学位申請論文

大井 徹

Population Organization of Wild Pig-Tailed Macaques

(<u>Macaca</u> <u>nemestrina</u> <u>nemestrina</u>) in West Sumatra.

Running head: Population organization of

pig-tailed macaques

Toru OI

Primate Research Institute
Kyoto University
Inuyama
Aichi
484 Japan

ABSTRACT

A field study of wild pig-tailed macaques was conducted in
West Sumatra, Indonesia, during three periods from January 1985
to February 1987. During the nine months of the first two
periods, unprovisioned monkeys were traced and observed. During
the eight months of the last period, monkeys were provisioned and
observed mainly at the baiting sites. Three troops and ten
solitary males appeared at the two baiting sites. Some males
immigrated into and emigrated from the troops. The troops had a
multi-male multi-female composition. The size of the various
troops was 74, 49, and 81 individuals, respectively, and the mean
adult sex ratio in the troops was 1:6.3, remarkably biased
towards females. The home ranges of two of the troops overlapped
considerably. When the troops encountered each other at the
baiting sites, a clear dominance relationship was recognized.
The troops differed in their integration as ranging units; two of
the troops did not form subgroups (temporal fission and fusion of
a troop), while the other troop frequently split into subgroups.
Recent field studies of pig-tailed macaques have suggested
multi-leveled society with harem-type unit groups. However, in
the present study, the groups observed had neither a substructure
similar to harem-type groups nor a superstructure that emerged as
a result of fusion of the groups. The unit group of the
pig-tailed macaques in West Sumatra appears to be a multi-male,
matrilineal group.

INTRODUCTION

Because of the furtive behavior of pig-tailed macaques
(Macaca nemestrina nemestrina) and their invisibility in their
natural habitat, the ecology and social behavior of these monkeys
has been difficult to analyze from field observations (Bernstein,
1967; Caldecott, 1986; Robertson, 1987).

Bernstein (1967) observed groups which had a multi-male and
multi-female composition, and solitary males, at Lima Belas in
Malaysia, and such multi-male groups appeared to him to represent
stable foraging and reproductive units. By contrast, Caldecott
(1986) suggested that pig-tailed macaques (pigtails) had a fluid,
multi-leveled society with "super-groups", "groups", "sub-groups",
and solitary males. The "group" has a multi-male configuration;
it temporarily splits into "sub-groups" and temporarily fuses
into a "super-group". Caldecott also mentioned that such
grouping tendencies "may be explicable in terms of aggregation
and separation of one-male harem units with permanent female
membership" though he deliberately avoided offering this possible
explanation as a definitive conclusion. Robertson (1987), who
conducted field studies in the Alas Valley, northern Sumatra,
concluded that pigtails had "a society which contained three or
more hierarchically organized group levels". The term "level"
implied "band" defined as a bisexual group whose members shared
the same home range center, "sub-group" composed of one or more
adult females and their offsprings, and "mixed-band" in which
neighboring "bands" or some of their component units associated.
Furthermore, from observations that "bands" which contained two

2

or three breeding males frequently split into "sub-groups" which contained only one breeding male, he proposed that a "band" may have been sub-structured into harems or polygynous one-male groups. However, because of the fragmental nature of their observations without individual identifications in the tropical forest, the aforementioned hypotheses should be reconsidered on the basis of more detailed observations.

After observing wild, unprovisioned pigtails for about nine months, I provisioned and observed the animals for about eight months. At the baiting sites, I collected detailed information about the social relationships from individual identifications which were hard to make from observations in the forest. The aims of the present report is to clarify the configuration of the unit group (as defined by Iṭani, 1977) of this species and its social organization, by an analysis of the roll books of individuals who visited the baiting sites, of movements of groups in the forest, and of social interactions among the groups.

STUDY AREA

The study area is situated at the northern foot of Mt. Kerinci (3,805 m above sea level), West Sumatra Province, Indonesia (1·40'S, 101 20'N) (Fig. 1). The altitude of the area ranges from 850 m to 1,000 m above sea level. Most of the area is gently undulating or flat. The gradient ranges from 3% to 7% (DIT AGRARIA PROP SUMBAR, 1970). The annual rainfall at the study site was 5,570 mm in 1986. The rainfall changed seasonally;

3

there were two periods of relatively high rainfall (March-May, October-January) and two periods of low rainfall (February, June-September) (Fig. 2).

The floristic zone of this area corresponded to an ecotone between hill dipterocarp forest and upper dipterocarp forest (Whitmore, 1984). However, the original vegetation in this area was significantly disturbed by the establishment of tea and coffee plantations by the Dutch during the period from 1927 to 1941. Because of the abandoned tea plantations, and lumbering by the selective cutting method, the present vegetation can be said to be a mosaic of primary and secondary vegetation (Fig. 3). Secondary vegetation was typified by species such as Melasotoma, Trema, Villebrunea, etc., giant herbs such as wild gingers, bananas and rinju (Compositae), and giant woody climbers such as rattans.

Six primate species inhabited this area: pig-tailed macaques (Macaca nemestrina), crab-eating macaques (Macaca fascicularis), siamangs (Hylobates syndactylus), agile gibbons (Hylobates agilis), banded langurs (Presbytis melalophos) and slow loris (Nycticebus coucang). The local people said the crab-eating macaques had intruded into this area within the ten years that preceded the study.

METHODS

The field study was conducted during three periods: from January to March 1985, from June 1985 to March 1986, and from

4

July 1986 to February 1987.

The study area of around 5 km² was divided by the observation paths into a grid with sides of 100 m. Through the entire study period, pigtails were traced by one or more tracker teams which included local assistants, and their ranging routes were mapped. The contact time with the groups which ranged naturally amounted to 858 hours (309 encounters).

From 22 January to 2 March 1986, and from 17 July 1986 to 13 February 1987, I provisioned and observed the animals at the baiting sites. Three baiting sites (Sites I, II, and III) were set up in the study area but the last one was abandoned when the monkeys stopped visiting it after pitching of the blind. Each site was a square with 20 m side in a wood of Jambu Raden trees (<u>Melastoma</u> <u>sp.</u>), the fruit of which was one of the natural foods of the pigtails. The bait, 5~15 kg peanuts with pods, was supplied on every occasion during which observations were made. At the beginning of provisioning, the bait was supplied continuously without any observations of the animals, for about a month. When I had confirmed that the animals visited the site regularly to eat the bait, I pitched a blind. After two or three days, when the animals had become accustomed to the blind, I waited for the animals in the blind and observed them through the peepholes.

An attempt was made to identify and record all the individuals that appeared at the sites. I use the term "troop" to refer to a complete unit group and "group" to refer to any aggregate of the animals for which I could not determine whether it was a subset of the entire troop or an entire troop (Crockett and Wilson,

5

1980). The troop as a unit group was recognized in terms of the stability of its membership and the social interaction between the groups. Three troops (Troops A, B, and C), two groups (Groups E and F), and 10 solitary males were observed at the sites. An additional troop, Troop D, was composed of about 40 animals and ranged in the western part of the study area. However, Troop D did not visit the baiting site.

Groups E and F were recognized because they were composed of individuals not known to be part of Troops A, B, and C. However, as Groups E and F visited Site II just once, I was unable to judge whether they were troops or not. The age-sex composition of Group E was three adult males, two adolescent males, six adult females, nine juveniles, and three infants, while Group F was composed of one adult male, one adolescent male, three adult females, and one adolescent female (for a definition of the age-sex class, see below).

Table 1 shows the number of occasions on which observations were made, and duration of observations for each troop, group, and solitary animals. Prior to the end of September 1986, the adolescents, the adults, and some juveniles of Troops A and B had been identified, and all adult males, some adolescent males and some adult females had been identified in Troop C.

Age-sex classes were distinguished by the body size and secondary sexual characteristic of the monkeys. Adult male: estimated age of over 9 years old, with complete secondary sexual traits; red-colored penis, muscular especially around the shoulders, and a body size of 1.5-2 times that of adolescent males. Adolescent male: estimated age of 5-9 years old; suspension of

6

testicles. <u>Adult</u> <u>female</u>: estimated age of over 5 years old, periodical swelling of sexual skin, parous, nipples elongated by suckling. <u>Adolescent</u> <u>females</u>: estimated age of 3.5-6 years old, periodic swelling of sexual skin, nulliparous. <u>Juvenile</u>: estimated age of 1-4.5 years old for males, 1-3.5 years old for females. Infant: less than 1 year old, blackish fur. .

The names of the individuals are represented by two alphabets; codes of two capital letters represent names of males and codes of a capital letter and a small letter represent names of females.

RESULTS

Size and Age-sex Composition of Troops

A multi-male, multi-female composition emerged as the configuration of a unit group (troop), through examination of stability of membership, and intergroup interactions, as mentioned in the following sections (Table 2). The average number of animals in the troops was 68 (range: 49-81). The mean ratios of immature to mature animals (<u>adult and adolescent:juvenile and infant</u>) was 1:1.2.

Though each troop contained three or four adult males, the sex ratio was biased by the presence of a larger number of females than males. The mean adult sex ratio (adolescent and adult sex ratio) in a troop was 1:6.3 (1:2.9).

With regard to the factors that distorted the sex ratios of troops, we need to examine the sex ratio of the population of

7

this area. The sex ratio of the population was calculated from the number of all the individuals from five years up that appeared at the baiting sites. This sex ratio was 1:1.6, and this figure implies the possibility that the number of females was greater than that of males in the population. However, as there might have been some solitary males who did not appear at the baiting sites, this difference might be slight.

The population density of this area (<u>the number of individuals observed in this area</u> / <u>study area</u>) was approximately 53 individuals per km². In the upper part of the study area, the slopes became steeper and primary forest occupied a much larger proportion of the area. I penetrated up to 1500 m a. s. l. on three occasions, but since I never found any pigtails on these expeditions, the density is probably very low in the upper part of the area.

Integration of Troops as Foraging Units

Two types of troop, in terms of their integration, were recognized: troops that always appeared at the baiting site with almost the complete complement of members and seemed to forage as a tightly knit group even outside the baiting site (Troops A and B), and the other type of troop, which appeared at the baiting site with fluid membership within the troop and seemed to participate in frequent subgrouping (Troop C).

Group sizes of Troops A, B, and C were counted mainly at the baiting sites from February 1986 to February 1987 (Fig. 4). The group sizes of Troops A and B were stable. The size of the group of Troop A was concentrated around 50 level ($\bar{x}=54$, SD=5.3, n=12);

that of Troop B was concentrated around 30 level ($\bar{x}=37$, SD=3.7, n=12), and these values almost coincided with the troop sizes: 59 for Troop A, and 40 for Troop B. By contrast, the group sizes of Troop C fluctuated from the 20 level to the 70 level ($\bar{x}=51$, SD=16, n=16).

Each individual who appeared as a member of a given troop never appeared with other troops, except for the case of one adolescent male, DK. The attendance rate for each individual in Troops A and B at the baiting site was calculated (Table 3). As the time of completion of identification for each individual differed, the periods during which the data were obtained for analysis differed according to sex: for males since July 1986 (Troop A: n=96, Troop B: n=83) and for females since October 1986 (Troop A: n=61, Troop B: n=66).

A difference between the sexes was recognized in the attendance rates. The rate for any of the females was almost 100%. St of Troop B had a rate of 78.8% because one of her legs was damaged by a snare, and for a while, she could not keep up with the movements of the troop. In contrast to the case with females, the attendance rates for males differed according to the individuals in question. The individuals could be grouped into three categories by their rates of attendance: (1) those with attendance rates of more than 80%, who moved stable as troop members, (2) those with attendance rates of around 60%, who usually moved as troop members but who often separated from the troop, i. e., loosely attached troop individuals, (3) those with attendance rates of less than 25%, who joined the troop temporarily. The former two categories define troop individuals,

9

and the last category defines temporal troop individuals. In the previous paragraph, only the troop individuals were included in the counting of the sizes and compositions of troops. Two adolescent males (KM, AK) in Troop A belonged to the class of loosely attached troop individuals. Temporal troop individuals included two young adult males (DO, KR in Troop A) and four adolescent males (MN, PR in Troop A, NP in Troop B, and DK in both Troops A and B). These individuals were comparatively young and low-ranking.

Thus, most of the members foraged together with the exception of the temporal troop individuals in Troops A and B. In particular, stable troop individuals were scarcely ever absent from the troops. ID, the 3rd-ranking adult male in Troop B was temporarily absent from Troop B from 29 January 1987 to 2 February 1987, and appeared again in Troop B on 9 February 1987. On one occasion, in Troop B, two adult males (RS, ID), three adult females (St, Hn, Ks), one adolescent female (Kn), some juveniles, and an infant disappeared simultaneously (1 Feb. 1987). They may have temporarily split from the other members of the troop.

Although the attendance rates for Troop C could not be calculated, it is quite certain that the group size of this troop varied enormously from 21 to 81 (Table 4), and these variations indicate that members of Troop C repeatedly formed subgroups. Five adult males (KK, HS, MS, IM, HT) observed in this troop have been identified since the first observation. The attendance rates for these five males with the females of Troop C were: for KK, 89.5%; HS, 89.5%; IM, 52.6%; MS, 89.5%; HT, 5.2%. While KK, HS, MS always visited the site together (16 visits out of 19

10

visits of Troop C), only MS was observed in the group when 26
individuals were counted at the baiting site on 3 October 1986.
IM was frequently absent from the groups in which KK, HS, MS were
present (6 visits out of 19 visits of Troop C), and on such
occasions the group sizes tended to be smaller (Mann-Whitney U=2,
$N_1=8$, $N_2=6$, p<0.01, one-tailed).

While the trackers followed the natural foraging of Troops
A, B, and D, they did not notice any signs of subgrouping (during
202 hrs of contact time after 57 encounters from August 1986 to
February 1987). However, when Troop C was followed, the groups
sometimes split and moved in different directions (9 cases in 298
hrs contact time, after 61 encounters, from August 1986 to
February 1987). However, the composition of the groups and the
ways in which they moved and fused again were uncertain.

Males' Immigration into and Emigration from the Troops

Immigration into and emigration from the troop were restricted
to males, and such behavior by females was never observed.
Temporal troop males might be males who joined the troop for a
short time. Although the temporal troop males were tolerated by
the troop individuals, and in particular by troop males, solitary
males were never tolerated.

As temporal troop males, two adult males (DO, KR) and three
adolescent males (MN, DK, PR) appeared in Troop A; an adolescent
male (NP) appeared in Troop B; an adolescent male (DK) appeared
in both Troops A and B (Figure 5). Only DO and KR were observed
leading a solitary life before or after they appeared in Troop A.
In the case of Troop C, it was difficult to determine immigrants

11

and emigrants because of frequent subgrouping.

Males appeared to leave troops when they were more than four years old, because the sex ratio for individuals of four years old and under in Troop B, in which the sex of all individuals was known, was 13:14. This value implies that males in this age class have not yet emigrated from the troop. Furthermore, the estimated age of solitary males and temporal troop males ranged from 5 to 16 years (n=14). It is noteworthy, in this context, that individuals of 5 and 6 years of age were observed not as solitary males but only as temporal troop males.

Interactions Between Troops and Solitary Males

Interactions between troops and solitary males were generally antagonistic. Especially, the dominant troop males were antagonistic to the solitaries. However, estrous females and peripheral individuals, such as young males, sometimes showed a permissive attitude towards the solitaries who frequently approached their troop. The solitary males occasionally copulated with estrous females and interacted non-agonistically with the peripheral males of the troop.

BK, an adult male, visited Site I (69 cases). When BK fed at the site, it happened occasionally that either of Troop A (9 cases) or Troop B (14 cases) would appear at the site. In all of these cases, BK retreated from the site immediately without any direct confrontation. On two occasions, BK shook a tree without articulating any sounds against the troop individuals. The alpha or the beta males of Troop A and Troop B then rushed in that direction, and agonistic voices "go, go, go" and the sound of

12

violently swaying branches were heard. These males may have attacked BK. BK was observed to copulate with Kn, an estrous adult female of Troop B, on one occasion. After Troop B left to go southwards, Kn approached BK, who was outside the site on the north side and copulated with him.

At Site II, several encounters between Troop C and solitary adult males (GD, DS) occurred. When troop males came to the site with troop individuals, the solitaries retreated. However, GD appeared at the site with an estrous female of Troop C, and copulated with her on one occasion, and DS appeared at the site with an estrous females on two occasions. Consortship between solitary males and troop females was temporary, and the females returned to the troop afterwards.

.

Interactions among solitary males

Sometimes more than one solitary male appeared at a site simultaneously (7 cases). Their attitudes could be categorized into three patterns, according to the degree of proximity, which seemed to reflect the degree of acquaintanceship or familiarity between them. First, an individual B who had fed at the site left the site as soon as a dominant individual A approached him, and then A started to feed alone (2 cases). Second, three individuals were seen around the site, but none of the individuals entered the site, as if each was nervous about the other (1 case). Third, two individuals fed simultaneously, but they did not come close to each other while feeding (4 cases). A kind of greeting behavior was performed, such as puckering (Bernstein, 1966, 1967) and non-copulatory mounting (2 cases). The directions

13

in which they left, and their attitudes to each other indicated they had just happened to meet at the site.

