season. ²Sugiyama, 1972, pp. 253, 259. ³Koyama, 1973, p. 228.

Survivorship of neonates to age one year probably is only about 50% (table 14). Sugiyama (1972, p. 253) records that one of six neonates in one troop disappeared within eight days of birth, and Simonds (1974a, p. 154) records that two of five neonates in another troop died within one month after birth. Singh & Pirta (1978, p. 267) report that two infants born during an unusual troop migration disappeared within five days. Other authors (Hutton, 1949, p. 689; Rajagopal, 1965, p. 233; Rahaman & Parthasarathy, 1969b, p. 157) report seeing near-dead neonates that were abandoned by their mothers and dead neonates that were carried by their mothers for several days. Nolte (1955, p. 85) observed that a helpless infant was abandoned (?temporarily) by its mother when the mother joined in a troop attack on an unidentified predator; such abandoned infants sometimes may be retrieved by juvenile or subadult males (Sugiyama, 1972, p. 261). The fact that most births occur at the end of the dry season (fig. 9), when food and water are relatively scarce, may be a factor that contributes to the high infant mortality rate.

The annual age-specific mortality rate from age one year to at least age four years evidently is much lower than during the first year of life, with the result that most one-year-olds probably survive to age four years (table 14). This generalization is based on detailed age data available for Dharwar area Troops D and E (table 14), but it is also supported by less precise data available for 33 additional troops listed in Table 10; the ratio of infants to juveniles age one to three years in Troops D and E (13 infants: 18 juveniles = 0.72) is reasonably close to the corresponding ratio in 33 additional troops listed in Table 10 (149.5 infants: 182 juveniles = 0.82).

Evidence from Dharwar area Troop D, supported by comparable but less complete evidence from Troop E, indicates that age four to five years, like age birth to one year, is a period of unusually high mortality risk (table 14). In Troop D, the number of individuals in the infant cohort (age one year) is six; the average number of individuals in each cohort from age one through four years is about three; and the average in each cohort from age five years to approximately age 19 years is about one. Age four to five years, as previously indicated, is the age of puberty, and the high mortality rate that apparently characterizes this age presumably is a result of hazards related to entering the breeding population. For males, these probably are hazards associated with dominance

fighting and with shifting from one troop to another; for females, the nature of the hazards of puberty are less clear, but they may be obstetrical hazards of primiparity. Higher male mortality risk during this period of adolescence probably is the main reason why troop breeding populations usually include more females than males (fig. 8).

Following the demographic crisis of puberty, the mortality rate in *M. radiata* apparently declines, with the result that most monkeys that reach age six to seven years probably survive at least 10 years more, to old age. This span, from age six to seven years to about age 15 years, probably is the prime of life, the period when individuals reach their highest level in the dominance hierarchy. In one long-term study, it was observed that two of six high-ranking males survived at least nine years after reaching adulthood (table 11).

Finally, some time after age 15 years, the cumulative effects of old age, among which worn teeth may be especially important, result in another period of high mortality. A 20-year-old bonnet macaque probably is near the upper age limit for survival in the wild. Under artificial conditions of captivity, however, individuals may survive to about age 30 years (Prater, 1971, p. 36). Average life expectancy at birth under natural conditions probably is about five years (table 14).

Causes of morbidity and mortality that have been directly observed in *M. radiata* include fights within and between troops, attacks by predators, infectious diseases, and old age. Of these, wounds sustained in the course of intratroup fights have been most frequently reported (Simonds, 1965, pp. 179–180; Rahman & Parthasarathy, 1968, p. 261; 1969b, p. 151; Krishnan, 1972, pp. 540, 550; Sugiyama, 1972, p. 256; Simonds, 1974b, p. 178); these fights usually are related to competition for food and/or dominance position and often result in serious injury or death. Intertroup fights are less frequently reported, but these also may be extremely violent and produce serious casualties (Rajagopal, 1965, p. 230; Yoshida in Sugiyama, 1972, p. 263). A predatory attack by domestic dogs that resulted in the death of an infant bonnet macaque has been reported by Simonds (1965, p. 179). Fatal diseases that have been reported or identified in *M. radiata* include bubonic plague, which is said to have killed large numbers of bonnet macaques near Gadag, 50 km east of Dharwar (Shortridge in Wroughton, 1912, p. 1176), and Kyasanur Forest disease, a tick-borne virus infection that has been isolated in individuals of this species that were found dead in forests in Shimoga District, 100 km south of Dharwar (Work & Trapido, 1957, p. 342; Work, 1958, p. 250). Old age is suspected as the cause of death of a senescent male that disappeared from the Somanathapur troop, south of Mysore, between January and April 1962 (Simonds, 1965, p. 179).

Individual survival and population size under natural conditions apparently are strongly influenced by predation pressure and by carrying capacity of the habitat. Population growth may be explosive in bonnet macaque groups that are artificially introduced in areas where there are no predators and no nearby troops to compete for resources. Krishnan (1972, p. 538) reports on such a group that was introduced in the Kodikadu Reserved Forest, Point Calimere. This group increased in five or six years from 30 individuals to about 100 individuals, which implies that 10 or 15 infants were born each year and that nearly all of these infants survived to the end of the five- to six-year period of observation (cf. table 14). A similar explosive population increase also may have occurred when *M. radiata* was introduced in the Mascarene Islands (see under Distribution).

Addendum.—Six important works, listed below, that relate to the natural history of *M. radiata* were published while the present paper was in press.

- GLICK, B. B. 1980. Ontogenetic and psychobiological aspects of the mating activities of male *Macaca radiata*, pp. 345–369. In Lindburg, D. G., ed., *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold, New York.
- HANDEN, C. E., AND P. S. RODMAN. 1980. Social development of bonnet macaques from 6 months to 3 years of age: A longitudinal study. *Primates*, 21 (3): 350–356.
- KURUVILLA, G. P. 1980. Ecology of the bonnet macaque (*Macaca radiata* Geoffroy) with special reference to feeding habits. *J. Bombay Nat. Hist. Soc.*, 75 (suppl): 976–988.
- MAKWANA, S. C. 1980. Observations on population and behavior of the bonnet monkey, *Macaca radiata*. *Comp. Physiol. Ecol.*, 5: 9–12.
- PIRTA, R. S., P. PRAKASH, AND M. SINGH. 1981. A population study of two species of non-human primates: *Macaca mulatta* and *Macaca radiata*. *J. Bombay Nat. Hist. Soc.*, 77 (3): 429–434.
- RAHAMAN, H., AND M. D. PARTHASARATHY. 1979. Behavioral variants of bonnet macaque (*Macaca radiata*) inhabiting cultivated gardens. *J. Bombay Nat. Hist. Soc.*, 75 (2): 406–425.