Interactions between Troops and Home Range

Troops A and B both visited Site I, and often encountered each other (21 cases). Usually, Troop A approached Troop B when the latter troop was feeding at the site, and Troop B retreated quickly, without aggressive interactions (10 cases) or with aggressive interaction, such as threats and chasing (11 cases). These observations imply that Troop A dominated Troop B (Cheney, 1981). As soon as Troop B retreated, Troop A usually began to feed. However, in two cases, Troop A pursued Troop B when the leftover of the bait was a little. The antagonistic encounters occurred before provisioning, also. On 26 July 1985, the group which I was tracking encountered another group which was being followed by another tracking team. After a brief interval, the groups crossed the road one after another, separated again, and moved off in different directions. Before and after two troops crossed the road, agonistic voices and tree-shaking were frequently heard.

Attacks were always started by individuals from Troop A, and they ended with the retreat of Troop B. Attackers included individuals of all dominance status, if juveniles and infants are excluded from consideration (Table 5). The alpha and beta males participated most frequently in the attacks. Females participated in 100% (10 occasions) of the aggressive interactions while males participated in 80% (8 occasions) of the interactions, and in one case the participants were unknown. Targets of attacks were not

14

obvious. The alpha male and the beta male of Troop B always retreated promptly, but in just one case they chased the members of Troop A; when Troop B was feeding at the site, the beta male and two females (3rd-ranking and 14th-ranking), who preceded the main body of Troop A, intruded onto the site, and the alpha male and beta male of Troop B chased them. However, as soon as the main body of Troop A approached, Troop B retreated.

Some individuals of the two troops fed together on two occasions. In one case, when females (middle- and low-rankings: 7th, 8th, 10th 14th) and some juveniles of Troop B were feeding after the main body of the troop had left the site, the 3rd-ranking male of Troop A joined them. Females from Troop B did not come close to him and the male did not chase the females. Finally, as soon as the main body of Troop A arrived, the females from Troop B retreated. In another case, when the females (low-rankings: 11th, 12th, 14th, 15th), some juveniles, and the 3rd-ranking male of Troop B were feeding, a middle-ranking (14th-ranking) female and an adolescent male (5th-ranking) from Troop A joined them. The two members of Troop A stayed together but avoiding the individuals from Troop B, but when the main body of Troop A finally arrived, all of the individuals from Troop B retreated.

Home ranges were determined by summing up enclosed quadrats (which were delineated by the observation paths at intervals of 100 meters) on and within the outermost traces of movement of the troops (Fig. 6). Troops A and B appeared only at Site I, and Troop C appeared at Site II (cf. Table I). Troops A and C used the coffee plantation on the northern side of the study area, but

15

the extent to which they intruded into that area was not certain. Therefore, the home range of Troop A was greater than 140 ha, and that of Troop C was greater than 153ha. The western part of the home range of Troop D was unknown. Only the range of Troop B was completely enclosed within the study area and was accurately estimated (127 ha). The home range of each troop overlapped considerably; 87% for Troop A, 79% for Troop B , 100% for Troop C. The extent of overlapping of home ranges between Troops A and B (area of overlapping part of home range between Troop A and Troop B x 100 / area where home ranges of Troop A and Troop B occupied) was less than 39%; for that between Troops A and C, it was less than 13.3%; for that between Troops B and C, it was less than 3.2%.

DISCUSSION

Troop Size and Sex Ratio

Troop sizes of pig-tailed macaques range from 6 to 81 individuals ($\bar{x}$=36, SD=22, n=17; MacClure, 1964; Bernstein, 1967; Rijksen, 1978; Rodman, 1979; Crockett and Wilson, 1980; Mackinnon and Mackinnon, 1980; Caldecott, 1986; this study). The troop sizes at Lima Belas (Bernstein, 1967; Caldecott, 1986; the "group" of Caldecott should coincide with our definition of troop), and at Mt. Kerinci (this study) are the largest among those reported, ranging from 47 to 81. If the data from these two sites are excluded, the mean troop size becomes 19 (range: 6-35, n=9). The most conspicuous difference in habitat between

16

these two sites and the others is that at the former sites, secondary forest occupied a large fraction of the area (Caldecott, 1986). The larger group size might be explicable in terms of such a forest structure. Secondary forest at a certain stage of succession has rather higher plant productivity than primary forest, and includes patches where the same one or a few species grow up together (Whitmore, 1984). Such patches serve large feeding sites for monkeys. Given that intratroop competition for food can prevent formation of large troops (van Schaick & van Hoof, 1983), large food patches in such secondary forest sustain the existence of large troops. Furthermore, in the past studies (e. g., MacClure, 1964; Crocket and Wilson, 1980) there is possibility that only part of the troops was counted and the troops may have been estimated to be of smaller size than they actually were.

The mean adult sex ratio in a troop was 1:6.3, markedly biased towards females in the same way as that for the Malayan pigtails (1:8), that Caldecott (1986) studied. There are some possibilities that the hunting pressure might distress the male population, although such effect may not be so significant since the approximate adolescent and adult sex ratio of the population (1:1.6) indicated only a comparatively small bias. Using the pigtails for picking of coconuts, the Minankabau tribe, the main dwellers in West Sumatra, hunt many pigtails. Although no monkeys were hunted during the study, some abandoned traps were found in the study area.

A more important factor in this distortion of a 1:1 sex ratio among matures in the troop might be males' immigration into

17

and emigration from the troop. Solitary males have been observed at many study sites (Bernstein, 1967; Rijksen, 1978; Crockett and Wilson; 1980; Caldecott, 1986; this study). The mobility of males suggests that the unit group (troop) should be matrilineal.

There is a clear difference in the adult and adolescent sex ratios in a troop between Japanese and pig-tailed macaques. On the western coast of Yakushima Island, the population of Japanese macaques showed similar features to that on Mt. Kerinci: high troop density [Yakushima, 1 troop/km^2 (Iwano, 1983); Mt. Kerinci, 0.94 troops/km^2] ; high individual density [Yakushima, 33 individuals/km^2 (Maruhashi, 1982); Mt. Kerinci, 52.8 individuals/km^2] , and no physical barriers to prevent intertroop transfer by males (Takasaki and Masui, 1984). However, the adult and adolescent sex ratio in a troop of Yakushima was nearly 1:1 (Maruhashi, 1982; Furuichi, 1985), while that of a troop on Mt. Kerinci was 1:2.9, a much higher values than the approximated sex ratio of the whole population on Mt. Kerinci (1:1.6). The difference in the sex ratio within a troop, between Japanese and pig-tailed macaques, might result from the difference in the troop individuals' tolerance of solitary males between these two species. I postulate that this difference should be ascribed to the difference in mating systems between the two species. Since the Japanese macaque is a seasonal breeder and the pig-tailed macaque is a year-round breeder, available females as mates were fewer for pigtail males than for Japanese macaque males, and pigtail males are more competitive for females (Oi, submitted).

Just as male Japanese macaques leave their natal troops at three to five years of age and transfer to other troops or become

18

solitaries (Nishida, 1966; Sugiyama, 1976), male pigtails leave
their natal troops at around five years of age. Males of 5-6
years of age lived as temporal troop individuals, not yet as
complete solitaries. After repeating temporal stays in some
troops, they may become complete solitaries at an older age. In
the present study, solitaries, BK, DS, and MK appeared at the
same baiting site for periods of a month to seven months. Like
them, some solitary males of pigtails stay for long periods in
one fixed area (Rijksen, 1978). Although some solitaries
happened to meet at the baiting site, they did not organize into
male groups. Robertson (1987) observed cases of a "sub-group
composed of two or three sub-adult males and/or large juvenile
males". Such a group might correspond to the male group of
Japanese macaques which peripheralized males or new immigrant
males organize (Yamada, 1966; Norikoshi & Koyama, 1975)

Subgrouping

The attendance rates of females in Troops A and B were
almost 100%, and females were the most stable members of the
troops, while attendance rates of males were variable. If
temporal troop males are excluded, Troops A and B maintained
their integrity as single ranging units through the females,
their offspring, and higher-ranking males. By contrast, Troop C
formed subgroups frequently, i. e., females, who were the most
stable members of Troops A and B, temporarily split from the main
troop. Among four top-ranking adult males (KK, HS, MS, IM) of
Troop C, KK, HS, MS almost always visited the baiting site with
females, while IM was frequently absent. Even when all of four

19

adult males, including IM, appeared together (17 October, 12 November, 13 November 1986), the number of animals in the group was smaller than the possible total, which indicated the occurrence of subgrouping. This observation implies that IM and the other three adult males did not play a positive role in the formation of subgroups as harem-type units. Rather, they just followed the female subgroups, as was observed during the fission process in the case of Japanese macaques (Oi, 1988). If the harem-type units, which are organized by a special bond between a male and some females in a group (Caldecott, 1986; Robertson, 1987), were the units of subgrouping observed in this study, the absence and attendance of four adult males (KK, HS, MS, IM) should work together with the number of attending females in Troop C. As the observed result did not coincide with this assumption, the hypothesis of the harem-type unit can be rejected. In pigtails, the multi-male troop is essentially a stable foraging and reproductive unit. This conclusion is also supported by observations that the mating partners of each dominant male include the females from the whole estimated kin groups; there was no fixed mating bond between a male and some females (Oi, submitted).

Previous workers have stressed subgrouping as the grouping tendency of pigtail macaques (Rijksen, 1978; Crockett and Wilson, 1980; Caldecott, 1986; Robertson, 1987). In the present study, the tendency towards formation of subgroups varied in each troop; Troops A and B did not form subgroups while Troop C formed them frequently. This intertroop variation indicates that subgrouping might occur under certain sociological or demographic conditions,

20

as observed in the process of fission of a Japanese macaque troop (Maruhashi, 1982). The data strongly suggest that Troop C was in the process of social change; the dominance relationship between two top-ranking males (KK, HS) has reversed, while the dominance rank order among top-ranking males in Troops A and B was stable and strictly linear.

Ecological factors, such as intratroop competition for food, might combine with sociological and demographic factors to cause subgrouping (van Schaick & van Hooff, 1983). Troops A and B significantly overlapped in terms of their home range, but their home ranges overlapped slightly with that of Troop C. There might be some significant environmental differences between the home ranges of Troop A and Troop B, and that of Troop C, which the present study did not detect. To examine this possibility, a detailed study of the food environment and actual conditions of competition for food is necessary.

Intertroop Relationships

Caldecott (1986) described that pigtails tended to spend most of their time in a "group". Since the society of pigtails that I observed did not include any harem-type units which Caldecott has assumed as the substructure of the "group", his term "group" should coincide with troop as used in the present study. He also suggested that "super-groups" emerge as the result of temporal fusion of "groups". However, the present study showed that pigtail troops were antagonistic to each other and that the subordinate troop foraged while avoiding the dominant troop. Troop fusion, based on non-antagonistic relationships between the

21

troops was never observed.

In interactions between troops, the higher-ranking individuals participated actively. The alpha and beta males, in particular, evidently showed an antagonistic attitude towards non-troop individuals, including solitaries. Furthermore, females, from lower- to higher-ranking members of Troop A, were also involved in these antagonistic interaction. However, middle- and low-ranking females of Troop B occasionally happened to feed together with the 3rd-ranking male, middle-ranking females, and adolescent males of Troop A. Their attitude might be said to be opportunistic. However, the configuration of the troop was rigidly maintained by individuals who discriminated between the members of their own troop and those of other troops.

Bernstein (1967) reported that the home ranges of two troops overlapped to some degree, and that their encounters were peaceful. The "super-group" of Caldecott (1986) and the "mixed-group" of Robertson (1987) might encompass groups which were observed during peaceful encounters between troops. From the antagonistic relationships observed in the present study, we might conclude that intertroop relationships vary in this species. The relationships between troops has been suggested to vary diacronically and syncronically according to the ecological situation, e.g. density of individuals (Yamagiwa, 1987), history of establishment of the troops, history of interactions between troops, and history of exchanges of members among troops (Cheney, 1981). We need not to treat the changeable nature and patterns of intertroop relationships as the super-structure of the society.

REFERENCES

Bernstein, I. S., 1966. An investigation of the organization of pigtail monkey groups through the use of challenges. Primates, 7: 471-480.

Bernstein, I. S., 1967. A field study of the pigtail monkey. Primates, 8: 217-228.

Caldecott, J. O., 1986. An Ecological and Behavioural Study of

the Pig-tailed Macaque. Contributions to Primatology, 21,
F. S. Szalay (ed.), Karger, Basel.

Cheney, D. L., 1981. Intergroup encounters among free-ranging
vervet monkeys. Folia primatol., 35: 124-146.

Crockett C. M. and W. L. Wilson, 1980. The ecological
separation of Macaca nemestrina and M. fascicularis in
Sumatra. In: The Macaques, D. G. Lindburg (ed.), Van
Nostrand Reinhold, New York, pp. 148-181.

DIT AGRARIA PROP SUMBAR, 1970. Lereng Perkebunan Bukit Malin-
tang (Skala 1:10,000)

Furuichi, T., 1985. Inter-male associations in a wild Japanese
macaque troop on Yakushima Island, Japan. Primates, 26:
219-237.

Itani, J., 1977. Evolution of primate social structure. J.
Hum. Evol., 6: 235-243.

Iwano, T., 1983. Concluding remarks on the socioecological
characteristics of Yakushimazaru. The Nihonzaru, 5: 86-95. (in
Japanese)

MacClure, H. E. 1964. Some observations of primates in climax
dipterocarp forest near Kuala Lumpur, Malaya. Primates, 5:
39-58.

MacKinnon, J. R. and K. S. MacKinnon, 1980. Niche
differentiation in a primate community. In: Malayan Forest
Primates, D. J. Chivers (ed.), Plenum, New York, pp. 167-190.

Maruhashi, T., 1982. An ecological study of troop fissions of
Japanese monkeys (Macaca fuscata yakui) on Yakushima Island,
Japan. Primates, 23: 317-337.

Nishida, T., 1966. A sociological study of solitary male

monkeys. Primates, 7: 141-204.

Norikoshi, K. & N. Koyama, 1975. Group shifting and social
organization among Japanese monkeys. In: Proceed. Symp.5th
Congr. Int. Primatol. Soc., S. KONDO, M. KAWAI, A.
EHARA, & S. KAWAMURA (eds.), Japan Science Press, Tokyo,
pp. 43-61.

Oi, T., 1988. Sociological study on the troop fission of wild
Japanese monkeys (Macaca fuscata yakui) on Yakushima Island.
Primates, 29: 1-19.

Oi, T., submitted. Sexual behavior and mating system of the wild
pig-tailed macaque (Macaca nemestrina nemestrina) in West
Sumatra.

Rijksen, H. D., 1978. A Fieldstudy on Sumatran Orang Utans
(Pongo pygmaeus abelii, Lesson 1827): Ecology, Behavior and
Conservation, H. Veenman & Zonen B. V., Wageningen, The
Netherlands.

Robertson, J. M. Y., 1987. On the evolution of pig-tailed
macaque societies. Doctoral dissertation, University of
Cambridge.

Rodman, P. S., 1979: Skeletal differentiation of Macaca
fascicularis and Macaca nemestrina in relation of arboreal and
terrestrial quadrupedalism. Am. J. Phys. Anthrop. 51:
51-62.

van Shaick C. P. & J. A. R. A. M. van Hoof, 1983. On the
ultimate causes of primate social systems. Behaviour, 85:
91-117.

Sugiyama, Y., 1976. Life history of male Japanese monkeys. In:
Advaces in the Study of Behaviour VII, J. S. Rosenblatt & R.

A. Hinde (eds.), Academic Press, London, pp. 255-284.

Takasaki, H. and K. Masui, 1984. Troop composition data of wild Japanese macaques reviewed by multivariate methods. Primates, 25: 308-318.

Whitmore, T. C., 1984. Tropical Rain Forest of the Far East, Oxford Univ. Press, New York.

Yamada, M., 1966. Five natural troops of Japanese monkeys in Shodoshima Island (I) -distribution and social organization-. Primates 7: 315-362.

Yamagiwa, J., 1987. Intra- and inter-group interaction of an all-male group of Virunga mountain gorillas (Gorilla gorilla beringei). Primates, 28: 1-30.

Table 1. Duration of observations at the baiting sites.

Name of units	Site	N. of visits	Time(min.)
Troop A	I	110	2322
Troop B	I	102	4534
Troop C	II	19	794
Group E	II	1	78
Group F	II	1	18
DO(sol.)*	I	2	34
KR(sol.)*	I	3	24
BK(sol.)	I	69	766
BT(sol.)	I	7	31
JR(sol.)	I	1	5
EX(sol.)	I	1	7
MY(sol.)	I	1	6
DS(sol.)	II	15	185
GD(sol.)	II	3	48
MK(sol.)	II	18	132

N. of visits: number of visits by the social units to the sites.
The author stayed in the blinds for observations a total of 171
times at Site I, and 64 times at Site II. sol.: solitary male.
*: DO and KR joined Troop A on some occasions.

Table 2. Sizes and age-sex composition of troops

Troop name	AdM	AdlM	AdF	AdlF	J	I	Total
Troop A	3	5	22	2	27	15	74
Troop B	3	4	14	1	18	9	49
Troop C	4	4	26	2	34	11	81

AdM: adult male; AdlM: adolescent male; AdF: adult female; AdlF: adolescent female; J: juvenile; I: infant

Table 3. Attendance rate of each individual in each troop.

	Troop A					Troop B			
NC	Age	N.	n.	A. rate		NC	Age	N.	n.	A. rate
NU	adult	96	92	95.8		AM	adult	83	82	98.8
NS	adult		89	92.7		RS	adult		81	97.6
NR	adult		93	96.9		ID	adult		76	91.6
DO	adult		21	21.9		JN	adole		82	98.8
KR	adult		6	6.3		SR	adole		83	100.0
KM	adole		62	64.6		HG	adole		83	100.0
IK	adole		91	94.8		PT	adole		80	96.4
KA	adole		85	88.5		NP	adole		1	1.2
AK	adole		66	68.8						
IN	adole		94	97.9						
MN	adole		8	8.3						
DK	adole		1	1.0		DK	adole		2	2.4
PR	adole		1	1.0						
Cw	adult	61	61	100.0		St	adult	66	52	78.8
Ef	adult		61	100.0		Hn	adult		65	98.5
Mr	adult		61	100.0		Kg	adole		64	97.0
Mi	adult		61	100.0		Ks	adult		63	95.5
Dn	adult		61	100.0		Ab	adult		65	98.5
Mo	adult		61	100.0		Kn	adult		66	100.0
Em	adult		61	100.0		Tr	adult		65	98.5
Mm	adult		61	100.0		Yt	adult		66	100.0
Up	adult		61	100.0		Po	adult		66	100.0
Uu	adult		61	100.0		Na	adult		65	98.5
Hr	adult		61	100.0		Ni	adult		66	100.0
Ww	adult		60	98.4		Ng	adult		64	97.0
Rt	adult		61	100.0		Tk	adult		66	100.0
Ii	adult		61	100.0		Gi	adult		64	97.0
La	adult		61	100.0		Mg	adult		66	100.0
Li	adult		61	100.0						
Pi	adult		60	98.4						
Me	adult		60	98.4						
Ma	adult		61	100.0						
Bt	adult		61	100.0						
Ys	adult		61	100.0						
Ae	adult		61	100.0						

N: the number of observations of each troop. n: the number of
observation days for each individual. A. rate: attendance rate
which is given by "n/N x 100". NC: codes of individual names;
the codes presented with double capitals are for males, and those
presented with a capital and a small letter are for females. The
individuals are arranged from top to bottom almost according to
their dominance rank order within the same sex class. adole:
adolescent.

Table 4. Sizes and composition of groups of Troop C

Date	AdM (Individuals)		AdlM	AF	AdlF	J	I	Total
				Age-sex class				
86/08/18	4	(KK,HS,MS, -,HT)	3	7	1	19	1	35
86/08/29	3	(KK,HS,MS, -, -)	2	17	1	34	3	60
86/08/30	3	(KK,HS,MS, -, -)	1	10		19	2	35
86/09/23	3	(KK,HS,MS, -, -)	3	12		28	4	50
86/09/25	3	(KK,HS,MS, -, -)	3	14	1	25	4	50
86/10/03	1	(-, -,MS, -, -)	3	8	0	12	2	26
86/10/10	4	(KK,HS,MS,IM, -)	1	23	0	34	2	64
86/10/17	4	(KK,HS,MS,IM, -)	2	14	0	33	2	55
86/10/24	3	(KK,HS,MS, -, -)	1	7	0	10	0	21
86/11/06	4.	(KK,HS,MS,IM, -)	2	26	0	40	5	77
86/11/07	4	(KK,HS,MS,IM, -)	2	21	0	26	3	56
86/11/12	4	(KK,HS,MS,IM, -)	4	18	1	37	3	67
86/11/13	4	(KK,HS,MS,IM, -)	3	14	4	37	9	71
86/11/15	4	(KK,HS,MS,IM, -)	4	20	2	34	10	74
86/12/02	4	(KK,HS,MS,IM, -)	4	26	2	34	11	81
86/12/13	2	(KK,HS, -, -, -)	4	17	3	34	11	71

The codes in parentheses represent the code names of adult males who were present in the groups, and "-" in the column of AdM represents the absence of the individuals. Abbreviations are listed in Table 2.

Table 5. The number of aggressive encounters
in which each male or female participated as
an aggressor.

	Male			Female	
Attacker	Rank	N.	Attacker	Rank	N.
Troop A					
NU	1	4	Mr	3	1
NS	2	4	Mi	4	1
NR	3	3	Li	16	1
KR	6	1	Pi	17	1
AdlU	?	1	Ad	22	2
			AdU	?	1
Troop B					
AM	1	1			
RS	2	1			

Rank: dominance rank order within the same sex
class.
N.: the number of the aggressive encounters in
which an individual participated as an aggressor.
The total number of aggressive encounters was 11.
AdlU: an unidentified adolescent.
AdU: an unidentified adult.

FIGURE LEGENDS

Figure 1. Location of the study area, indicated by an arrow.

Figure 2. Seasonal changes in rainfall and temperature in the study area in 1986. As a rule, I myself measured the rainfall and temperature, but two field assistants did so in his absence.

Figure 3. Vegetation in the study area, based mainly on vegetation in 270 systematically sampled plots (10 × 10 m^2). Cc: cultivated area or open area; Cp: coffee plantation; Sh: covered with tall (> 2 m) herbs and shrubs; St: secondary forest recovering from evacuated tea plantation, 10%-85% of trees (5 cm $\leq$ DBH) are tea. Sc: Secondary forest recovering from heavy cutting, stands of trees with 5 cm $\leq$ DBH < 50 cm; Pl: selectively logged primary forest, stands of some trees with DBH $\geq$ 50 cm and some large stumps; Pr: Primary forest, stands of some trees with DBH $\geq$ 50 cm.

Figure 4. Distribution of group sizes for Troops A, B, and C. The groups were counted when entering the baiting sites, when feeding at the sites, when crossing a road (two occasions for Troop A). The number infants were excluded from quantification of groups. The sample sizes are 12 for Troop A, 12 for Troop B, and 16 for Troop C.

Figure 5. Observation of temporal troop males. Vertical lines and squares indicate that the period when each male was observed.

The symbol "S" indicates the male was observed as a solitary; "A", as a member of Troop A; "B", as a member of Troop B.

Figure 6. Home ranges of the pigtail troops.

EQUATOR

West Sumatra

Jambi

▲ Mt. Kerinci

N

0   200   400km

Fig. 1

Fig 2

Key:

▓	Cc
▦	Cp
▤	Sh
☐	St
▨	Sc
▨	Pl
▨	Pr

▲ Site I
▼ Site II
■ Site III

N

0   500m

1 2 3 4 5 6 7 8
A
River   River
B
River   Road
C
River
D
E
F
G
H

Fig. 3

Fig 4

Fig 5

Key:

☐ Troop A

☐ Troop B

☐ Troop C

⬚ Troop D

▦ Group E, F

▲ Site I ▼ Site II ■ Site III

N

0   500m
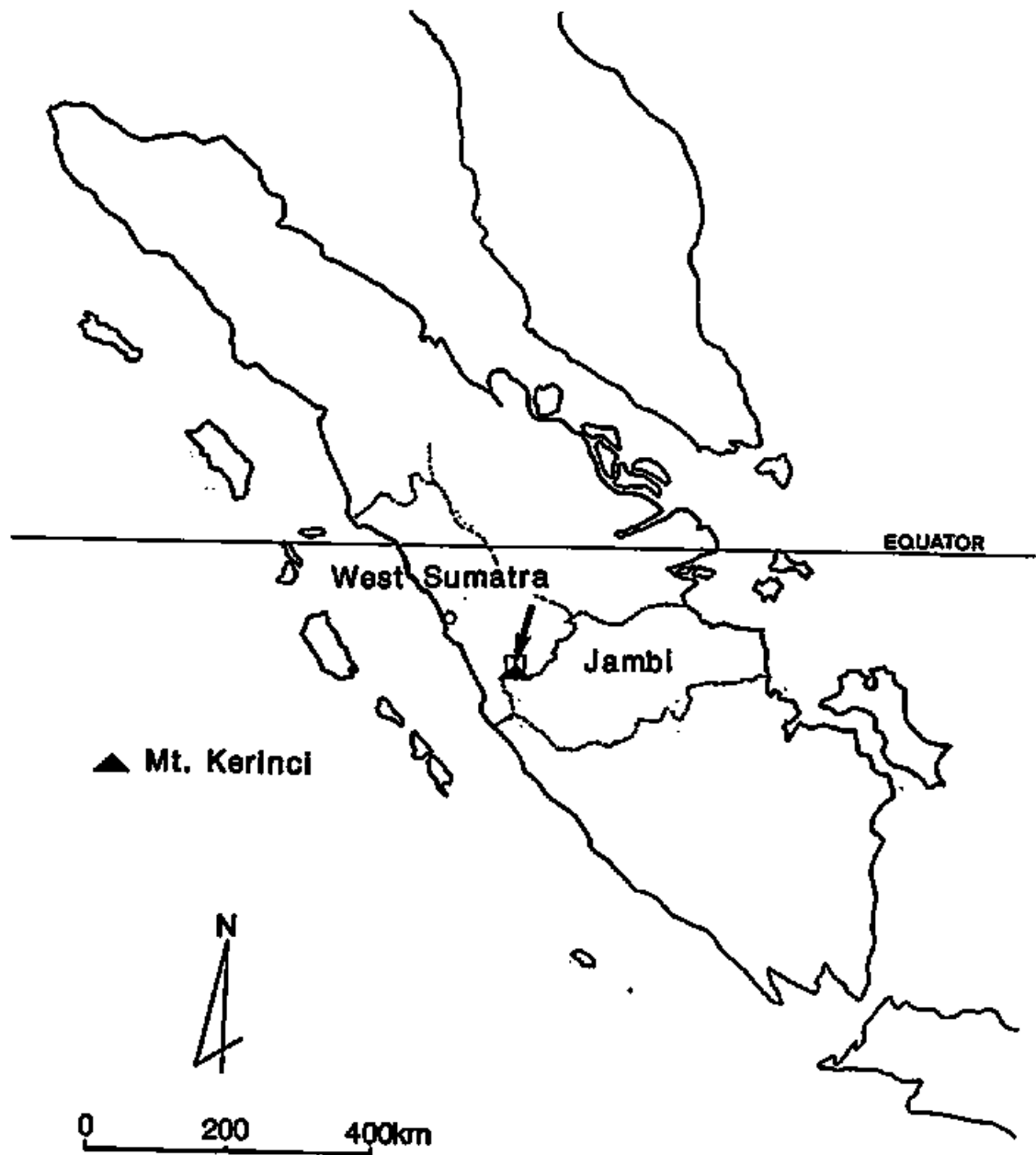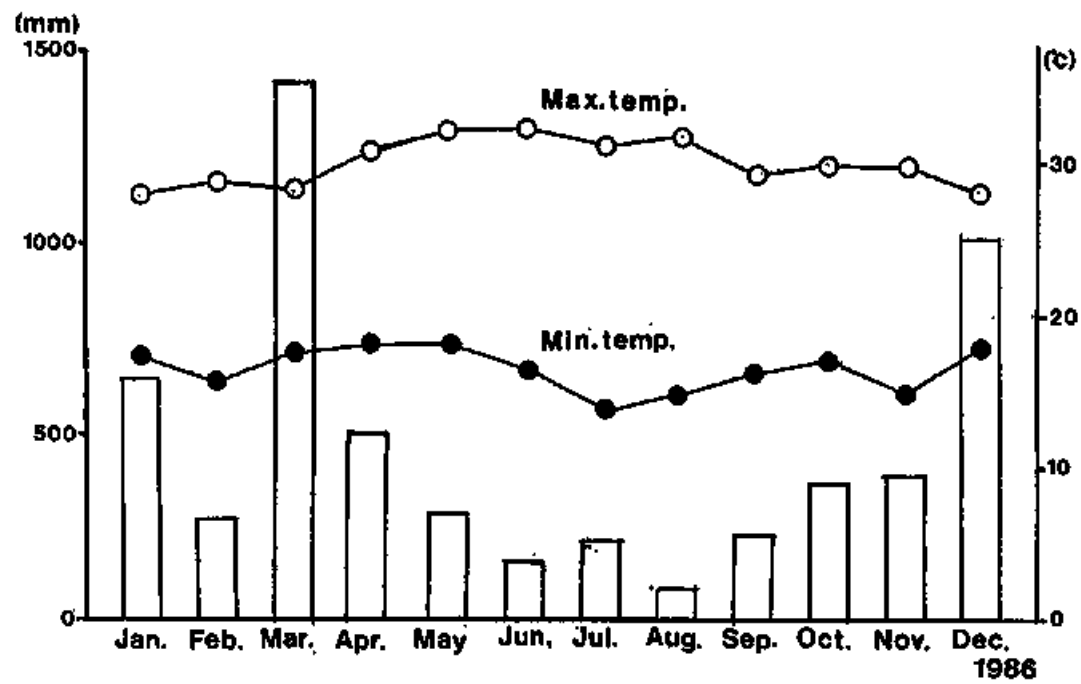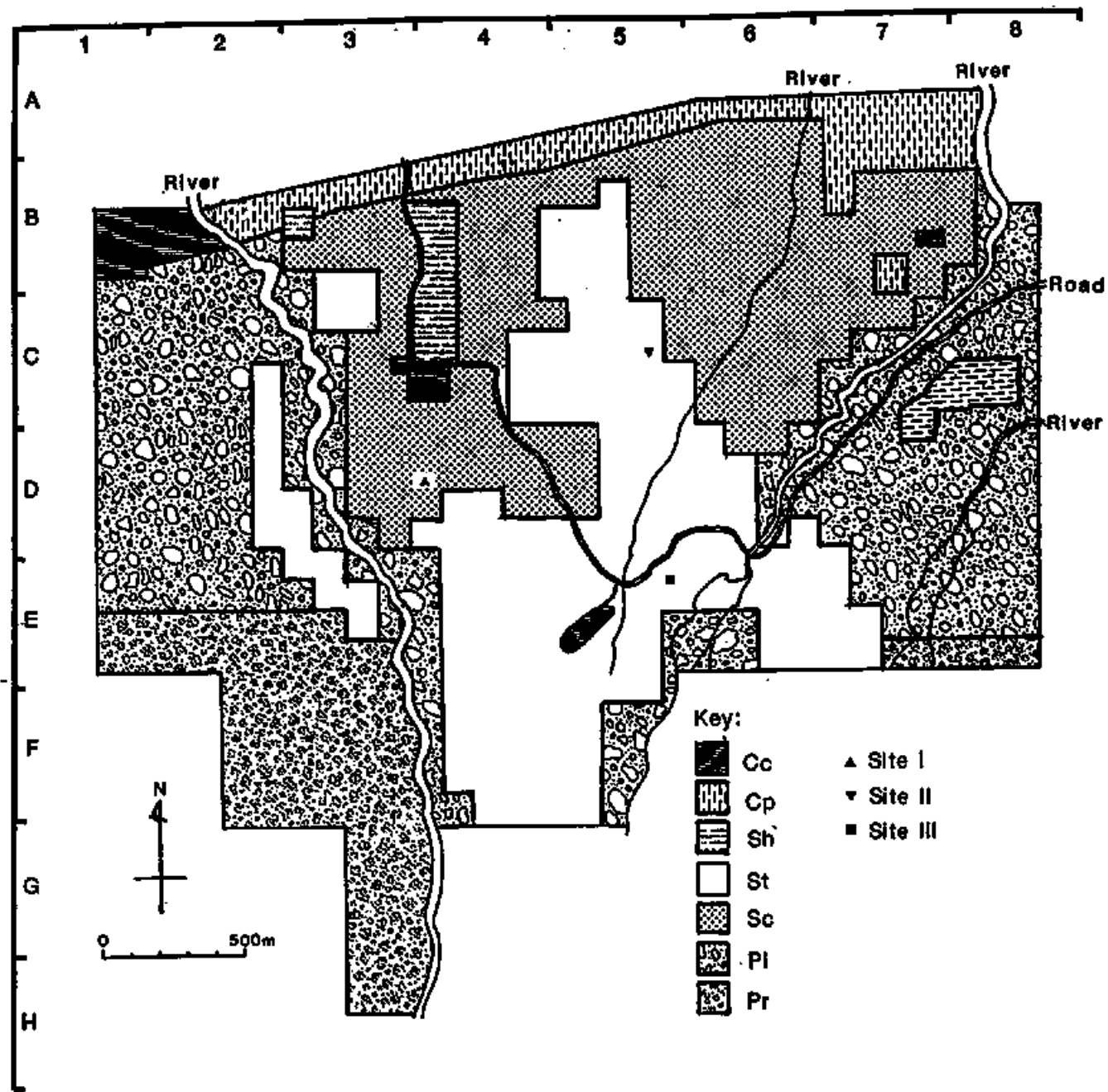
Fig 6

Title:

Social behavior of wild pig-tailed macaques

(<u>Macaca</u> <u>nemestrina</u> <u>nemestrina</u>) in West Sumatra.

Running head: Social behavior of

wild pig-tailed macaques.

Toru OI
Primate Research Institute
Kyoto University
Inuyama
Aichi
484 Japan

Key words: wild pig-tailed macaque, dominance relationships,

male co-existence, conciliatory behavior, sexual differences.