Macaca radiata radiata (E. Geoffroy, 1812)

- Cercocebus radiatus*: E. Geoffroy, 1812, p. 98—external characters; cranial comparisons with *M. silenus*; distribution, India; specific name is an adjective referring to the radiate arrangement of crown hairs.
- [P]ithecus *radiatus*: Desmarest, 1817, p. 325—external characters; taxonomic history; distribution, India.
- [M]acacus *radiatus*: Desmarest, 1820, p. 64—taxonomy; distribution, India.
- Cercopithecus radiatus*: Kuhl, 1820, p. 13—external characters; distribution, eastern India.
- [Simia] M[acacus] *radiatus*: Griffith, 1827, p. 17—external characters; taxonomy; distribution, India.
- [Simia] *radiata*: G. Cuvier, 1829, p. 95—external comparison with *M. sinica*.
- [Inuus] *radiatus*: Wagner, [1839], p. 140—external characters; distribution, Malabar Coast.
- M[acacus] *radiatus* (affinis): Blyth, 1863, p. 8—distribution, "Formosa."
- M[acaca] *radiata*: Hinton and Wroughton, 1921, p. 815—nomenclature.
- [Zati; genus or subgenus] *radiata*: Pocock, [1926], p. 1572—taxonomy; distribution, southern India.
- M[acaca] *radiata radiata*: Pocock, 1931b, p. 276—part, external, and cranial characters; taxonomy.
- Macaca (Zati) radiata*: Hill, 1932, p. 314—external characters. Hill, 1974, pp. xiv, xv, 694—taxonomy.
- Toque: F. Cuvier, 1820, p. 1 (part), plate (animal, color)—taxonomy; penial characters; distribution, Malabar Coast.
- Simia sinica* . . . var.: Griffith, 1821, p. 110 (not Linnaeus, 1771)—taxonomy.
- M[acacus] *sinicus*: I. Geoffroy, 1851, p. 26 (not L.)—taxonomic history; type history; distribution, India, Mauritius ("vraisemblablement importée").
- [Inuus] *sinicus*: Wagner, 1855, p. 56 (not L.)—external characters; distribution, peninsular India.
- Pith[ecus] (Mac[acrus]) sinicus*: Dahlbom, 1856, p. 117 (not L.)—external characters; distribution, India.
- [Cynamolgus] Z[ati; subgenus] *sinicus*: Reichenbach, 1862, p. 130, pl. 23 (figs. 27–29; animals in color) (not L.)—taxonomic history; distribution, India, Mauritius (introduced).
- Cercocebus sinicus*: Schlegel, 1876, p. 99 (not L.)—part, external characters; distribution, Deccan.
- Macacus (sinicus), affinis*: Anderson, 1879, p. 91 (not L.)—doubtful species; distribution, Formosa (probably introduced).
- Simia sinica*: Wroughton, 1912, p. 1176 (not L.)—locality records; vernacular names; field notes. Hinton and Wroughton, 1921, p. 813—name not properly applicable to this species.
- Pithecus sinicus*: D. G. Elliot, [1913], p. 221 (not L.)—external and cranial characters; distribution, southern India.
- M[acaca] *sinica*: Wroughton, 1918, p. 555 (not L.)—external characters; locality records.

Zati sinicus: Pocock, 1921, p. 227, figs. g-k (penis) (not L.)—penial comparisons; taxonomy.

Silenus . . . *sinicus*: Stiles and Nolan, 1929, p. 535 (not L.)—parasites.

Macacus pileatus: Newton, 1893, p. 217 (not Kerr, 1792, p. 69)—introduced in Mauritius.

Pithecus albibarbatus: D. G. Elliot, [1913], cranial pl. xxiv (skull) (not Kerr, 1792)—misidentification (see Pocock, 1939, p. 68).

Types.—Of the type series examined by E. Geoffroy (1812, p. 98), two specimens have been preserved. The lectotype, designated by I. Geoffroy (1851, p. 26), is a mounted skin (MNHN 353/223, Type Cat. No. 56a; skull inside) of an adult male that was presented alive to the Paris Menagerie by Mme. Regnault de Saint Jean d'Angély in 1801; the monkey died in captivity in December 1803 or January 1804 (Nivôse, an XII, French Republican calendar). The paralectotype is a mounted skin (MNHN 356/226, Type Cat. No. 56b; no skull) of a captive immature male that died in the Paris Menagerie in 1815 (cf. Rode, 1938, p. 222); when examined by E. Geoffroy (1812, p. 98), this monkey evidently was still alive. Another mounted specimen (MNHN 355/227) in the Paris Museum also is tagged "Type," but this is the skin of a juvenile that died in captivity in 1837, and therefore it obviously was not available to E. Geoffroy (1812, p. 98) when he described this species.

Type-locality.—Peninsular India. E. Geoffroy's (1812, p. 98) statement concerning the provenance of this species is "Habite l'Inde," which is the locality notation on the tag of the lectotype (MNHN 353/223). The spurious notation "Bengalé" is written on the underside of the stand of the paralectotype (MNHN 356/226).

Distribution (fig. 1).—Peninsular India from the northern limit of the species (above, p. 2) southward as far as the Palni Hills and the Shevaroy Hills.

Diagnostic pelage color characters (prime pelage).—Crown grayish brown, cap hairs frequently tipped with blackish; upper back drab grayish brown, variably washed with pale yellowish, hair banding relatively inconspicuous; lower back with a variably defined dark brown to blackish median streak; outer surface of arms and legs ochraceous gray; skin of ventral surface broadly and deeply pigmented dark bluish gray.

Specimens examined.—Total, 122.

Skins and skulls, 53—Localities Nos. 10 (3), 12(2), 14 (1), 15 (6), 19 (2), 26 (3), 33 (4), 40 (2), 43 (1), 45 (1), 59 (2), 62 (1), 63 (2), 64 (1), 66 (2), 71 (1), 72 (3), "Ceylon" (2: ANSP, 1; USNM, 1), "Formosa" (1), "Madras" (1), "Southeastern Asia," (2: AMNH), "Travancore" (1), no locality data (9: FMNH, 1; IRSN, 1; MNHN, 1; NHMB, 1; RMNH, 5).