ABSTRACT

Social organization of a wild troop of pig-tailed macaques
was studied by provisioning, on the basis of individual
identifications, in West Sumatra, Indonesia.

Closely associated clusters were recognized among females
close in rank, through an analysis of co-feeding, grooming within
the troop. These clusters may correspond to close-kin groups.
Estrous females tended to temporarily separate from these groups
and associate with the mating partners.

Each male showed different association patterns with females,
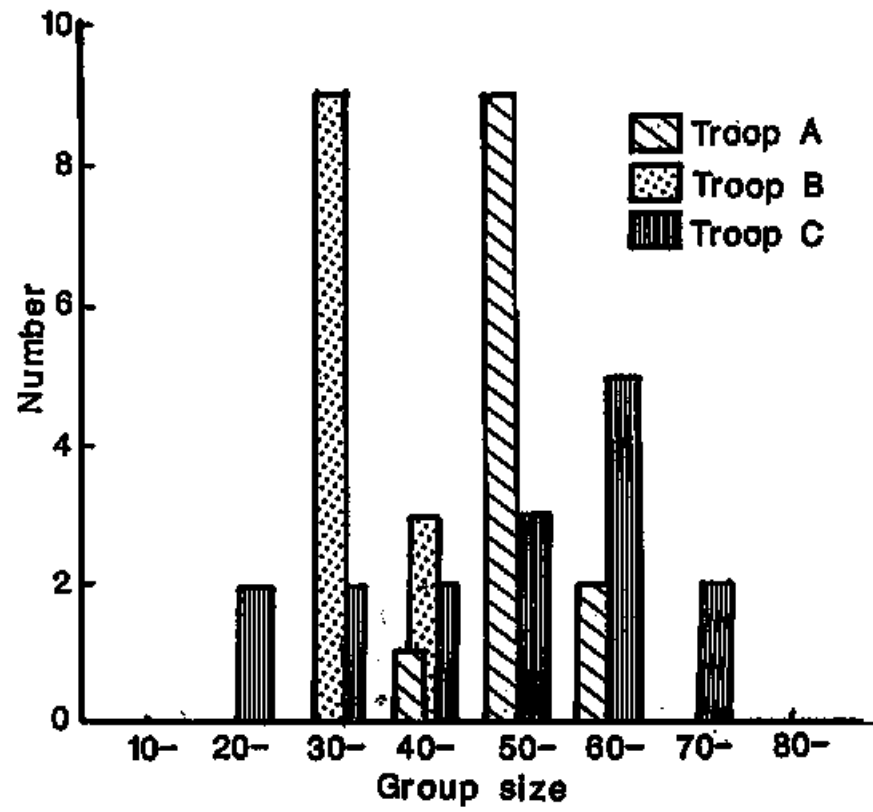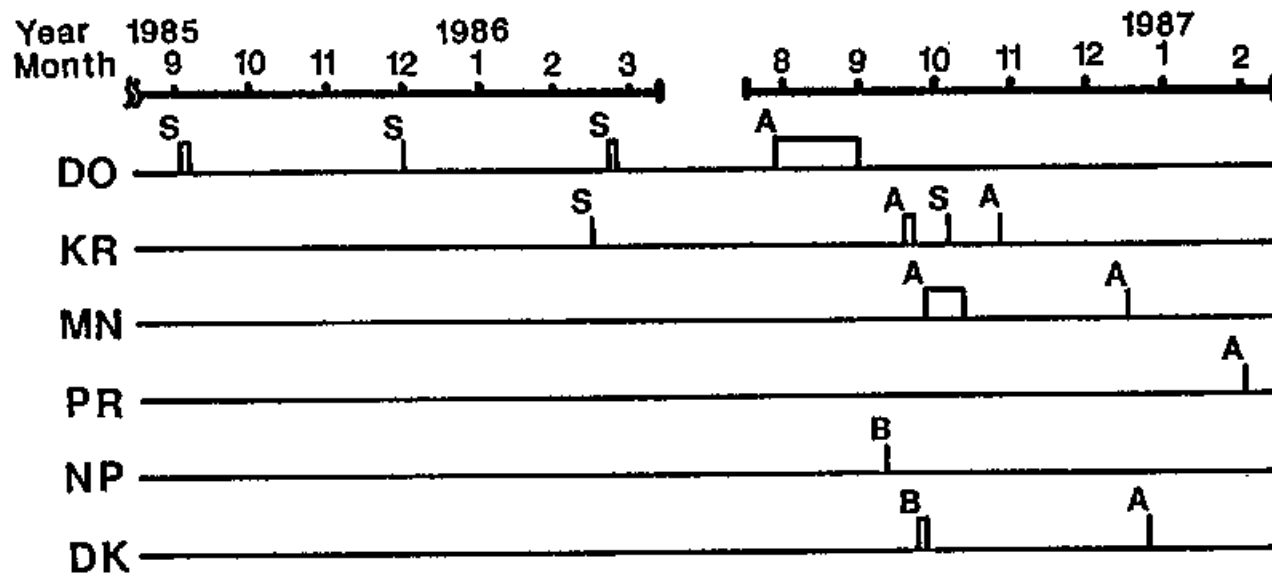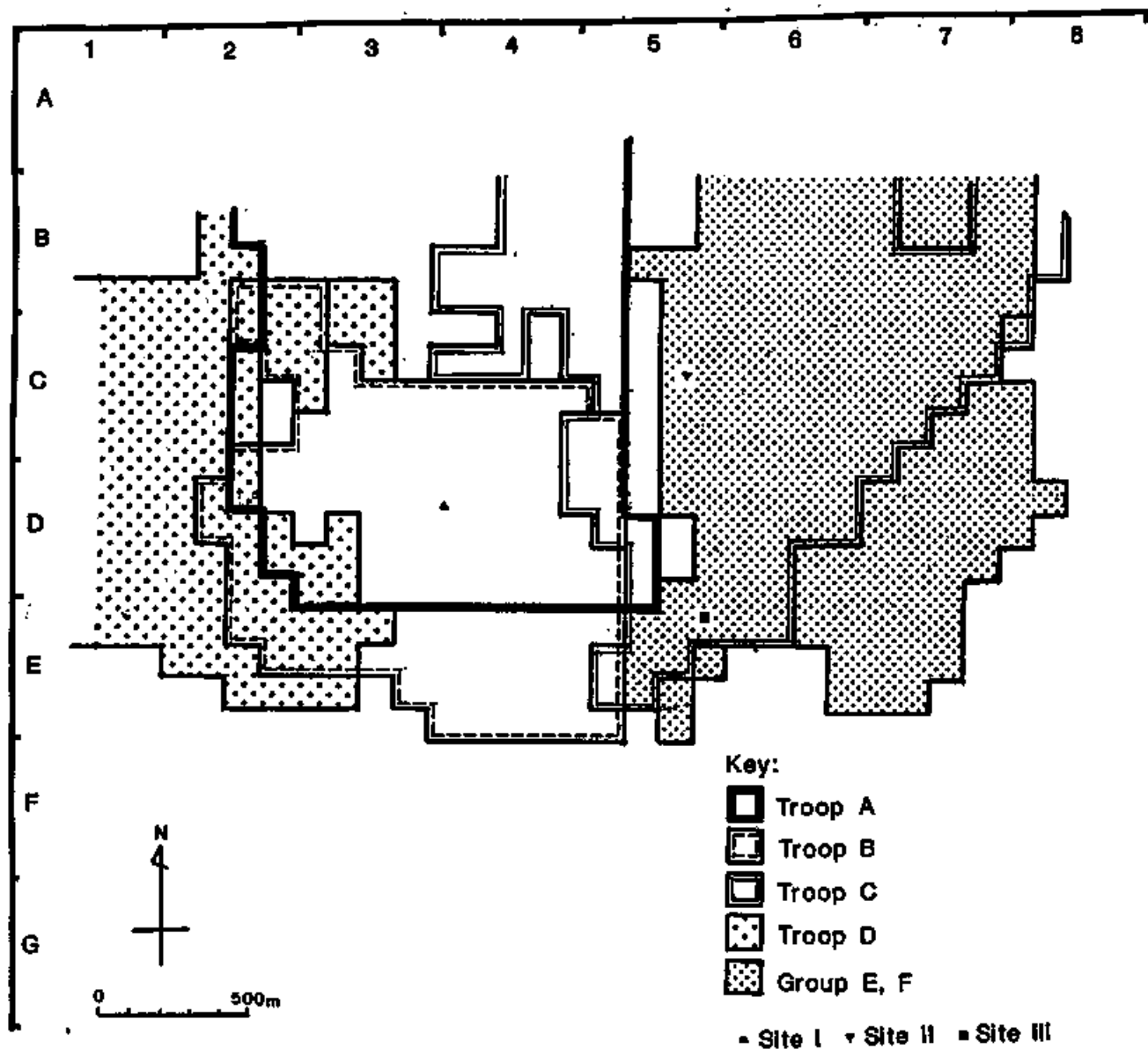that appeared in intersexual grooming and allies of agonistic
interactions. Males other than the alpha male, in particular,
low-ranking males suffered from the allied attacks by females
more frequently. The alpha male performed loser-support in
triadic agonistic interactions more frequently than other
individuals.

Grooming, non-copulatory mounting, and kissing occurred in
the context of conciliation, probably based on cognition of
dominance relationships by the participants. Sexual differences
were recognized in the quality and pattern of these behaviors;
for example, among males, non-copulatory mounting tended to be
performed in the direction from the subordinate to the dominant,
while among females, it tended to be performed in the reverse
direction; and grooming performed within kin-group seemed more
important for conciliation among females. Subordinate-to-dominant
mounting seemed to be more elaborate and designed to express
tolerance, in a way that might be manipulated by the dominant.

1

Thus, given the less aggressive attacks among males, it could be said that social interactions among troop males were more inhibitory and conciliatory than those among females. Furthermore, it was suggested that dominant male played an important role in coexistence among males by manipulating the pattern of conciliatory behavior such as the direction of non-copulatory mounting. A comparison by species of the directionality of non-copulatory mounting implies that severer social tensions exist between pigtail males than in the case of males of other macaques.

INTRODUCTION

Like all species of macaques studied thus far, pig-tailed macaques form matrilineal unit groups (troops) (Oi, submitted a). Caldecott (1986a, 1986b) described variations in the adult sex ratio in troops of macaques, which might be related to variations in male association patterns within the troops (Shively et al. 1982; Caldecott, 1986a). I (submitted b) explained this variation in terms of interspecies difference in competition between males for mates. If the multi-male troop evolved from the single-male troop by addition of males (Eisenberg et al., 1978), it may be significant to study behavioral features of males to constitute a multi-male troop.

A field study of the wild pig-tailed macaques in West Sumatra, Indonesia was conducted over the three periods: from January to March, 1985; from June 1985 to March 1986; and from July 1986 to February 1987. The present paper is based on

2

observations at close quarter attained by provisioning during the last study period. It aims to clarify the social organization of a troop and determine the ways in which males co-exist in a troop, by an analysis of both agonistic and non-agonistic interactions, and in particular, of conciliatory behaviors (de Waal & Yoshihara, 1983; de Waal, 1984). This is the first study of the social organization of wild pig-tailed macaques that has been based on individual identifications.

MATERIAL AND METHODS

Observation of wild pig-tailed macaques were made at two baiting sites. The baiting sites were square clearings of 20 m x 20 m with a blind from which all observations were made. On observation days, 5-15 kg of unshelled peanuts were distributed at the site. Although three troops visited the sites, the current analyses concern only Troop B, for which observation time was greatest.

Troop B visited the site on 102 occasions and was observed a total of 4534 minutes, from July 1986 to February 1987. The average duration of each visit was 44 minutes (range: 3-102 min.). A general description of the troop and the study area is given in Oi (submitted a).

The troop was composed of three adult males (fully mature, estimated age of over 9 years), four adolescent males (mature, estimated age of 5-9 years), 14 adult females (parous, estimated age of over 5 years), one adolescent female (nulliparous,

3

estimated age of 3.5-6 years), 18 juveniles (estimated age of 1-4 years for males and 1-3.5 years for females), and nine infants (aged less than one year). The adolescents and the adults were all identified individually, as were some of the juveniles.

In the text, tables, and figures, codes with two capital letters are used for male individuals, and codes with one capital and one lower case letter for females. Adults and adolescents were the main subjects of analysis, and the terms "males" and "females" refer to both adults and adolescents. The social interactions, and the sampling methods were as follows.

1. Agonistic interactions:

The participants and directions of all agonistic interactions were recorded. Aggressive behaviors included chasing, slapping, holding down and biting, and submissive responses by the recipients included retreating, screaming and grimacing. The agonistic interactions were classified into three levels according to their intensity (Thierry, 1986): level 1, facial threat, approach with consequent retreat by the opponent; level 2, brisk rush and contact attack, such as slapping and holding; level 3, biting.

Relative dominance was assessed from the outcome of dyadic agonistic interactions. If there were insufficient data for any particular pair, for example, individuals $\underline{A}$ and $\underline{C}$, their dominance relation was assessed according to the following premise: if individual $\underline{A}$ dominated individual $\underline{B}$, and $\underline{B}$ dominated $\underline{C}$, then $\underline{A}$ was considered dominant to $\underline{C}$.

Winner-support and loser-support were distinguished in

4

triadic agonistic interactions (de Waal, 1978). Agonistic interactions in which more than three individuals participated could be divided into triadic interactions.

2. Co-feeding:

This methods were used to examine co-feeding relationships. In method A), 5 kg peanuts were spread evenly within a circle of 3 m radius. Every 2.5 minutes the identity of every individual who was eating in the circle was recorded. An experimental session began when the first individual entered the circle, and ended when the last individual left. Each session was divided into four (subsessions of equal duration). A total of 12 sessions (277 point samples) were recorded from 23 October to 23 January. The distribution of the number of observation points (OP) in each subsession for each individual was compared and categorized.

In method B), 15 kg peanuts were spread evenly in three circles of 2.1 m radius, the centers of which were separated from each other by 10 m. Individuals feeding in the same circles were recorded every 2.5 minutes. Five sessions (96 point samples) were recorded from 3 January to 12 February 1987. The relative time that any two individuals co-fed in the same circle was given by "$S_c = 2 F(\underline{A} \cap \underline{B}) X 100 / \{ F(\underline{A}) + F(\underline{B}) \}$, where $F(\underline{A})$ is the total number of observation points for individual $\underline{A}$, and $F(\underline{A} \cap \underline{B})$ is the number of observation points when individuals $\underline{A}$ and $\underline{B}$ co-fed in the same circle. A dendrogram (single cluster analysis) was constructed by using "S_c" as a similarity index (Sneath & Sokal, 1973).

5

When method B) was used, tolerance rather than antagonism affected the coexistence between individuals, while when method A) was used, the antagonism had a stronger effect, because of more dispersed distribution of the bait in method B).

3. Grooming:

One grooming bout was defined as a continuous series of grooming actions by an individual (Dunbar, 1976). The participants and direction of all the grooming bouts were recorded.

4. Non-copulatory mounting:

Non-copulatory mounting was defined as mounting without intromission. The participants and the direction of all mounting were recorded. Solicited mounting was preceded by solicitation, such as presenting and puckering (Bernstein, 1966, 1967), whereas forced mounting was defined as mounting without prior solicitation.

5. Kissing:

An individual sometimes brought its mouth into contact with the mouth of another. The participants and direction of kissing were recorded.

Chi-square tests (one-tailed) were used to examine statistical significance. The significance level was set at $p < 0.05$. To determine whether a given type of interaction occurred more frequently with a pair in each age-sex class than would be expected by chance, a cell-by-cell chi-square test was used (Fagen and Mankovichi, 1980). The expected values were calculated

6

under the null hypothesis that the age-sex class of the actor is independent of the age-sex class of the recipient. In the chi-square test of the distribution of victims of agonistic interactions, the expected values were calculated under the null hypothesis that the distribution of agonistic interactions in each age-sex class depends on the number of individuals in the particular age-sex class. The expected values for the direction of grooming, non-copulatory mounting and kissing were examined under the null hypothesis that the direction of a given type of interaction is independent of the dominance relationships of the participants.

RESULTS

AGONISTIC INTERACTIONS

2117 agonistic interactions were observed (27.9 per hour). Of these, 1959 (92.5%) were level 1 interactions, 110 (5.2%) were level 2, and only 48 (2.3%) were level 3. 45 (93.8%) of the level 3 interactions occurred among females and juveniles, including 26 among females. By contrast, level 3 agonistic interactions never occurred between males.

Aggression seemed to be much more common at the baiting sites than under natural conditions. The frequency of agonistic interactions detected by vocalization while tracing the troops during natural foraging was only 0.6 cases per hour. At the baiting sites, 2105 agonistic interactions (99.4%) occurred over food or space, and 12 agonistic interactions (0.6%) occurred over

mates.

<u>Dyadic</u> <u>Agonistic</u> <u>Interactions</u> <u>and</u> <u>the</u> <u>Dominance</u> <u>Rank</u> <u>Order</u>.

  Agonistic interactions within the same age-sex class occurred
more frequently than expected. By contrast, agonistic interactions
initiated by juveniles against adult males and adolescent males,
by females against adolescent males, by adolescent males against
females, and by adolescent males against juveniles were less
frequent than expected (Table 1).