Skins only, 26—Localities Nos. 7 (2), 10 (1), 38 (1), 63 (1), "Bengalé" (1), "Decan" (4, including 2 with skull inside), "India" or equivalent (4: IRSN, 1, skull inside; MNHN, 2, including 1 with skull inside; ZSBS, 1), "Malaya Peninsula" (1: AMNH), "le Maurice" (1, skull inside), Réunion (1), no locality data (9: IRSN, 1; MNHN, 1; RMNH, 5; ZMUZ, 1; ZSI, 1).

Skulls only, 43—Localities Nos. 1 (1), 2 (2), 57 (1), "India" (2: BM, 1; NHRM, 1), no locality data (37: AIUZ, 17; BM, 10; FMNH, 1; IRSN, 3; USNM, 1; ZSI, 5, including 1 mandible only).

For details, except where museum is specified here, see Figure 1 and Gazetteer.

Macaca radiata diluta Pocock, 1931

Cercocebus sinicus: Schlegel, 1876, p. 100 (not Linnaeus, 1771)—part, locality record, Pondicherry.

Macaca sinica: Wroughton, 1921, pp. 546, 549 (not L.)—locality records, Kambam, Bhu-tapandi.

M[acaca] radiata radiata: Pocock, 1931b, p. 278—part, external characters of specimen collected at "Cumbum" [Kambam].

M[acaca] radiata diluta Pocock, 1931b, p. 278—external characters, distribution, "Boothapaundy" [Bhutapandi]; subspecific name is an adjective alluding to the coloration, which is characterized as paler than in the nominate subspecies.

Macaca (Zati) radiata diluta: Hill, 1937, pp. 205, 212—external characters; field notes.

Types.—The holotype designated by Pocock (1931b, p. 279) is the stuffed skin, with skull, of an adult female (BM 1937.5.26.1, Coll. No. 158), collected at Bhutapandi by R. S. N. Pillay, 18 Nov. 1915 (cf. Wroughton, 1921, p. 549). This specimen, however, is not currently tagged as type; instead, the paratype (BM 30.11.1.31, Coll. No. 171, adult female, skin and skull, same locality and collector, 20 Nov. 1915) erroneously is so tagged (cf. Hill, 1974, p. 708). The basis for determination of the authentic holotype (Int. Code Zool. Nomencl., Art 73b) is explained below.

Pocock (1931b, p. 278) based this subspecies solely on two adult female specimens (table 15). Although no specimen numbers are mentioned, each of the two specimens is identifiable by its recorded external measurements, which are specified by Pocock. (Following his standard practice, Pocock converted measurements recorded by the collector in millimeters to inches by dividing by 25.) Of the two specimens, the one with the smaller measurements (BM 1937.5.26.1) is designated by Pocock (p. 279, table) as "Type of *diluta*." This same type designation ("the smaller specimen, the type") is repeated by Pocock (1939, p. 42) in a subsequent account of *M. r. diluta*, thereby unequivocally confirming his original selection. These two published designations of the smaller specimen as holotype clearly establish that tagging of the larger specimen as "Type," which probably was done by Pocock himself, was an unfortunate curatorial lapsus.

Type-locality.—Bhutapandi, Tamil Nadu (state), extreme southern India; cited by Pocock (1931b, p. 278) as "Boothapaundy in Travancore."

Distribution (fig. 1).—Southeastern peninsular India; known northern marginal records of this subspecies are Alleppey (few miles S; ca. 9°25'N, 76°20'E), Kambam (9°44'N, 77°18'E), and Pondicherry (11°56'N, 79°49'E).

TABLE 15. External measurements of type-series of *Macaca radiata diluta* Pocock, 1931.

Source of data	Length	
	Head and body	Tail
Pocock, 1931b, p. 279:		
"Type of <i>diluta</i> ," ♀	1' 1 1/5" ¹ [330 mm] ²	1' 9" [525 mm] ²
Paratype, ♀	1' 4 4/5" [420 mm] ²	1' 10 4/5" [570 mm] ²
Specimen tags:		
BM 1937.5.26.1 ³ ♀	328 mm ⁴	524 mm
BM 30.11.1.31 ⁵ ♀	420 mm	571 mm

¹This is the measurement given in Pocock's (1931b, p. 279) table; the slightly different measurement, 1' 1 3/5", given in the text on the same page evidently is the result of a typographical error.

²Pocock's conversion factor: 1 inch = 25 mm.

³Collector's No. 158, collected by R. S. N. Pillay at "Bhoothapaundi, Travancore," 18 Nov. 1915.

⁴This measurement, which was taken and recorded by the collector, probably is in error (see table 1); however, the error was not noticed by Pocock and consequently does not affect his type designation. In any case, measured as dry skins, BM 1937.5.26.1 (HB = 510 mm) is clearly smaller than BM 30.11.1.31 (HB = 565 mm).

⁵Collector's No. 171, collected by R. S. N. Pillay at "Bhoothapaundi, Travancore," 20 Nov. 1915.

Diagnostic pelage color characters (prime pelage).—Crown pale yellowish brown; upper back brightly colored, pale yellowish brown to golden brown, hairs conspicuously banded dark brown basally and bright yellowish distally; lower back slightly drabber than upper back; outer surface of arms and legs pale grayish brown; skin of ventral surface mostly unpigmented whitish in four specimens examined (Bhutapandi, BM, 2; Kambam, BM, 1; Travancore, ZSI, 1; not examined in Pondicherry specimen, RMNH).

Specimens examined.—Total, 6.

Skins and skulls, 3—Locality Nos. 77 (1), 87 (2).

Skins only, 3—Locality Nos. 73 (1, skull inside), 82 (1), "India" (1: BM).

For details, except where museum is specified here, see Figure 1 and Gazetteer.

GAZETTEER OF *MACACA RADIATA* LOCALITIES

Locality names listed as primary entries in this gazetteer preferentially are the standard names approved in U.S. Board on Geographic Names (USBGN) Gazetteer: India (1952), with diacritical marks omitted. Primary entries for macaque localities that are not included in USBGN: India are spelled here either as in U.S. Defense Mapping Agency world map sheets, Series 1301, scale 1:1,000,000, or as in the original source. Secondary entries, with cross references to corresponding primary entries, give variant spellings or alternate locality names that appear on specimen tags or in published literature on *M. radiata*.

The sequence of information presented in each primary entry is as follows:

1. locality name
2. altitude, if available
3. name of state (capitalized)
4. coordinates of locality, usually taken from USBGN: India
5. name of collector or observer followed by parenthetical reference to published locality notes, if any
6. date of collection or observation
7. abbreviated name of museum where specimens are stored and number of specimens available (with indication of part preserved, if skin and skull are not both present) or bibliographic reference to literature record
8. italicized locality number as shown in distribution map (fig. 1)

Macaca radiata radiata

Anamalai Hills. See Anaimalai Hills.

Anaimalai Hills, N, 1,500–3,000 ft; KERALA; ca. 10°20'N, 76°50'E; observed by C. R. Stonor (1944, p. 591), 12 Feb.–10 March 1944. 69

Avalgodu; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20

Bairankuppe. See Byrankuppe.

Bandipur; KARNATAKA; 11°40'N, 76°38'E; observed by M. Krishnan (1972, p. 536), date unknown. 54

Bandipur, 1 mile NE, 3,000–3,500 ft; KARNATAKA; 11°40'N, 76°38'E; observed by P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 54

- Bandipur, 1 mile W, 3,000–3,500 ft; KARNATAKA: 11°40'N, 76°38'E; observed by P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 54
- Bandipur National Park. See Bandipur Wildlife Sanctuary.
- Bandipur Wildlife Sanctuary; KARNATAKA; ca. 11°40'N, 76°38'E; observed by H. C. Sharatchandra and M. Gadgil (1976, p. 646; Nair et al., 1978, p. 420), 1974–75, and M. A. R. Khan (1977, p. 517), 1975–76. 54
- Bangalore, 4,000 ft; KARNATAKA; ca. 13°00'N, 77°35'E; collected by Ripley Indian Expedition, 18 March 1947 (AMNH, 2); observed in Bangalore City by A. S. Rajagopal (1965, p. 228), date unknown, and H. Rahaman and M. D. Parthasarathy (1967, p. 252; 14 troops), Aug. 1964–Jan. 1965. 40
- Bangalore-Krishnagiri road; KARNATAKA or TAMIL NADU; ca. 12°45'N, 77°45'E; several troops observed by A. S. Rajagopal (1965, p. 228), date unknown. 41
- Bellary. See Vijayanagar.
- "Bengalé"; ca. 22°–27°N, 84°–90°E; spurious locality notation (MNHN, 1 [skin only]).
- Biligiri Rangan Hills; KARNATAKA: 11°54'N, 77°14'E; collected by "H. C. Raven, Hopwood Chindwin Exp.," 26 March 1935 (AMNH, 1 skin only). For basis of doubt concerning identity of collector, see Morris, 1936, p. 668. 38
- Billigirirangan Hills. See Biligiri Rangan Hills.
- Bombay. See Yeur.
- Byrankuppe, near; KARNATAKA; 11°52'N, 76°12'E; two troops observed by A. Nolte (1955, p. 77; 1956, p. 177), April–May 1953. 47
- Cauvery River. See Ranganathitoo Sanctuary.
- Channapatna. See Malur.
- Chica Nayakana Hully. See Chiknayakanhalli, vicinity.
- Chiknayakanhalli, vicinity; KARNATAKA; 13°26'N, 76°37'E; sight record (identification equivocal), reported by F. Buchanan (1807, p. 55), 21 Aug. 1800. 32
- Cochin. See Sharnelli Estate.
- Coonor-Mettupalaiyam road, milestone 12 [km]; TAMIL NADU; 11°19'N, 76°56'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 60
- Coonor-Mettupalaiyam road, milestone 17 [km]; TAMIL NADU; 11°18'N, 76°56'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 60
- Coromandel coast; ANDHRA PRADESH; ca. 14°00'N, 80°10'E; collected by F. Eydoux and L. F. A. Souleyet (1841, p. xiv), 5 April–12 June 1837 (MNHN, 2; not seen, reported by I. Geoffroy, 1851, p. 26). 28
- Dakhan. See Deccan.
- Decan. See Deccan.
- Deccan; MAHARASHTRA, ANDHRA PRADESH and KARNATAKA; ca. 10°–15°N, 75°–80°E; reported by W. H. Sykes (1831, p. 99); collector unknown, 1862–75 (RMNH, 4 [2 skulls in skins, 2 skins only], including at least two captives). Not mapped.
- Devikop, 2,000 ft; KARNATAKA; 15°08'N, 74°56'E; collected by G. C. Shortridge (in Wroughton, 1912, p. 1176), 21 Nov. 1911 (BNHS, 1). 14
- Dharwar, 2,300 ft; KARNATAKA; ca. 15°28'N, 75°02'E; collected by G. C. Short-

ridge (in Wroughton, 1912, p. 1176), 14 Nov. 1911 (BM, 2; FMNH, 1; ZSI, 1 [skin only]). 10

Dharwar, 4.4–17.5 km SW; KARNATAKA; ca. 15°25'N, 74°55'E; nine open-land troops observed by Y. Sugiyama (1972, p. 255), June–Sept. 1961; six troops observed by N. Koyama (1973, p. 225), 2 Jan.–14 March 1963. 9

Dharwar, 18.4–29.5 km SW; KARNATAKA; ca. 15°20'N, 74°50'E; three forest troops observed by Y. Sugiyama (1972, p. 255), June–Sept. 1961. 8

Dodderi; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20

Dukhun. See Deccan.

Eastern Ghats, near Nellore; ANDHRA PRADESH; ca. 14°45'N, 79°10'E; specimen examined by T. C. Jerdon (1867, p. 13), date unknown. 27

“Formosa”; TAIWAN; ca. 22°–25°N, 120°–122°E; living captive sent by R. Swinhoe, 1859 (ZSI, 1; see Blyth, 1860, p. 87, and 1875, p. 8). Not mapped.

Gadag; KARNATAKA; 15°25'N, 75°37'E; reported by G. C. Shortridge (in Wroughton, 1912, p. 1176), Nov.–March 1911. 11

Gaday. See Gadag.