  Participants (adult and adolescent) were identified in 931
cases out of a total of 1259 cases (Table 2). No agonistic
interactions occurred in three dyads out of the 21 possible
combinations of males, in 16 dyads out of the possible 105
combinations of females, and in 21 dyads out of the possible 105
combinations between males and females. In four pairs, attacks
occurred bidirectionally. Dominance reversal was attributed to
two pairs (Yt vs. Tr, Ab vs. Kn), and unfixed dominance was
attributed to the other two pairs (ID vs. JN, ID vs. SR). All
these pairs were composed of individuals of close dominance
rank.

  A linear dominance rank was recognized; in males, AM > RS >
[ID, (JN > SR)] > HG > PT; and in females, St > Hn > Kg > Ks >
(Ab, Kn) > (Tr, Yt) > Po > Na > Ni > Ng > Tk > Gi > Mg, where
individual <u>A</u> > individual <u>B</u> indicates that <u>A</u> is dominant over <u>B</u>,
and a change in dominance or unfixed dominance was recognized
between the individuals placed within the same parentheses.
During the study, the estrous condition of seven females (Hn, Kg,
Ab, Kn, Na, Ni, Tk) did not affect the dominance rank order.

8

Adult males (AM, RS, ID) seemed dominant over females. AM and RS attacked almost all females on occasion, including the first-ranking female (St). However, the females and the juveniles attacked RS and ID on occasion. Most of the attacks were initiated by females or juveniles while emitting a scream, which might be a kind of call for help from the third individual. The initiators could repel the victim adult males, possibly exploiting the influence of a third individuals whom I could not detect. Thus, essentially, such interactions might be classified as triadic agonistic interaction. ID suffered from attacks by the females most frequently among adult males (21 cases).

Excluding the pairs of ID versus JN and ID versus SR, the adult males dominated the adolescent males. Of the four adolescent males, JN and SR were dominant to some females and subordinate to others, while the other two (HG, PT) were subordinate to all females. In Japanese macaques, which also form matrilineal unit groups, the dominance ranks of natal juvenile and adolescent males are often close to those of their mothers (Koyama, 1967). It may be that JN and SR were natal males, who could still depend on the support of their mothers in disputes with lower-ranking females, while HG and PT were non-natal, and hence subordinate to all females.

Agonistic interactions occurred more frequently between pairs of males. The agonistic interactions between HG and PT were most frequent (63 cases). When only the two adolescents were feeding together, HG did not take an aggressive stand against PT. However, when a third individual appeared, HG abruptly attacked PT. Interactions between the alpha male (AM)

9

and the beta male (RS) was frequent (29 cases), as were those between ID and HG (18 cases) and between ID and PT (17 cases).

Only adult males were involved in agonistic interactions over mates. All cases involved the alpha male (AM) directing aggressive behavior towards his potential rivals, the second-ranking (11 cases) and the third-ranking males (one case).

Triadic Agonistic Interactions

189 cases of winner-support, and 37 cases of loser-support were observed. In winner-support, alliances involved females, juveniles or both were directed towards males (Table 3a). For example, when females attacked males, other females joined them in 34 cases, and juveniles joined in 20 cases. Similarly, when juveniles attacked males, females joined them in 12 cases, and juveniles joined in 16 cases.

Generally, males tended to support females (40 cases), females tended to support females (39 cases) and juveniles (31 cases), and juveniles tended to support other juveniles (26 cases), though only the latter tendency was significantly more frequent than the expected value (p<0.01). By contrast, males supported juveniles, and juveniles supported males less frequently than expected (p<0.01 and p<0.02, respectively). Adult males were the victims in 78 triadic interactions, adolescent males in 55 cases (both more frequently than expected by chance, p<0.001), females in 40 cases and juveniles in 16 cases.

In all cases of loser-support, adult males, females and juveniles supported females and juveniles, but the numbers of the

10

interactions in each age-sex combination are not significantly different from the expected values. Supportive interactions were never observed among males (Table 3b). Adult males were victims in 12 cases; adolescent males in 10 cases; females in 7 cases; juveniles in 8 cases. Males and juveniles were the victims of these attacks more frequently than expected ($p<0.001$ and $p<0.05$, respectively).

Males were the victims of supported aggression in 155 cases and in dyadic interactions in 385 cases. By contrast, females and juveniles were the victims in dyadic interactions far more frequently (1506 cases) than in triadic interactions (71 cases). The number of attacks initiated by females or juveniles on males comprised 85.2% (132 cases) of the triadic interactions in which males were victims.

In 81 out of a total of 110 cases of winner-support, all participants (adult and adolescent) were identified (Table 4a). Initiators of the interactions did not attack dominant animals, with the exceptions of attacks by females and adolescent males on RS, ID, SR. The victims were also subordinate to the supporters. When high-ranking females (St, Hn, Ks) initiated the aggression, high-ranking males (AM, RS, JN, SR) supported them, and when middle- and low-ranking females (Ab-Mg) initiated the aggression, females of similar rank and high-ranking males supported them. Noticeably, ID, the lowest-ranking male, supported only low-ranking females.

Differences were found in the supporting behavior of males. The beta male (RS) joined attacks against females while the alpha male (AM) joined only against males. Furthermore, the alpha male

11

joined attacks only when the females were initiators, while the
other males joined also when the more dominant males initiated
the attack. The third-ranking male (ID) joined only when HG or
PT was a victim, and only when ID attacked PT did HG join. PT
was never observed to support an attack.

The status of victims was biased towards the lowest-ranking
males (ID, 25 cases; HG, 22 cases; PT, 11 cases), and
lowest-ranking females (Gi, four cases; Mg, eight cases).

All the participants (adult and adolescent) were identified
in 11 out of 14 cases of loser-support (Table 4b). The
interferers included the alpha male (AM) (six cases), the beta
male (RS) (two cases), the first-ranking female (St) and the
twelfth-ranking, oldest female (Ni) interfered.

In general, higher-ranking individuals were the victims of
loser-support, while lower-ranking individuals were the victims
of winner-support. The victims of loser-support were RS (three
cases), ID (two cases), SR (four cases) among males, and Hn (one
case), Yt (one case) among females.

NON-AGONISTIC INTERACTIONS

Co-feeding

Figure 1 shows the distribution of observation points for
each individual analyzed by method A). Among males, the
observation points were significantly correlated with the dominance
ranks ($\tau = -0.90$, $p < 0.01$, one-tailed). AM, RS, and JN, the
first-ranking to the third-ranking males, scored the highest

12

points in the first subsession, while SR and ID, the third

ranking-males, scored the highest points in the third subsession,

and HG, PT, the lowest-ranking males, scored points mainly in the

forth subsession.

Among females, the observation points were not correlated

with the dominance rank (τ =-0.18, p>0.05, one-tailed). St, Hn,

Kg, Ks, Ab, Kn, Tr, the first-ranking to the seventh-ranking

females, scored the highest points in the first subsession. Yt,

Po, Na, Ng, Ni and Mg, the eighth-ranking to the 12th-ranking and

the 15th-ranking females scored the highest points in the second

subsession, and Tk, Gi, the 13th-ranking and the 14th-ranking

females scored the highest points in the third subsession.

Estrous females did not always co-feed with the males,

though the total numbers of observation points for the females

(Kn, Na, Ni, Tk) who showed estrous signs during the experiment,

were higher than those for other females close in rank.

Figure 2 shows a dendrogram of the co-feeding relationships

when method B) was employed. Clusters that emerged at similarity

14 seem to reflect some grouping tendency, and individuals who

appeared in the same cluster also tended to show the same

distribution patterns in the analysis by method A).

High-ranking males (AM and RS) and one adolescent male (SR)

appeared in the clusters with females. By contrast, lower-ranking

males (JN, ID, HG, and PT) were not part of any clusters; ID, HG,

and PT were not well tolerated by others and tended to feed alone

in the latter half of the experimental session, while JN fed

freely anywhere.

Close-ranking females tended to appear in the same clusters,

13

in particular, middle-ranking females tend to belong to larger clusters. By contrast, the high-ranking females (St, Hn and Ks) were not included in any clusters. The high-ranking females were able to feed freely, as was JN. The remaining three clusters were large; one included middle-ranking females (Ab, Kn, Tr, Yt, Po), another included middle- and low-ranking females (Ng, Ni, Gi, and Tk) and RS and SR, and the third cluster included the alpha male (AM) and an estrous female (Na).

Estrous condition seems to be related to the clustering of adult males and the females. Na who appeared in the cluster including AM was fully estrous in two sessions, and Ni, who appeared in the clusters including RS ended the full estrus just before the start of the experiment. Kn was fully estrous in one session, and did not form a cluster with any males in the same cluster.

Grooming

112 grooming bouts occurred. 107 bouts (95.5%) were grooming in which a female was a groomer or a groomee, and it appeared that grooming interactions were distributed with females as the centers. Grooming between females (45 bouts), between juveniles and females (30 bouts), and between adult males and females (32 bouts) were most frequent, but with no significant differences from the expected values. Most grooming between females and juveniles (30 bouts) appeared to correspond to mother-child relationships. Among males, only one grooming bout was observed, between the third-ranking male (ID) and the second-ranking male (RS).

14

Most grooming was performed unilaterally. Only 14 bouts of mutual grooming were observed and these involved six pairs (two pairs of adult females, two pairs of an adult male and an estrous adult female. and two pairs of a juvenile and an adult female).

Nine grooming bouts (8.0%) occurred after agonistic interactions, and all involved the subordinate animal grooming the dominant. Eight grooming bouts were between females and the remaining one bout was grooming by a juvenile of a female.

The participants (adults and adolescents) were identified in 68 out of 78 bouts (Table 5). All the females (Ab, Na, Ni, Tk) groomed by males showed signs of estrus (in 14 bouts). Grooming directed from females with signs of estrus (Hn, Kn, Ni, Tk, Mg) to males accounted for 52.6% (10 bouts) of intersexual grooming by females, and the remaining 47.4% (nine bouts) were by females just before delivery (Kg, Ab, Ng). Adult males generally participated in grooming with females. Grooming of males by females with infants was not observed. Among females, grooming in the direction from the subordinate to the dominant were performed more frequently (28 bouts) than grooming in the opposite direction (6 bouts) ($p<0.001$).

Non-copulatory Mounting

192 cases of non-copulatory mounting were observed. 186 mounts (96.9%) were unilateral, and the remaining six (3.1%) were mutual. All of the latter occurred between juveniles in the context of play.

Mounting among juveniles occurred most frequently (75 cases), and more frequently than expected ($p<0.001$). Mounting

15

between males (26 cases), and females (25 cases) occurred more frequently than expected (p<0.001, p<0.01 respectively), while mounting by males of juveniles, and by juveniles of males, occurred less frequently than expected (p<0.01, p<0.001).

The function of most mounting among males seemed to be something other than instant repair of disrupted relationships caused by the agonistic interactions, and rather to reduce social tension, since out of a total of 26 cases of mounting among males, only one (3.8%) case occurred after agonistic interactions (Table 6). Among males, forced mounting was never observed, and agonistic interactions were never observed to follow mounting.

By contrast, of the 25 cases of mounting among females, 20 cases (80%) occurred after agonistic interactions in which at least one of the participants had been involved, and out of 11 cases of mounting between males and females, six (54.5%) occurred after agonistic interactions. Furthermore, out of 11 cases (55%) of post-aggression mounting among females were forced mounts, and on one occasion, an aggressive act occurred just after female-female mounting. Thus, more than half of the mounts among females were performed as an extension of agonistic behaviors.

There was also a sexual difference in the direction of mounting. 20 (76.9%) out of 26 cases of male-male mounting were in the direction from the subordinate to the dominant (p<0.001). By contrast, in 9 (81.8%) of 11 cases of male-female mounting, and in 17 (68.9%) of 25 cases of female-female mounting, the direction was from the dominant to the subordinate (p<0.05). When the subordinate mounted the dominant, presenting by the dominant followed presenting by the subordinate (20 cases), or

16

presenting by the dominant followed an approach with puckering by the subordinate (nine cases).

Subordinate females mounted the dominant males twice. In one case, after the agonistic interaction, an unidentified female mounted the alpha male. In the other case, after the alpha male inspected an unestrous female (Kn), she mounted the alpha male.

Both participants (adults and adolescents) were identified in 50 cases out of 62 cases of non-copulatory mounting (Table 7). The most frequent dyads were RS and ID (six cases), AM and RS (five cases), and AM and ID (four cases), among the males. The most frequent mountee was the alpha male (AM).

Kissing

The function of kissing may be to express affinity or conciliation, since the approach from the subordinate to the dominant occurred in this interaction without inducing aggression. 50 cases of kissing were observed. In two cases, kissing occurred after agonistic interactions. In one case, the dominant approached and kissed the subordinate, and in the other case, the subordinate approached and kissed the dominant. The rest of the kissing occurred in non-agonistic contexts, and was not followed by positive social interactions. Kissing occurred most frequently among females (29 cases) and from juveniles to females (11 cases), with no significant difference from the expected values. Five cases of kissing took place among males; three cases took place between males and females; one case took place between males and juveniles; and another case took place among juveniles.

Participants (adults and adolescents) were identified in 34

out of 37 cases (Table 11). Among females, kissing tended to occur more frequently in the direction from the dominant to the subordinate (23 cases) than in the reverse direction (five cases) ($p<0.001$). Three instances of kissing were observed among males in the direction from subordinate (ID) to dominant (AM and RS).

DISCUSSION

The pig-tailed macaque has a unit group of a multi-male, multi-female composition. Migration of males, as well as the existence of solitary males, suggests that the unit group is matrilineal (Oi, submitted a).

The groups (St, Hn, Kg, Ks), (Ab, Kn, Tr, Yt, Po), (Na, Ni, Ng, Tk, Gi) probably consisted of close kin, such as mothers, daughters and sisters, as affinitive behaviors are most common amongst close kin in other species of macaque (Yamada, 1963; Chapais, 1983; Furuichi, 1984) and in confined pig-tailed macaques (Rosenblum, 1971; Defler, 1978). The females within each group had similar priority of access to bait, and were able to feed close to each other with a high degree of tolerance as suggested from co-feeding relationships. Further, they were close in dominance rank, and grooming and non-copulatory mounting occurred more frequently between members of the same group than between members of different groups. (chi square-test, $p<0.001$, df=1). The same was not true of triadic agonistic interactions and kissing, however ($p>0.05$). The small clumps of animals within the wild pigtail troops reported in previous studies

(Crockett & Wilson, 1980; Caldecott, 1986b; Robertson, 1987)
might also have been groups of close kin.

Estrus of females may possibly affect their cohesion to the groups, as was indicated by the co-feeding experiment B). A female might temporarily separate from her kin group to consort with males. Heterosexual grooming was exchanged between estrous females and males, and pregnant females occasionally groomed the males. Males might first have a grooming relationship with estrous females. Next, the pregnant females with whom they copulated might groom them. Since different females come into estrus one after another (Oi, submitted b), high-ranking males might change their female grooming partners according to their estrous condition.

A linear dominance rank order seems to be a general characteristic of macaque societies (Takahata, 1988), and one that was apparent in the study troop. Even though females in estrus tended to be proximate to the males, female dominance rank did not change in relation to estrous condition. However, by being close to the dominant male, the estrous females could engage in more advantageous feeding than the females of similar rank. Furthermore, dominance reversal occurred between only two pairs during the study. These data demonstrate the stability of the dominance hierarchy in pigtail troops (Bernstein, 1969).

Winner-support took place when the dominant animals formed an alliance and attacked a subordinate, with the exception of cases where alliances of females and adolescent males attacked the males. Such patterns of attacks might maintain the present dominance relationships (Datta, 1983).

19

The males were most frequent victims (68.3%), and 85.2% of these attacks were initiated by females and juveniles. In pigtails, males are markedly larger than females, and they are strong competitors of females and juveniles during feeding (Caldecott, 1986a). Thus, females and juveniles might try to take advantage in competition for food by excluding the males by concerted attack. The male victims of these attacks scored comparatively low rates of attendance in the unit group (Oi, submitted a). The frequent aggression from the females and juveniles against the males might be one of the factors that influences the emigration of males from the troop.

The special concerns of high-ranking males for females appeared to be involved in triadic interactions. In winner-support, the alpha male supported only females, and only the two top-ranking males, particularly the alpha, took part in loser-support. Control behavior by the alpha male has also been reported for pigtails in the laboratory (Bernstein, 1966; Tokuda & Jensen, 1968; Massey, 1977) and in other macaques (M. mulatta, Bernstein & Sharpe, 1966; M. radiata, Simonds, 1965; M. fuscata, Watanabe, 1979). Furthermore, the alpha twice chased away a female who approached too closely to the blind. The two top-ranking males, and especially the alpha male, positively interfered with dangerous behavior by troop members, which might result in maintaining the security of the troop (Caldecott, 1986b; Watanabe, 1979).

Grooming, non-copulatory mounting, and kissing have been regarded as conciliatory behavior (de Waal, 1984). In the present study, most such behaviors seemed to occur without direct

20

relation to agonistic context. Thus, their functions might be considered to reduce social tension (de Waal, 1984) which is induced, for example, by feeding at a crowded baiting site or by male competition for mates. Furthermore, these behaviors might be performed in recognition of the dominance relationships between the participants, since they tend to be performed unidirectionally.