Gersoppa, sea level; KARNATAKA; 14°15'N, 74°39'E; collected by G. C. Shortridge (in Wroughton, 1913, p. 30), 27–29 May 1912 (BM, 2 [1 skin only]). 19

Ghatmatha; MAHARASHTRA; 17°25'N, 73°40'E (Moore & Tate, 1965, p. 320); collected by S. H. Prater (in Wroughton, 1916, p. 311), 17 Dec. 1914 (BM, 1 [skin only]); collector unknown, 15 Dec. 1914 (BNHS, 1 [mounted specimen on exhibit]). 7

Gudalur-Theppakadu, forest country between; TAMIL NADU; ca. 11°33'N, 76°32'E; collected by C. Donovan (1920, p. 718), May–June 1919 (specimens not preserved). 55

Gundalapettu-Chamarajnagar. See Gundlupet-Chamrajnagar road.

Gundlupet-Chamrajnagar road, milestone 1, 2 [km]; KARNATAKA; 11°49'N, 76°41'E; two troops observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 52

Gudulur. See Gudalur-Theppakadu.

Haleri, 3,555 ft; KARNATAKA; ca. 12°27'N, 75°48'E; collected by G. C. Shortridge (in Ryley, 1913b, p. 489), 20 Dec. 1912, 16 Jan. 1913 (BM, 4). 33

Halery. See Haleri.

Halgali; KARNATAKA; 14°21'N, 75°06'E; (Work, 1958, p. 273); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849) specimen not preserved. 17

Hampi. See Vijayanagar.

Hangala, 2,500–3,000 ft; KARNATAKA; 11°45'N, 76°39'E; observed by P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 53

Haravadike; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20

Hosabale; KARNATAKA; 14°19'N, 75°02'E (Work, 1958, p. 272); collected by

- Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20
- Jalarpet; TAMIL NADU; 12°34'N, 78°35'E; observed by M. Krishnan (1972, pp. 509, 537), date unknown. 44
- Kabbanir-Fluss. See Byrankuppe.
- "Kachh" [Kutch]; GUJARAT; ca. 23°–24°N, 68°–72°E; imported captive observed by F. Stoliczka (1872, p. 220), 1871–72. Not mapped.
- Kakkenahala; KARNATAKA; 11°37'N, 76°35'E; observed by P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 54
- Kanara [district]. See Gersoppa.
- Kanara Forest. See Devikop.
- Karchikoppa; KARNATAKA; 14°18'N, 75°08'E (Work, 1958, p. 273); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 18
- Kargudi. See Theppakadu-Kargudi area.
- Karjikoppa. See Karchikoppa.
- Karumbapatti. See Kurumbapatti.
- Karwar, forest; KARNATAKA; ca. 14°48'N, 74°08'E; observed by M. Krishnan (1972, p. 536), date unknown. 13
- Kauveri River. See Ranganathitoo Sanctuary.
- Keladi; KARNATAKA; 14°13'N, 75°00'E (Work, 1958, p. 272); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 21
- Khandala, rocky cliffs and forests; MAHARASHTRA; 18°45'N, 73°23'E; reported by C. McCann (1933, p. 810). 5
- Kilkotagiri. See Kotagiri.
- Kodaikanal. See Palni Hills, 5,500 ft.
- Kolar, 2,786–4,026 ft; KARNATAKA; 13°08'N, 78°08'E; collected by G. C. Shortridge (in Ryley, 1913a, p. 283) 29 Sept. 1912 (BM, 1). 43
- Konkan; MAHARASHTRA; ca. 18°05'N, 73°25'E; reported by R. M. Dixon (1894, p. 104). 6
- Kotagiri, 5,120 ft; TAMIL NADU; 11°26'N, 76°53'E; collected by P. Gosse (in Wroughton & Davidson, 1920, p. 1031), 25 June 1918 (BM, 2). 59
- Koyna Valley. See Ghatmatha.
- Kummur. See Kummuru.
- Kummuru; KARNATAKA; 14°25'N, 75°06'E (Work, 1958, p. 273); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 17
- Kuppe; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20
- Kurnool. See "Malakondapenta, Kurnool District."
- Kurumbapatti; TAMIL NADU; 11°45'N, 78°15'E (Moore & Tate, 1965, p. 324); collected by N. A. Baptista, 21 April 1929 (BM, 1). 62

- Kuruvari; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20
- Kyasanur Forest, 580–650 m; KARNATAKA; 14°17'N, 75°02'E; diseased specimen reported by T. H. Work (1958, pp. 250, 272), 28–29 March 1957; 172 specimens collected in general area by Virus Research Centre, Poona (Trapido et al., 1964, pp. 765, 768, 769), 1957–61, examined for ticks, monkeys not preserved. 20
- Machchur, Palni Hills, 4,000 ft; TAMIL NADU; 10°16'N, 77°35'E; (Survey of India, 1:126,720, Sheet 58 F/SE); collected by C. McCann (in Lindsay, 1926, p. 592), 5 April 1922 (ZSI, 1). 72
- Machur. See Machchur.
- Maddathoray. See Mattathur.
- "Madras" [formerly a state]; ANDHRA PRADESH or TAMIL NADU; ca. 8°–20°N, 75°–80°E; collected by T. C. Jerdon, date unknown (BM, 1; possibly same specimen as that reported by Jerdon [1867, p. 13] from Eastern Ghats, near Nellore). Not mapped.
- Malabar coast; KERALA; ca. 10°15'–12°20'N, 75°00'–76°00'E; two specimens collected by M. Housard, date unknown (apparently not preserved; see F. Cuvier, 1820, p. 1). Not mapped.
- "Malakondapenta, Kurnool District," probably equivalent to Marla Konda-Marlapenta, Kurnool District (cf. Pocock, 1931a, p. 51); ANDHRA PRADESH; 15°48'N, 79°01'E (Survey of India, 1:126,720, Sheet 57 M/NW); collected by N. A. Baptista, 14 May 1930 (BM, 3 [including 1 skull in BNHS, No. 5053]). 26
- Malagaladde; KARNATAKA; 14°18'N, 75°05'E (Work, 1958, p. 272); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 18
- Malur, Channapatna [subdistrict]; KARNATAKA; 13°00'N, 77°55'E; observed by A. S. Rajagopal (1965, p. 228), date unknown. 42
- Manali Theppakadu, forest; TAMIL NADU; ca. 11°35'N, 76°34'E; observed by P. E. Simonds (1973, p. 600), 1961–63 or 1970. 55
- Mangata, 3,000–3,500 ft; KARNATAKA; 11°39'N, 76°40'E; observed by P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 54
- Marasa; KARNATAKA; 14°12'N, 75°03'E (Work, 1958, p. 272); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 22
- Marla Konda. See "Malakondapenta, Kurnool District."
- Marlapenta. See "Malakondapenta, Kurnool District."
- Matheran; MAHARASHTRA; 18°59'N, 73°16'E; collected by H. M. Phipson, April 1888 (BNHS, 1 [skull only]); collected by J. Banty, May 1892 (BNHS, 1 [skull only]). 4
- Mattathur; KERALA; 10°23'N, 76°20'E (USDMA, series 1301, Sheet NC43) reported as host of pseudoscorpion by E. Ellingsen (1914, p. 10), 17 Nov. 1908; host of tick, *Haemaphysalis bispinosa* (Nuttall & Warburton, 1915, p. 432). 65
- Maurice. See Mauritius.