In pigtails in the laboratory, grooming among females is performed mutually and more frequently among kin (Defler, 1978). The same tendency was found in Japanese macaques, which also have a matrilineal unit group (Furuichi, 1984). However, in the present study, most grooming among females were performed unilaterally. Thus, this grooming is considered to be, not only an expression of affinity among the females, but also a way of reducing social tension. These conciliatory behaviors were also performed more frequently among kin in rhesus macaques (de Waal & Yoshihara, 1983).

In non-copulatory mounting by the subordinate of the dominant, the tolerance by the dominant individual of the subordinate seemed to be expressed quite elaborately. Manipulation by the dominant seems to be important in the performance of the mounting by the subordinate since this type of mounting includes a behavioral element, i. e., presenting by the dominant.

Directionality of mounting in terms of dominance relation was not completely one-sided in each sex-combination of the participants. This implies that directionality does not depend on the sex-combination of the participants but on the social context (Hanby, 1974). Contrasting results in Tokuda et al.

21

(1968) on the directionality of male-male mounting also support this idea. Tokuda et al. (1968) reported that male-male mounting in confined pigtails tended to be directed towards the lower-ranking males. The data were obtained just after a dominance reversal between the alpha and beta males. In the reorganized confined troop, the new alpha male might be frequently in a social context where he has to express his dominance rather than tolerance by the dominant-to-subordinate mounting. By contrast, in a well-established troop under natural condition, such as Troop B, the alpha male might frequently be in a social context where he should express tolerance by the subordinate-to-dominant mounting. It could be said that the dominant male has the option of using either of the two types of mounting according to the social context.

Pigtail males seemed to use rather elaborate non-copulatory mounting for conciliatory purpose more frequently than other macaque males. The <u>unidirectional</u> subordinate-to-dominant mounting observed among pigtail males is in contrast to the <u>undirectional</u> mounting observed among rhesus macaque males (Reinhardt et al., 1986) and male Japanese macaques (Hanby, 1974). However, even in mounting by Japanese macaques, the initial presenting was performed by the subordinate (Hanby, 1974), as in the case of the mounting by the pigtails. This result suggests that mounting by macaques are performed with expression of the dominance relation in some behavioral component of mounting. I concluded that pigtail males were more competitive for mates than Japanese macaques and rhesus macaques, and that the priority of dominance in access to the mates was more rigidly established (Oi,

22

submitted b). Under such social conditions, pigtail males may have developed more elaborate ways to reduce such severe social tension by using subordinate-dominant mounting frequently.

Since forced mounting was not preceded by presenting, the motivation for this behavior could be a demonstration of dominance by the performer. This type of mounting was performed only among females, and females performed it more frequently than solicited mounting. This tendency was in contrast to mounting among troop males which reflected a tolerant relationship.

The sex difference found in quality and pattern of conciliatory behavior, and in the intensity of aggression may reflect a difference in the social relationships of each sex. The interactions among males tend to be better-controlled, and the dominant males play a positive role in coexistence with the subordinate males by expressions of tolerance. It might be necessary for coexistence of males who are competitive for mates and have no kin bonds, as do females, that the dominant should express tolerance of the subordinate in non-resource-oriented behaviors, in order to permit a concerted defense of females and their offspring against potent solitary males and predators. The subordinate males, by living in the troop, may have more opportunities to mate with females than solitaries, who might also be in greater danger from predators.

Females seemed to adjust their social relationships by grooming rather than mounting, however, mainly within close kin, and the subordinate females appeared to make approaches to the dominant females by acting as groomers. For matrilineal troops, troop fission is one way in which the troop size is regulated

(Maruhashi, 1982), and such troop fission is realized by the disruption of affinitive relationships based on the kin-bonds (Oi, 1988). To be fierce in agonistic interactions, and to express aggression in non-copulatory mounting would help to disrupt the kin bonds and may result in smaller-sized troops when the social tension induced by intra-troop conflicts becomes high.

CONCLUSIONS

In the matrilineal pig-tailed macaque troop, females tend to form some spacially cohesive associations within a group, assumed to be of close kin, in which affinitive interactions were exchanged. Each male showed different association patterns with females. High-ranking males tended to associate with females in the contexts of grooming and agonistic alliances, while low-ranking males tended to be hindered from these associations, and to frequently suffer from allied attacks involving females and juveniles. Among males, conciliatory behavior was well developed which might work to reduce social tension among troop males probably caused by strong competition for mates. These behaviors seemed to work successfully since the fierce attacks were never observed among troop males. Unidirectionality of conciliatory behavior implies cognition of dominance relationships by the participants. Furthermore, context-dependent directionality of male-male mounting and the role of the dominant in performing subordinate-to-dominant mounting, suggest that the dominant male has the option of two types of mounting according to the social

context. This implies that the dominant male plays an important role in coexistence of pigtail males in a troop.

ACKNOWLEDGMENTS

REFERENCES

Bernstein, I. S., 1966. An investigation of the organization of

25

pigtail monkey groups through the use of challenges.
Primates 7: 471-480.

Bernstein, I. S. & L. G. Sharpe, 1966. Social roles in a rhesus
monkey group. Behaviour, 26: 91-104.

Bernstein I. S., 1967. A field study of the pigtail monkey.
Primates, 8: 217-228.

Bernstein I. S., 1969. Stability of the status hierarchy in a
pigtail monkey group (Macaca nemestrina). Anim. Behav., 17:
452-458.

Caldecott, J. O., 1986a. Mating patterns, societies and the
ecogeography of macaques. Anim. Behav., 34: 208-220.

Caldecott, J. O., 1986b. An Ecological Study and Behavioural
Study of the Pig-Tailed Macaque. Contributions to Primatology
21, F. S. Szalay (ed.), Karger, Basel.

Chapais, B., 1983. Dominance, relatedness and the structure of
female relationships in rhesus monkeys. In: Primate Social
Relationships. R. A. Hinde (ed.), Blackwell Scientific
Publications, Oxford. pp. 208-219.

Crockett C. M. & W. L. Wilson, 1980. The ecological separation of
Macaca nemestrina and M. fascicularis in Sumatra; In: The
Macaques. D. G. Lindburg (ed.), Van Nostrand Reinhold, New
York, pp. 148-181.

Datta, S. B., 1983. Relative power and the maintenance of
dominance. In: Prmate Social Relationships. R. A. Hinde
(ed.), Blackwell Scientific Publications, Oxford, pp. 103-111.

Defler, T. R., 1978. Allogrooming in two species of macaque
(Macaca nemestrina and Macaca radiata). Primates, 19: 153-167.

Dunbar, R. I. M., 1976. Some aspects of research design and

their implications in the observational study of behaviour. Behaviour, 58: 78-98.

Eisenberg, J. F., N. A. Muckenhirn, & R. Rudran, 1978. The relation between ecology and social structure in primates. Science, 176: 863-874.

Fagen R. & N. J. Mankovichi, 1980. Two-act transitions, partitioned contingency tables, and the 'significant cell' problem. Anim. Behav., 28: 1017-1023.

Furuichi, T., 1984. Symmetrical patterns in non-agonistic social interactions found in unprovisioned Japanese macaques. J. Ethol., 2: 109-119.

Hanby, J. P., 1974. Male-male mounting in Japanese monkeys (Macaca fuscata). Anim. Behav., 22: 836-849.

Koyama, N., 1967. On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates, 18: 189-216.

Maruhashi, T., 1982. An ecological study of troop fission of Japanese monkeys (Macaca fuscata yakui) on Yakushima Island, Japan. Primates, 11: 317-337.

Massey, A. 1977. Agonistic aids and kinship in a group of pigtail macaques. Behav. Ecol. Sociobiol. 2: 31-40.

Oi T., 1988. Sociological study on the troop fission of wild Japanese monkeys (Macaca fuscata yakui) on Yakushima island. Primates, 29: 1-19.

Oi T., submitted a. Population organization of wild pig-tailed macaques (Macaca nemestrina nemestrina) in West Sumatra.

Oi T., submitted b. Sexual behavior and mating system of the wild pig-tailed macaque (Macaca nemestrina nemestrina) in West Sumatra.

Reinhardt V., A. Reinhardt, F. B. Bercovitch & R. W. Goy, 1986. Does intermale mounting function as a dominance demonstration in rhesus monkeys? Folia. Primatol., 47: 55-60

Robertson, J. M. Y., 1987. On the evolution of pig-tailed macaque societies. Ph. D. thesis, University of Cambridge.

Rosenblum, L. A., 1971. Kinship interaction patterns in pigtail and bonnet macaques. In: Proc. 3rd Int. Congr. Primat., Zurich 1970, vol. 3, Karger, Basel, pp. 79-84.

Shively, C., S. Clarke, N. King, S. Schapiro & G. Mitchell, 1982. Patterns of sexual behavior in male macaques. Am. J. Primatol. 2: 373-384.

Simonds, P. E., 1965. The bonnet macaque in South India. In: Primate Behavior. I. DeVore (ed.), Holt, Rinehart and Winston, New York, pp. 175-196.

Sneath, P. H. A. & R. R. Sokal, 1973. Numerical Taxonomy, The Principal and Practice of Numerical Classification. W. H. Freeman & Co., San Francisco.

Takahata, Y., 1988. Dominance rank order of adult female Japanese monkeys of the Arashiyama B troop. Primate Res., 4: 19-32. (in Japanese, with English summary)

Thierry B., 1986. A comparative study of aggression and response to aggression in three species of macaque. In: Primate Ontogeny and Social Behaviour. Proceed. 10th Congr. Int. Primatol. Soc. vol. 3, J. G. Else & P. C. Lee (eds.), Cambridge University Press, Cambridge, pp. 307-313.

Tokuda K., R. C. Simons and G. D. Jensen, 1968. Sexual behavior in a captive group of pigtailed monkeys (Macaca nemestrina).

Primates, 9: 283-294.

Tokuda K. and G. D. Jensen, 1969. Determinants of dominance hierarchy in a captive group of pigtailed monkeys (Macaca nemestrina). Primates, 10: 227-236.

de Waal, F. B. M., 1978. Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. Behaviour, 66: 268-312.

de Waal, F. B. M. & D. Yoshihara, 1983. Reconciliation and redirected affection in rhesus monkeys. Behaviour, 85: 224-241.

de Waal, F. B. M., 1984. Coping with social tension: sex differences in the effect of food provision to small rhesus monkey groups. Anim. Behav., 32: 765-773.

Watanabe, K., 1979. Alliance formation in a free-ranging troop of Japanese macaques. Primates, 20: 459-474.

Yamada, M. 1966. Five natural troops of Japanese monkeys in Shodoshima Island (I)-Distribution and social organization-. Primates, 7: 315-362.

Table 1. Dyadic agonistic interactions among age-sex classes.

| Actor | Recipient | | | | |
	AdM	AdlM	F	Juve	Total
AdM	40(27.9)*	95(83.9)	277(305.1)	137(132.1)	549
AdlM	8(10,2)	83(30.7)***	78(111.7)**	32(48.4)*	201
F	46(43.7)	85(131.6)***	547(478.5)**	183(207.2)	861
Juve	2(14.2)**	26(42.8)*	149(155.6)	103(67.4)***	280
Total	96	289	1051	455	1891

The numbers in parentheses are the expected values.
significance levels by cell-by-cell, chi-square test, one-tailed:
* p<0.02, ** p<0.01, *** p<0.001.
AdM: adult male, AdlM: adolescent male, F: adult and adolescent
female, Juve: juvenile.

Table 2. Direction of dyadic agonistic interactions at the individual level.

Actor		AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ni	Ng	Tk	Gi	Mg	Total
AM	(Ad)	-	29	3	10	3	3	I	4	11	10	11	12	9	14	9	5	6	9	1	8	5	3	166
RS	(Ad)	0	-	8	7	8	0	2	3	3	7	9	6	10	9	7	8	4	10	3	3	7	1	115
ID	(Ad)	0	0	-	1	1	18	17	0	0	0	0	0	0	0	1	1	0	1	0	1	0	9	50
JN	(Adl)	0	0	3	-	6	0	1	1	0	0	0	2	1	7	2	9	1	1	2	2	11	3	52
SR	(Adl)	0	0	1	0	-	4	0	0	0	0	2	0	0	0	0	3	0	0	1	5	9	11	36
HG	(Adl)	0	0	0	0	0	-	63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	63
PT	(Adl)	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
St	(Ad)	0	0	1	0	3	1	0	-	13	13	1	4	4	1	3	1	3	5	2	1	2	1	59
Hn	(Ad)	0	1	4	3	0	1	1	0	-	6	0	6	3	4	4	2	2	5	4	2	4	6	58
Kg	(Adl)	0	1	0	1	0	0	0	0	0	-	5	2	1	5	3	3	1	2	0	0	1	1	26
Ks	(Ad)	0	0	0	0	1	1	0	0	0	0	-	0	0	0	1	0	0	1	0	2	1	0	7
Ab	(Ad)	0	0	3	0	6	3	2	0	0	0	0	-	1	1	15	7	5	3	4	0	3	2	55
Kn	(Ad)	0	0	3	0	4	2	0	0	0	0	0	1	-	10	10	4	4	7	8	3	5	7	68
Tr	(Ad)	0	3	2	0	5	0	0	0	0	0	0	0	0	-	7	6	1	4	4	1	7	10	50
Yt	(Ad)	0	0	3	0	3	1	3	0	0	0	0	0	0	2	-	5	5	7	1	1	7	9	47
Po	(Ad)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	2	0	0	3	6
Na	(Ad)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	1	0	1	3	1	7
Ni	(Ad)	0	1	2	0	1	3	4	0	0	0	0	0	0	0	0	0	0	-	1	0	2	14	28
Ng	(Ad)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	1
Tk	(Ad)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	-	9	6	17
Gi	(Ad)	0	0	3	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	7	13
Mg	(Ad)	0	1	0	0	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	7
Total		0	36	36	22	43	44	97	8	27	36	28	33	29	53	62	54	32	57	33	31	76	94	931

Ad: adult, Adl: adolescent
The horizontal line separates the males from the females.

Table 3a. Direction of winner-support among age-sex classes: an initiator attacks a victim, and a participant joins in attacking the victim.

initiator	participant →	AdM				YM				F				Juv				Total
	victim →	AM	YM	F	J	AM	YM	F	J	AM	YM	F	J	AM	YM	F	J	
AdM		0	1	2	1	0	2	1	0	0	7	0	1	0	0	0	0	15
YM		0	2	1	0	0	1	0	0	2	7	2	1	1	0	0	1	18
F		5	8	8	1	6	7	4	1	31	3	4	1	18	2	7	4	110
Juv		0	0	0	0	0	2	2	0	7	5	3	1	8	8	6	4	46
Total			29				26				75				59			189

Table 3b. Direction of loser-support among age-sex classes: an actor (later the victim) attacks a beneficiary, then an interferer attacks the victim.

beneficiary	interferer →	AdM				YM				F				Juv				Total
	victim →	AM	YM	F	J	AM	YM	F	J	AM	YM	F	J	AM	YM	F	J	
AdM		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YM		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F		4	3	1	4	0	0	0	0	4	1	1	1	4	0	0	0	23
Juv		0	2	1	0	0	0	0	0	0	2	4	3	0	2	0	0	14
Total			15				0				16				6			37

YM: adolescent male

Table 4a. Direction of winner-support at the individual level.

Init.	AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ni	Ng	TK	Gi	Mg	Total
																		Participant					
AM	-	Kn Hn	HG																				3
RS		-		Gi																			1
ID			-	HG		PT									PT			HG3		PT			7
JN				-				ID												ID			2
SR		HG			-									HG	HG					Gi			4
HG		PT	PT			-								PT				PT				PT	5
PT							-																0
St				ID	Tk			-												ID			3
Hn	RS3	Ab		HG					-					ID									6
Kg										-										ID			1
Ks			ID								-												1
Ab		Mg Tk	HG						ID			-		ID2									6
Kn		Mg											-					Mg		Mg2			4
Tr	RS				Mg2 HG									-									4
Yt		Na Gi			Gi										-			ID					4
Po															SR HG	-					ID		3
Na					HG												-						1
Ni	ID	Mg	HG2 PT	ID				ID							ID			-		ID			9
Ng					HG														-				1
Tk	HG		HG													ID		ID		-			4
Gi					HG											ID					-		2
Mg			PT2		HG2				ID					HG ID				ID		ID	ID	-	10
Total	6	9	10	7	10	1	0	2	2	0	0	2	0	6	3	3	1	7	0	9	2	1	81

Init.; Initiator
Name codes in each cell are victims of alliance attacks   The figures in each cell are the
number of attacks. Codes with no figures indicate that the attack occurred just once.

Table 4b.   Direction of loser-support at the individual level.

Bef.	AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ni	Ng	Tk	Gi	Mg	Total
													Interferer										
AM	-																						0
RS		-																					0
ID			-																				0
JN				-																			0
SR					-																		0
HG						-																	0
PT							-																0
St								-															0
Hn	RS3								-														3
Kg										-													0
Ks											-												0
Ab								Hn				-											1
Kn	SR	SR											-										2
Tr														-									0
Yt															-								0
Po		SR														-		SR ID					3
Na	Yt																-						1
Ni																		-					0
Ng																			-				0
Tk																				-			0
Gi																					-		0
Mg	ID																					-	1
Total	6	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	11

Bef.; Beneficiary
Name codes in each cell are victims of alliance attacks. The figures in each cell are the numbers of the attacks. Codes with no figures indicate that the attack occurred just once.