- Mauritius; MASCARENE ISLANDS: 20°18'S, 57°36'E; *M. r. radiata* introduced (see above, p. 2); presented by M. l'abbé Bascou, 1851 or earlier) (MNHN, 1 [skin only]). Not mapped.
- Moyar River. See Mangata.
- Moyar Valley. See Nilgiri Hills, N, overlooking Moyar Valley.
- Mudumalai Wild Life Sanctuary, 3,000–3,800 ft; TAMIL NADU; ca. 11°37'N, 76°31'E; reported by J. J. Spillett (1969, p. 640), 1965–66; observed by M. Krishnan (1972, p. 536, pl. 4), 27 Sept. 1966, and M. A. R. Khan (1977, p. 517), 1974–76, and S. S. C. Nair et al. (1978, p. 420), July–Oct. 1975. 55
- Mysore, Horticulture Department field; KARNATAKA; 12°18'N, 76°39'E; observed by M. Singh and R. Sachdeva (1977, p. 605) and M. Singh and R. S. Pirta (1978, p. 265), 1974–77, 48
- Mysore-Bandipur. See Somanathapur, 1 mi. W.
- Mysore-Bandipur Sanctuary; KARNATAKA; 12°18'N, 76°39'E–11°40'N, 76°38'E; reported by J. J. Spillett (1968b, p. 318), 27–29 Nov. 1966. 48–53
- Mysore-Bangalore road, milestone 28, 30, 32 [km]; KARNATAKA; 12°30'N, 76°50'E; three troops observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 36
- Mysore-Bangalore road, milestone 34, 36 [km]; KARNATAKA; 12°32'N, 76°52'E; two troops observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 37
- Mysore-Bangalore road, milestone 83 [km]; KARNATAKA; 12°44'N, 77°17'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 39
- Mysore-Mangalore road, milestone 94, 96 [km]; KARNATAKA; 12°23'N, 75°50'E; two troops observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 34
- Nadahalli. See Nadhalli.
- Nadhalli; KARNATAKA; 14°22'N, 75°04'E (Work, 1958, p. 272); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 17
- Nagarhole Wildlife Sanctuary; KARNATAKA; 12°05'N, 76°05'E (Spillett, 1968b, map 2); observed by M. A. R. Khan (1977, p. 517), 1975–76. 46
- Nagarjunakonda valley; ANDHRA PRADESH; 16°31'N, 79°14'E; erroneously reported by R. Subrahmanyam and V. V. Rao (1975, p. 6), who also erroneously report the liontail macaque, "*Innus silenus*" (= *Macaca silenus*), at the same place (cf. Fooden et al., 1981, fig. 1). Not mapped.
- Nelliampathy Hills, northern cliffs; KERALA; ca. 10°35'N, 76°45'E; reported by A. P. Kinloch (1921, p. 939; 1923, p. 552), 1911–1923. 67
- Nelliampathy Hills, southern slopes; KERALA; ca. 10°25'N, 76°45'E; reported by A. P. Kinloch (1921, p. 939; 1923, p. 552), 1911–1923. 68
- Nellore. See Eastern Ghats, near Nellore.
- "Nepâl"; NEPAL; ca. 27°–30°N, 80°–88°E; spurious report by B. H. Hodgson (1834, p. 96), based on misidentified *M. mulatta* (cf. Hodgson, 1832, p. 339). Not mapped.
- Nilghiris. See Nilgiri Hills.
- Nilgiris. See Nilgiri Hills.
- Nilgiri Hills; KERALA or TAMIL NADU; ca. 11°20'N, 76°30'E; collected by W. Davison, date unknown (BM, 1 [skull only]). 57