Table 5. Direction of grooming at the individual level.

Performer	AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ni	Ng	Tk	Gi	Mg	Total
AM	-											1					1	3		3			8
RS		-																3					3
ID		1	-															2					3
JN				-														1					1
SR					-																		0
HG						-																	0
PT							-																0
St								-															0
Hn	3							1	-														4
Kg	2	1							1	-		4											8
Ks											-												0
Ab			2									-											2
Kn	1	1											-										2
Tr										1		2	2	-	1								6
Yt												1		1	-								2
Po														2	2	-							4
Na																	-	1					1
Ni		6															1	-					7
Ng		1										1						1	-				3
Tk		1																1		-			2
Gi														1		1		2		5	-		9
Mg			1										1							1		-	3
Total	6	11	3	0	0	0	0	1	1	1	0	9	3	4	3	1	2	14	0	9	0	0	68

Table 6. Situations and types of non-copulatory mouting.

Situation preceding mounting	Type of mounting	Direction of mounting		Sex combination		
				♂-♂	♂-♀	♀-♀
aggressive inter-action between both participants (20)	s-mt	D-S	2	0	1	1
		S-D	7	1	1	5
	f-mt	D-S	11	0	0	11
		S-D	0	0	0	0
aggressive inter-action embroiling one of the participants (7)	s-mt	D-S	3	0	2	1
		S-D	1	0	0	1
	f-mt	D-S	2	0	2	0
		S-D	0	0	0	0
	?-mt	D-S	1	0	0	1
approaching with conciliatory behaviour (29)	s-mt	D-S	8	5	2	1
		S-D	21	19	1	1
no distinct social situation (6)	f-mt	D-S	1	0	0	1
		S-D	0	0	0	0
	?-mt	D-S	3	0	2	1
		S-D	0	0	0	0
		?	2	1	0	1
Total	62		62	26	11	25

**s-mt: solicited mounting, f-mt: forced mounting, ?-mt: identification whether s-mt or f-mt was missed, D-S: the dominant mounted the subordinate, S-D: the subordinate mounted the dominant.

Table 7. Direction of non-sexual mountings at the individual level.

Performer	AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ng	Ni	Tk	Gi	Mg	Total
AM	-	1	1					2	1														5
RS	4	-	2																				6
ID	3	4	-		1																		8
JN		1		-															1		1		3
SR	1				-									1						2			4
HG	2		1			-																	3
PT	2	1	1				-																4
St								-															0
Hn									-	3													3
Kg										-													0
Ks										1	-												1
Ab												-	1						1				2
Kn	1											1	-									1	3
Tr														-									0
Yt										1				2	-								3
Po																-					1		1
Na																	-						0
Ng																		-					0
Ni																			-				0
Tk																				-	2	1	3
Gi														1							-		1
Mg																						-	0
Total	13	7	5	0	1	0	0	2	1	5	0	1	1	4	0	0	0	0	2	2	4	2	50

Table 8. Direction of kissing at the individual level.

Performer	Recipient																						Total
	AM	RS	ID	JN	SR	HG	PT	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Ni	Ng	Tk	Gi	Mg	
AM	-																						0
RS		-																					0
ID	1	2	-																				3
JN				-																1			1
SR					-																	1	1
HG						-																	0
PT							-																0
St								-						1									1
Hn									-	1				1									2
Kg										-													0
Ks											-												0
Ab												-		2			1	2					5
Kn					1								-					3					4
Tr												2		-	1			2			1	1	7
Yt															-			1					1
Po																-		2					2
Na																	-			1			1
Ni																		-					0
Ng																			-		1		1
Tk										1										-	1	1	3
Gi															1						-		1
Mg															1							-	1
Total	1	2	0	0	1	0	0	0	0	2	0	2	3	3	1	0	1	10	0	2	3	3	34

FIGURE LEGENDS

Figure 1. Distribution of observation points (OP) in the four feeding subsessions for each individual.

Figure 2. Co-feeding clusters found by single-link cluster analysis.
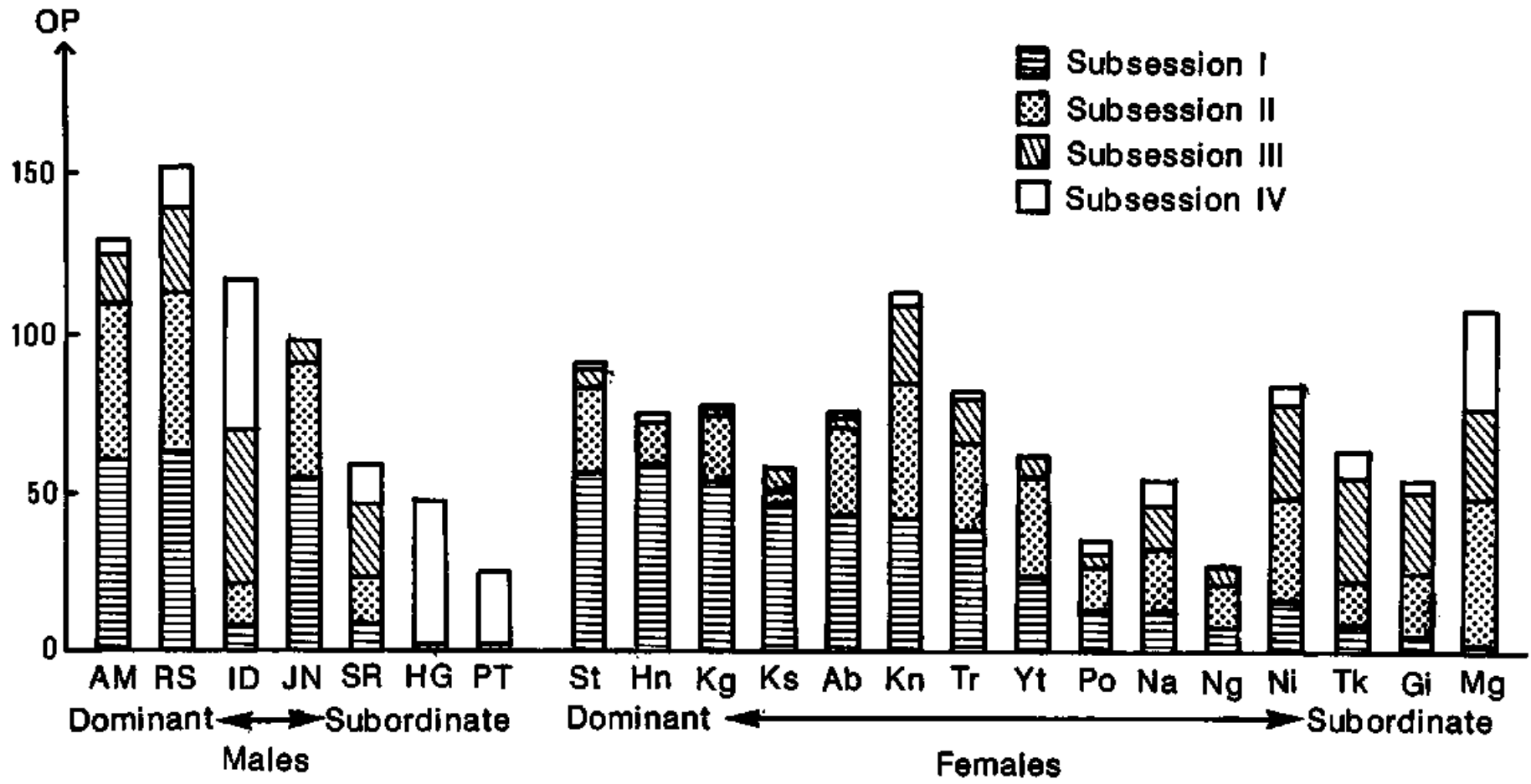
Fig. 1
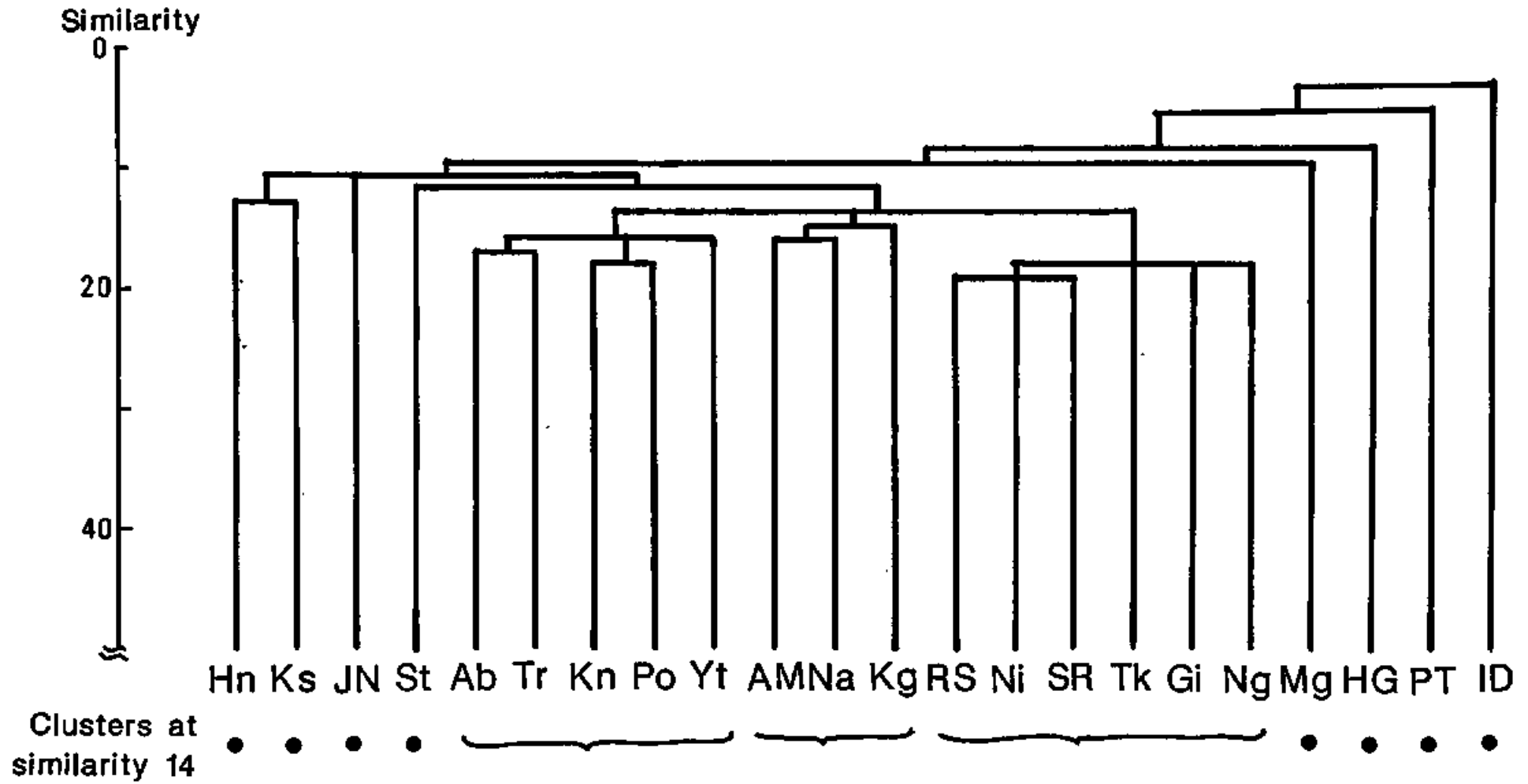
Fig 2

Sexual Behavior and Mating System of the Wild Pig-tailed

Macaque (<u>Macaca</u> <u>nemestrina</u> <u>nemestrina</u>) in West Sumatra.

Running head: Sexual behavior and mating system of

pig-tailed macaques

Toru OI

Primate Research Institute
Kyoto University
Inuyama
Aichi
484 Japan

ABSTRACT

Sexual behavior and mating relationships were studied in three provisioned troops of wild pig-tailed macaques in West Sumatra, Indonesia, based on identification of individual monkeys.

Estrous females showed conspicuous sexual swelling and had a mean cycle length of 39 days. Swelling was accompanied by sexual behaviors both by the females themselves and by males. Most copulations consisted of a single mount. Both the mean duration between the last swelling and parturition, and the duration of post-partum anestrus were 170 days. Estrus occurred throughout the year, with a peak in the middle of the rainy season.

The number of females who were simultaneously in estrous was generally low, and high-ranking males were usually able to monopolize them. As the number of estrous females in a troop increased, however, attempts to monopolize them became less successful.

The mating systems of macaques varies from the monopolization of estrous females by high-ranking males to promiscuity. Among species with mate throughout the year there are usually few females in estrous at any one time. High-ranking males are able to monopolize these females and within a group there tend to be many more adult females than males. Among species which have a restricted breeding season it is common for several females to be in estrous at the same time. These species display high degree of promiscuity and their social groups have a more balanced sex ratio. Such intra-genus variation in mating systems might be explicable in terms of the process of deployment, of each

1

species, into seasonal and non-seasonal environments.

INTRODUCTION

The sexual behavior and mating system of pig-tailed macaques
(pigtails) have been studied most frequently under laboratory
conditions (e.g., Kuehn et al., 1965; Tokuda et al., 1968).
Studies on the sexual behavior of wild pigtails are few in number
and are based on fragmentary observations (Bernstein, 1967;
Caldecott, 1986b). Perhaps because social behavior, is flexible
and may be influenced by external factors, results from the
laboratory and those from the natural habitat do not always agree
(e. g., Yamagiwa, 1986). Therefore, results from the laboratory
need to be verified and reinterpreted in the light of results
from studies in field.

Some behavioral differences have been recognized between
phylogenetic groups (species groups) of Macaca (Fooden, 1980;
Shively et al., 1982; Caldecott, 1986a). Macaque species have
the widest distribution among non-human primates, ranging from
tropical to subfrigid zones. Some variation in macaque behavior
and society may be related to differences in their habitats. One
example of this is the relationship between seasonality of the
environment and mating seasonality (Vandenbergh and Vessey, 1968;
Van Shaick & Van Noordwijk, 1985). Mating seasonality can be
thought of as a serial distribution of estrous females over time.
As estrous females can be considered to be a limited resources
for males (e. g., Emlen & Oring, 1977, Wrangham, 1979, 1980;

2

Ridley, 1986, Newton, 1988), mating seasonality will have important effects on competition between males for access to mates.

In the current paper, I describe the sexual behavior of pigtails, and analyze the relationships between the pattern of estrus in females and mate monopolization by males. Based on the analysis, I discuss the variation among macaque species in troop adult sex ratios and promiscuity in relation to mating seasonalities.

MATERIALS AND METHODS

Three troops of wild pigtails were studied in West Sumatra Province, Indonesia, during three periods: from January 1985 to March 1985, from June 1985 to March 1986, and from July 1986 to February 1987. A detailed description of the study area is given in Oi (submitted a).

From 22 January to 2 March 1985, Troop A was preliminarily provisioned, and from July 1986 to February 1987, all three troops including Troop A were provisioned and observed regularly. In the present paper, data obtained on 158 observation days, from June 1986 to February 1987, are analyzed. During this period, Troops A, B, and C visited the baiting site on 104 occasions (2109 minutes), on 102 occasions (4534 minutes), and on 19 occasions (794 minutes), respectively. Troop A stayed at the site for 20 minutes on average (range: 2-49 min.), Troop B for 44 minutes (range: 3-102 min.), and Troop C for 42 minutes (range:

3

15-66 min.). Table 1 shows the age-sex composition of the three troops. Adult males (fully mature, estimated age of over 9 years), adolescent males (mature, estimated age of 5-9 years), adult females (parous, estimated age of over 4 years), and adolescent females (nulliparous, estimated age of 3.5-6 years) were the subjects for analysis (for detailed definition, see Oi (submitted a).

The two baiting sites were square, with sides of 20 m, and the animals were observed from a blind. 5-15 kg of unshelled peanuts were distributed of the site before observations. All adult and adolescent animals in Troops A and B were known on sight. As Troop C was observed much less frequently, only certain individuals could be recognized. For analyses that required complete individual identification, only data for Troops A and B were used. Male dominance order was determined from the outcome of dyadic agonistic interactions (Oi, submitted b).

The estrous condition of each mature female was monitored and all births were recorded. All sexual behavior, including sexual solicitation, copulation, interference in copulation, and rejection of copulation, was recorded. Estrous females were easily distinguished by the conspicuous swelling of their sexual skin (Fooden, 1975). In the analyses, only females with maximal swelling of sexual skin were considered to be estrous. Bullock et al. (1972) reported that ovulation occurred between the day of peak swelling and the first day of detumescence of the sexual skin. For examination of seasonality of estrus, estrous females were monitored from July 1986 to February 1987. For the period from March to June 1986, the minimum number of estrous females

4

per month was calculated by counting back 171 days, the median gestation length (range: 154-230 days; Hadidian & Bernstein, 1979), from the dates of birth.

RESULTS

Copulatory Behavior

Copulatory behavior began with solicitation by either a male or a female. A male typically solicited an estrous female by approaching her while puckering (lowering his chest, with protruding mouth shut, and retracting his ears) and putting his hand on her rump. A female solicited a male by approaching him from behind, passing by his nose, and finally presenting her genitalia 0.5-1.5 m in front of him. In this posture the female often looked back over her shoulder at the male.