- Nilgiri Hills, 5,000–8,600 ft; TAMIL NADU; ca. 11°29'N, 76°34'E; "seen occasionally" by M. A. R. Khan (1977, p. 517), 1974–76. 56
- Nilgiri Hills, 7,000 ft; TAMIL NADU; ca. 11°29'N, 76°34'E; observed by P. E. Simonds (1965, pp. 175, 177), Oct. 1961–June 1962. 56
- Nilgiri Hills, N, overlooking Moyar Valley, 4,000 ft; TAMIL NADU; ca. 11°30'N, 76°33'E; collector unknown, Dec. 1919–Jan. 1920 (specimen not preserved; reported by C. Donovan, 1920, p. 721). 56
- Nilgiri Hills, northern and eastern slopes, ca. 6,000 ft; TAMIL NADU; ca. 11°25'N, 76°55'E; observed by F. E. Poirier (1970, p. 260), Sept. 1965–Aug. 1966. 59
- Nilgiri Hills, western slopes, 3,000–4,000 ft; TAMIL NADU; ca. 11°25'N, 76°30'E; observed by F. E. Poirier (1970, pp. 258–260), Sept. 1965–Aug. 1966. 56
- Nishrani; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20
- North Coorg. See Haleri.
- Ootacamund-Mysore road, milestone 92 [km]; KARNATAKA; 12°04'N, 76°40'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 51
- Ootacamund-Mysore road, milestone 107, 108 [km]; KARNATAKA; 12°10'N, 76°40'E; two troops observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 50
- Ootacamund-Mysore road, milestone 114 [km]; KARNATAKA; 12°15'N, 76°40'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 49
- Ootacamund-Mysore road, milestone 117 [km]; KARNATAKA; 12°17'N, 76°40'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 48
- Ootacamund-Mysore road, milestone 121 [km]; 12°18'N, 76°40'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 48
- Padamara, forest; TAMIL NADU; not precisely located, ca. 11°35'N, 76°35'E; observed by P. E. Simonds (1973, p. 600), 1961–63 or 1970. 55
- Palni Hills, 5,500 ft; TAMIL NADU; 10°16'N, 77°33'E; collected by C. McCann (in Lindsay, 1926, p. 592), 22–23 March 1922 (BM, 1; BNHS, 1). 72
- Palni Hills, northern slopes, 3,000 ft; TAMIL NADU; ca. 10°22'N, 77°35'E (Survey of India, 1:126,720, Sheet 58 F/SE); collected by J. Riley O'Brien (in Lindsay, 1926, p. 592), 1921–22 (BM, 1). 71
- Panniar, 1,000–1,250 m; KERALA; ca. 10°00'N, 77°00'E; observed by Y. Sugiyama (1968, p. 289), 5 Jan.–27 Feb. 1963. 70
- Perumel. See Palni Hills, 5,500 ft.
- Ranganathitoo Sanctuary, Cauvery River; KARNATAKA; 12°25'N, 76°40'E (Spillett, 1968b, p. 299); observed by M. Krishnan (1972, p. 536), date unknown. 35
- Réunion; MASCARENE ISLANDS: 20°06'S, 55°36'E; *M. r. radiata* introduced (see above, p. 2); collected by M. Pollen, 1865 (RMNH, 1 [skin only]). Not mapped.
- Sagar-Shimoga road; KARNATAKA; ca. 14°07'N, 75°09'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 24

Salem District. See Kurumbapatti.

Salsette Island, hills; MAHARASHTRA; ca. 19°12'N, 72°54'E; observed by C. McCann (1933, p. 810), date unknown. 2

Samasgi, 2,000 ft; KARNATAKA; 14°40'N, 75°00'E (Moore & Tate, 1965, p. 320); collected by G. C. Shortridge (in Wroughton, 1912, p. 1174), 12 March 1912 (BM, 3; BNHS, 2; FMNH, 1). 15

Satara. See Ghatmatha.

Segur Range. See Sigur Range.

Sharnelli Estate, 1,500 ft; KERALA; 10°32'N, 76°40'E (Survey of India, 1:126,720, Sheet 58 B/NE); collected by J. Riley O'Brien (in Lindsay, 1926, p. 592), 28 May, 6 June 1921 (BM, 1; BNHS, 1). 66

Shernelly. See Sharnelli Estate.

Shevaroy Hills, 4,500 ft; 5,400 ft; TAMIL NADU; ca. 11°50'N, 78°17'E; collected by N. A. Baptista, 19–25 May 1929 (BM, 1; BNHS, 1; ZSI, 1 [skin only]). 63

Shigga; KARNATAKA; 14°19'N, 75°10'E; diseased specimen reported by T. H. Work (1958, pp. 250, 273), 28–29 March 1957. 18

Shimoga District. See Kyasanur Forest.

Sholinghur, temple; TAMIL NADU; 13°07'N, 79°25'E; observed by M. Krishnan (1972, p. 536, pl. 3), 24 May 1960. 31

Siddharkoil. see Siddharkovil.

Siddharkovil; TAMIL NADU; 11°37'N, 78°04'E (Imp. Gaz. India, 14:401); observed by M. Krishnan (1972, p. 509), date unknown. 61

Sigur Range; TAMIL NADU; ca. 11°30'N, 76°42'E (USDMA, Series 1301, Sheet NC43); observed by M. A. R. Khan (1977, p. 517), 1975–76. 58

Somanathapur, 1 mile W, 2,500–3,000 ft; KARNATAKA; 11°43'N, 76°40'E; observed by E. P. Gee (1964, p. 20, pl. 8b) and P. E. Simonds (1965, p. 178), Oct. 1961–June 1962. 53

Sorab; KARNATAKA; 14°23'N, 75°06'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 17

Sorab-Banavasi road; KARNATAKA; ca. 14°28'N, 75°04'E; collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 16

Sorab-Shiralkoppa road; KARNATAKA; ca. 14°23'N, 75°10'E (Work, 1958, p. 273); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 17

South Arcot. See "Tenmali, S. Arcot."

"Southern Mahratta Country"; MAHARASHTRA and KARNATAKA; ca. 14°–19°N, 74°–77°E; reported by W. Elliot (1839, pp. 94, 95). Not mapped.

Srisailam; ANDHRA PRADESH; 16°05'N, 78°52'E; collected by Zoological Survey of India, 11 Feb. 1970 (ZSI, 1; not seen, reported by Agrawal & Bhattacharyya, 1976, p. 213). 25

Tada; ANDHRA PRADESH; 13°35'N, 80°02'E; observed by G. U. Kurup and J. Fooden, 24 May 1973. 30

Tavanadi; KARNATAKA; not precisely located, ca. 14°20'N, 75°00'E; collected

by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 20

“Tenmali, S. Arcot,” possibly equivalent to Timmalai, South Arcot District; TAMIL NADU; $11^{\circ}44'N$, $79^{\circ}08'E$ (Survey of India, 1:126,720, Sheet 58M/NW); collected by W. P. Howell and museum collector, date unknown (ZSI, 1 [skin, No. 12007; skull, No. 7089]). 64

Teppikadu. See Gudalur-Theppakadu.

Thana. See Yeur.

Theppakadu-Kargudi area; TAMIL NADU; ca. $11^{\circ}35'N$, $76^{\circ}35'E$ (Spillett, 1969, p. 663); observed by M. Krishnan (1972, p. 537, pl. 3), 21 Sept. 1970; P. E. Simonds (1973, p. 600), 1961–63 or 1970. 55

Theppakkadu. See Theppakadu-Kargudi area.

Timmalai. See “Tenmali, S. Arcot.”

Tirupathi. See Tirupati.

Tirupati; ANDHRA PRADESH; $13^{\circ}39'N$, $79^{\circ}25'E$; observed by A. S. Rajagopal (1965, p. 228) and M. Krishnan (1972, pp. 509, 537), dates unknown. 29

“Travancore” [formerly a state]; KERALA; specimen probably from Regent’s Park Zoo (Hill, 1937, p. 212), obtained from Mr. Bartlett, date unknown (BM, 1). Not mapped.

Trombay Hills; MAHARASHTRA; $19^{\circ}02'N$, $72^{\circ}56'E$; reported by C. McCann (1933, p. 810). 3

Veduru Guta, forest; TAMIL NADU; not precisely located, ca. $11^{\circ}35'N$, $76^{\circ}35'E$; observed by P. E. Simonds (1973, p. 600), 1961–63 or 1970. 55

Venu Gopal Wild Life Park. See Mysore-Bandipur Sanctuary.

Vijayanagar, 1,500 ft; KARNATAKA; $15^{\circ}19'N$, $76^{\circ}28'E$; collected by G. C. Shortridge (in Wroughton & Ryley, 1913, p. 60), 4 Aug. 1912 (BM, 2). 12

“Western Ghats.” See Deccan.

Wotekolli, 2,000 ft; KARNATAKA; ca. $12^{\circ}08'N$, $75^{\circ}47'E$; collected by G. C. Shortridge (in Ryley, 1913b, p. 489), 27 Dec. 1912 (BM, 1). 45

Wottekolle. See Wotekolli.

Yalgalali; KARNATAKA; $14^{\circ}08'N$, $75^{\circ}02'E$ (Work, 1958, p. 272); collected by Virus Research Centre, Poona, Nov. 1965–Nov. 1967 (Rajagopalan & Anderson, 1971, p. 849), specimen not preserved. 23

Yelagalale. See Yalgalali.

Yeur, jungle near; MAHARASHTRA; $19^{\circ}14'N$, $72^{\circ}57'E$ (Survey of India, 1:63, 360, Sheet 47 A/16); collected by R. E. Hawkins, 10 Aug. 1958 (BNHS, 1 [skull only], picked up along roadside; collector’s statement provided by H. Abdulali, letter, 23 May 1978). 1

Macaca radiata diluta

Alleppey, temple few miles S, on road to Quilon; KERALA; ca. $9^{\circ}25'N$, $76^{\circ}20'E$; observed by W. C. O. Hill (1937, p. 212), June 1936. 78

Aramboli, temple 5 miles S; TAMIL NADU; $8^{\circ}13'N$, $77^{\circ}34'E$; observed by W. C. O. Hill (1937, p. 212), June 1936. 88

Ashambo Hills. See Papanasam.

Ashambu Hills. See Papanasam.

Bhoothapaundy. See Bhutapandi.

Bhutapandi; TAMIL NADU; 8°16'N, 77°26'E; collected by R. S. N. Pillay (in Wroughton, 1921, p. 549), 18, 20 Nov. 1915 (BM, 2). 87

Boothaundy. See Bhutapandi.

Courtallam. See Kuttalam.

Cumbum. See Kambam.

Cumbun. See Kambam.

Kambam; TAMIL NADU; 9°44'N, 77°18'E; collected by S. H. Prater (in Wroughton, 1921, p. 546), 30 May 1917 (BM, 1). 77

Kodaicanal Road, milestone 23. See Kodaikanal Road, milestone 23 [km].

Kodaikanal Road; TAMIL NADU; 10°11'N, 77°56'E; observed by M. Krishnan (1972, p. 509), date unknown. 75

Kodaikanal Road, milestone 23 [km]; TAMIL NADU; ca. 10°10'N, 77°40'E; observed by P. E. Simonds (1974a, p. 157), 1961–63 or 1970. 76

Kodikadu Reserved Forest; TAMIL NADU; 10°17'N, 79°46'E; *M. radiata* introduced from Kambakonam vicinity, April 1965 (Daniel, 1968, p. 519; Krishnan, 1972, pp. 516, 538). Not mapped.

Kumbakonam, near; TAMIL NADU; ca. 10°58'N, 79°23'E; collector unknown, April 1965, ca. 30 living specimens obtained and subsequently transported to Kodikadu Reserved Forest (Krishnan, 1972, p. 538). 74

Kuttalam, forest; TAMIL NADU; ca. 8°55'N, 77°17'E; observed by K. Krishna-moorthy and M. Krishnan (1972, pp. 509, 536, 539), April 1967 and other dates unspecified. 84

Madura. See Kambam.

Naraikkadu Estate, vicinity; TAMIL NADU; ca. 8°30'N, 77°30'E; reported by C. G. Webb-Peploe (1947, p. 630). 86

Papanasam; TAMIL NADU; 8°42'N, 77°23'E; observed by M. Krishnan (1972, pp. 509, 537), date unknown; observed by H. Abdulali (letters, 23 May 1978, 26 June 1978) and R. Ali, April 1978. 85

Papavinasam. See Papanasam.

Periyar Lake, N; KERALA; ca. 9°34'N, 77°10'E; reported by J. Tanaka (1965, p. 111), 7 Jan.–5 Feb. 1963. 79

Periyar Wildlife Sanctuary; KERALA; ca. 9°28'N, 77°04'E; reported by G. U. Kurup (1971, p. 17). 79

Point Calimere Sanctuary. See Kodikadu Reserved Forest.

Pondicherry; PONDICHERRY; ca. 11°56'N, 79°49'E; collector and date unknown (RMNH, 1 [skull in skin]). 73

Pondichery. See Pondicherry.

Quilon. See Alleppey.

Srivilliputhur. See Srivilliputtur-Mudaliar Ootu.

- Srivilliputtur-Mudaliar Ootu, hill track between; TAMIL NADU; ca. 9°35'N, 77°34'E; reported by A. J. T. John Singh (1974, p. 376). 81
- Travancore; KERALA; ca. 9°00'N, 77°00'E; collected by Dr. N. Annandale, 28 Nov. 1908 (ZSI, 1 [skin only]). 82
- Trivandrum, vicinity; KERALA; ca. 8°29'N, 76°55'E; locally obtained living and preserved specimens examined in Trivandrum Zoo and Trivandrum Museum by W. C. O. Hill (1937, p. 212), June 1936. 83
- Varushnaad Valley, ca. 5,000 ft (one observation, more common at lower elevations); TAMIL NADU; ca. 9°35'N, 77°30'E; reported by A. F. Hutton (1949, p. 689). 80
- Vedaranyam. See Kodikadu Reserved Forest.

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