A mount with intromission usually followed sexual solicitation. The mean length of a mount was 9.0 ± 3.0 seconds (n = 92), and 14 ± 5.5 pelvic thrusts (n = 220) occurred in a single mount. Ejaculation could not be distinguished. Near the end of a mount, the female turned her face back towards the male and grasped his thigh or scrotum, though this "reaching-back behavior" is not always accompanied by ejaculation (Bullock et al, 1972). The male sometimes emitted a short scream, "kya", with a grimace, during the mount. In 246 of the 249 mounts observed, when the male had dismounted, the female rushed away from him, emitting the sounds "ga-ga-ga".

Though ejaculation could not be distinguished, the results of

the present study strongly suggest that the pigtail is a single-mount ejaculator. According to Nadler and Rosenblum (1973), pigtail males required 10 minutes to achieve ejaculation after a series of mounts in the laboratory. Therefore, I defined the termination of a copulation as either: (1) discontinuation of mounts for more than 10 minutes, or (2) solicitation or copulation with other individuals by either of the participants.

194 possible copulations consisting of 249 sexual mounts were observed in Troops A, B, and C. Of the copulations, 162 (83.5%) were single mounts, 20 (10.3%) were double mounts, eight (4.1%) were triple mounts, two (1.0%) consisted of five mounts, one (0.5%) of six mounts, and one (0.5%) of seven mounts. Between mounts, the animals often fed. Furthermore, during tracking of the troops before provisioning, two single-mount copulations were observed. Taking these results into account, I have treated one mount as one copulation in my analysis of sexual interactions.

Estrous Cycle of Pigtail Females.

Swelling of the sexual skin occurred in a series of marked sequential changes. First, the skin around the anus turned red; next, it became swollen; and, at its most extreme, the swelling extended to the caudal base. Two females in Troop A, one in Troop B, and two in Troop C experienced their first estrus during the observation period. All females who appeared to have reached 3.5-4 years of age showed swelling of the sexual skin when estrous. The two consecutive first days of maximal swelling were separated by 39 ± 17 days (n=10), and 10 ± 3.6 days (n=10) were required to reach the maximal swelling from the beginning of

6

swelling (tumescent phase). Maximal swelling continued for 13 ±
6.1 days (n=20) (full swelling phase), and then it gradually
deflated over 11 ± 5.8 days (n=16) (detumescent phase). A
complete absence of swelling was sometimes observed between the
detumescent phase and the next tumescent phase. Sexual
solicitation by both males and females, and copulation, occurred
most frequently during the full swelling phase (Table 2).
Females also became red around the anus for 43 ± 18 days (n=7)
before parturition, but did not show any swelling of sexual skin.
Sexual solicitation and copulation were not observed in this
period before parturition.

It took 170 ± 28 days (n=11) for a female to resume
post-partum sexual swelling, and 170 ± 9.6 days (n=5) for a
fertile female to give birth after full swelling ceased. The
females ceased their estrous cycles, possibly indicating
conception, after one or two consecutive estrous cycles in two
cases (10% of the consecutive cyclings). In other cases the
number of consecutive estrous cycles prior to conception could
not be ascertained since the initiation or termination of estrous
cycling was outside the observation period. However, in 11 cases
(55 %), two or more estrous cycles were observed before cessation
or conception. This result implies that at least half of the
individuals failed to conceive during the first estrous cycle.

Seasonality of Estrus and Births

There were 24 births in Troops A and B between May 1986 and
February 1987. 16 (73%) of the 22 adult females in Troop A, and
eight (57%) of the 14 females in Troop B, gave birth. Births

7

occurred throughout the period of observation (Fig. 1) and were not concentrated in any particular months. Data for Troop C were obtained between May and December 1986. 11 (42%) of 26 adult females gave birth, and 82% of these were in November.

Estrous females were present almost throughout the year, with an increase towards the end of 1986 in each troop (Fig. 2). The number of estrous females in Troop A reached its maximum, 7 (26% of mature females) in November and January, that in Troop B reached its maximum, 4 (22% of mature females) in November, and that in Troop C reached its maximum, 9 (30% of mature females) in May with a second peak in November. The peak in May in the data for Troop C was calculated from the pattern of births.

During observations, 14 females showed signs of estrus in Troop A, and seven females did so in Troop B. However, only a few females were in estrus simultaneously. The mean number of estrous females on a daily basis was 2.3 ± 1.1 (mode: 2, range: 0-7, n=96) in Troop A, and 0.83 ± 0.78 (mode: 1, range: 0-3, n=81) in Troop B (Fig. 3).

Sexual Solicitation and Copulation

In Troop A, there were 23 solicitations by males and 57 solicitation by females and 66 copulations. In Troop B, there were 79 solicitations by males and 196 solicitations by females and 157 copulations. In Troop C, there were six solicitations by males and 25 solicitations by females and 26 copulations.

The larger number of solicitations by females might be due to the fact that while the highest-ranking male could solicit any

8

estrous female at any time, the other males were inhibited from soliciting estrous females in the presence of the highest-ranking male. For example, when the alpha male was present, solicitation by other males occurred infrequently (0.037 solicit./hr; this rate is calculated from the number of solicitations by the males divided by the total number of hours of observation for each male), and only when the other male was not visible to the alpha. In the absence of the alpha, solicitations by other males increased (0.54 solicit./hr). By contrast, estrous females solicited any male, even in the presence of the alpha (0.38 solicit./hr). The solicited males ignored the females or moved around to escape from such females. However, the rate of sexual solicitation by females also increased, to 3.4 solicit./hr, in the absence of the alpha male.

Only high-ranking males performed sexual solicitations. In Troop A, only the three top-ranking adult males solicited estrous females, while in Troop B, the two top-ranking adult males and the 4th-ranking adolescent male did so. The rate of sexual solicitation by each male (abbreviated to MSR), given by the number of solicitations divided by the total number of hours of observation for each male, is significantly correlated with the dominance rank of males (Troop A: $\tau = -0.51$, $p < 0.05$; Troop B: $\tau = -0.81$, $p < 0.01$, one-tailed).

All adult males and three adolescent males were sexually solicited by females in Troop A, and the rate of such sexual solicitation of each male (abbreviated to FSR), given by the number of solicitations divided by the total number of hours of observation for each male, is significantly correlated with the

9

dominance rank of the males ($\tau=-0.69$, $p<0.01$, one-tailed). In
Troop B, all males except for one adolescent (SR) were sexually
solicited by females. A solitary male (BK) was also solicited by
an estrous female (Kn), who had temporarily separated herself
from the other troop members. The FSR for the 2nd-ranking male
(1.7 solicit./hr) surpassed that for the 1st-ranking male (1.3
solicit./hr) in Troop B, and the correlation between FSR and the
dominance rank of males is not significant ($\tau=-0.52$, $p>0.05$,
one-tailed).

Females seemed to seek more mating partners than males. In
46 cases (81%), a male solicited a single female in one
observation day, and in 11 cases (19%) a male solicited two
females in one observation day. The males who solicited two
females were the alpha (8 cases), and the beta (3 cases).
Females solicited a single male on one observation day in 62
cases (70%), two males in 15 cases, three males in nine cases,
and four males in three cases. In all, a female solicited more
than one male in any one observation day in 27 cases (30%).

50% and 75% of estrous females in Troops A and B,
respectively, copulated with more than one male, and all adult
males copulated with more than one female (Table 3). Long-term,
exclusive mating relationships between particular males and
females were not observed.

The rate of copulation for each male (abbreviated to CPR),
given by the number of copulations divided by the total number of
hours of observation for each male, is significantly correlated
with dominance rank of males (Troop A: $\tau=-0.82$; Troop B:
$\tau=-0.90$, $p<0.01$, one-tailed). In Troop A, all adult troop males

10

(NU, NS, NR), two adolescent males (KM, KA), and an adult male (DO) who was a temporary member of Troop A, and all adult males (AM, RS, ID), two adolescent males (JN, SR), and one solitary male (BK) in Troop B were observed to copulate (Table 3). 70% of copulations in Troop A and 90% of copulations in Troop B, were performed by the two top-ranking males in Troop B.

There was a tendency for dominant males to copulate more frequently as the number of estrous females on a daily basis (abbreviated to NFD), decreased. The lower-ranking males appeared to have more chances to copulate as NFD increased (Table 4). NFD ranged from 0 to 7 in Troop A, and from 0 to 3 in Troop B. When NFD was equal to one, most of the copulations were performed by the 1st-ranking male, and the rest by the 2nd-ranking and the 3rd-ranking males. When NFD was equal to two, the same tendency appeared, but the 4th-ranking male participated in 12% of the total copulations. When NFD was equal to three, the proportion of copulations performed by the 1st-ranking and 2nd-ranking males was nearly equal. When NFD was equal to four or more, the distribution of copulations was almost equal among the four ranks. However, 84% of the total number of copulations observed were monopolized by the 1st- and 2nd-ranking males.

Mean values for CPR, FSR, and MSR were calculated on a daily basis for each male dominance rank according to the NFD (CPR', FSR', MSR' respectively) (Fig. 4). When NFD was two, CPR' for the 1st-ranking male reached a maximum and was 5-80 times larger than that for the others. The CPR' decreased when NFD was equal to three (Cochran-Cox test, $p < 0.001$, two-tailed). The distribution of FSR' and MSR' for the 1st-ranking male were similar to that

11

for CPR'.

CPR' for the 2nd-ranking male reached a maximum when NFD was equal to three, and the rate was not significantly different from CPR' for the 1st-ranking male (Student t-test, $p > 0.05$, two-tailed). However, the CPR's were still 5-49 times larger than those for the other males. MSR' for the 2nd-ranking male increased as NFD increased. FSR' for the 2nd-ranking male increased until NFD increased to three.

CPR' for the 3rd-ranking male reached a maximum when NFD was four or more. In this case, CPR's of the three top-ranking categories seem to be almost equal (but were still significantly different; Student t-test, $p < 0.001-0.05$, two-tailed), and CPR's were only 4-10 times larger than those for the 4th-ranking male and those below him. FSR' for the 3rd-ranking male reached a maximum when NFD was four or more. MSR' increased slightly as NFD increased. CPR', FSR', MSR' for the 4th-ranking male and those below him remained at lower levels, than those for higher-ranking males, but CPR' reached a maximum when NFD was four or more.

There seems to be limiting value of NFD above which the 1st-ranking male's ability to monopolize females decreases. CPR' for the 1st-ranking male decreased when NFD was three or more. The 1st-ranking male copulated with more than one female on only nine observation days (7 cases with two females, 2 cases with three females). When NFD became three or more, the chances for the 2nd-ranking male to have access to and copulate with the extra female which the 1st-ranking male could not monopolize, were probably more frequent. As NFD increases above a certain number,

12

the difference in frequency of chances for copulation between the
dominant and the subordinate males becomes smaller.

Duration of Mating Relationships

As the duration of any set of observations was limited (20
to 42 minutes on the average), it is unknown how long a mating
relationship may have continued. However, as the frequency of
social interactions between a male and a female increased when
the female becomes estrous, the time during which they were in
proximity to each other might also increase. 130 grooming bouts
(Dunbar, 1976) were observed in Troops A, B, and C. 36 bouts
(28%) involved heterosexual pairs, of which 75% occurred when the
female was tumescent, and 22% occurred with pregnant females.

Interference in Mating Interactions

In all three troops, the higher-ranking males, especially
the alpha male, interfered with the mating interactions of other
males. The interference was directed either against a female or
a male. The object of the interference may be subtly influenced
by the male-male relationships.

Mating interactions are defined as sexual solicitations,
irrespective of whether copulations occur. In a total of 95
mating interactions in Troop A, one case of interference was
observed; the alpha male attacked the beta male who was
copulating with an estrous female.

In total of 319 mating interactions observed in Troop B,
interference occurred in 12 cases. In 11 cases, the alpha male
interfered between a pair composed of the beta male and an

13

estrous female. In most cases, the beta male just moved away from the female as soon as the alpha male interfered with the pair. A more severe encounter took place on one occasion: when the alpha male found the beta male copulating with an estrous female. The alpha approached the pair and presented to the female, then he chased her and the beta male joined the attack.

In Troop C, in total of 32 cases of mating interactions, one case of interference was observed. The former alpha male attacked an estrous female after she had copulated with the current alpha male.

Although these interference were effective in separating the mating pair at the time, it is uncertain whether they were also effective in the long-term because of the short duration of daily observations. In only two cases, a post-interference interaction among the three participants was observed: in one case, the interrupted pair copulated 27 minutes after the interference had occurred; in another case, the interferer copulated with the target female 22 minutes after the interference.

Rejection of Copulation by Females

Estrous females were able to reject solicitations by males, either by running away or by sitting down in order to prevent copulation. In Troop A, the alpha male was rejected by three females in four out of 35 attempts at copulatory mounting, and in Troop B, the alpha male was rejected by four females in eight out of 93 attempts, and the beta male was rejected by two females in two out of 57 attempts at copulatory mounting. In Troop C, no rejection was observed in 26 attempts at copulatory mounting.

14

All but one of the pairs in which a rejection had taken place
were observed to copulate on other occasions.

DISCUSSION

Sexual Behavior

Fooden (1980) classified Macaca into four species-groups
largely on the basis of the morphology of the sexual organs.
Furthermore, he suggested that these morphological characteristics
are related to mount-ejaculation patterns; males of some species
ejaculate after repeated mounts (multi-mount ejaculators), while
others ejaculate after a single mount (single-mount ejaculators).
Subsequent studies have supported Fooden's hypothesis to some
degree (Shively et al., 1982; Caldecott, 1986a). There have been
changes, however, in the classification of two macaque species in
terms of their mount-ejaculation patterns. The Barbary macaque,
which was previously considered to be a multi-mount ejaculator,
was shown to be a single-mount ejaculator (Taub, 1982); and the
crab-eating macaque, previously considered to be a multi-mount
ejaculator, was found to perform both types of copulation
(Shively et al., 1982). This changing perception suggests that
there is still much to be learned about mating patterns of males
macaques.

Laboratory studies indicated that pigtails are multi-mount
ejaculators (Tokuda et al., 1968; Nadler & Rosenblum, 1973).
Only Bernstein (1967) and Caldecott (1986b) have reported on
mount-ejaculation patterns observed in the field. Bernstein
mentioned that copulation occurred via multi-mount ejaculation,

15

but also reported "113 potentially reproductive mountings were observed, many in a single copulatory sequence. Many mountings, however, were isolated and probably indicative of tension produced by provisioning and observers rather than reproductive behavior". Caldecott, after observing only 17 mountings, concluded that copulation was composed of a series of mounts with an inter-mount interval ranging from 1-20 minutes. However, he stated that he did not observe a complete set of mountings, from the onset to the cessation of copulation, because of poor visibility. Since he could not discern when ejaculation occurred, Caldecott's results should not be taken as conclusive.

The present data suggest that each copulation was composed of a single mount. If the mounts that I observed were performed as part of a series, the inter-mount interval was more than 10 minutes, much longer than the values (3 minutes) reported by Tokuda et al. (1968). Furthermore, the behavior of females, whereby they separated from males after each mounting with emission of characteristic vocalizations, gave the strong impression that a single-mount ejaculation or, at least, a completed copulation had occurred. These results suggest that perhaps pigtails show intra-species variation in mount-ejaculation pattern, as do crab-eating macaques.

Observations in the laboratory have shown that , sexual behavior of females is most frequent (Goldfoot, 1971, cited in Caldecott, 1986b), and the ejaculation rate is highest (Bullock et al., 1972) when swelling is maximal. Although the ejaculation rate could not be determined in the present study, the frequency of sexual behavior by both males and females reached a maximum

16

which coincided with maximum swelling.

As the mean duration of gestation and of both post-partum
unestrus was 170 days, the period of anestrus after conception
continued for 340 days on average. Thus, females recovered
behavioral receptivity in 340 days, and so if the first estrous
was fertile, a female could give birth every year, as Hadidian &
Bernstein (1979) reported from their laboratory study. However,
since more than half of the females did not conceive except after
multiple cycles in the present study (1.7 cycles in the
laboratory, as reported by Kuehn et al., 1965), the birth
interval should be more than a year under natural conditions.

Mating Seasonality

Mating seasonality in primates living high latitudes is
related to the annual photoperiodic cycle (e. g., Nozaki &
Ohsima, 1987). The study area was at a latitude of around 1°,
where the duration of daylight does not fluctuate enough during
the year to influence the seasonality of mating. Parturition was
observed throughout the observation period. Furthermore, direct
observation and the distribution of births show that estrus
occurred throughout the year, with a peak from November to
January when the relatively heaviest rainfall was recorded during
the course of one year (Oi, submitted a). It may be that the
estrous condition of females is influenced by rainfall. Pigtails
in Malaysia also show an annual pattern in the occurrence of
estrus, with peaks just after the relatively dry season when high
productivity of fruits can be expected (Caldecott, 1986b).
Similarly, a peak in conceptions among lion-tailed macaques

17

(_Macaca_ _silenus_) in India coincides with the onset of the monsoon
(Kumar & Kurup, 1985b). In seasonal environments, where levels
of available food change dramatically, monkeys may adjust
conception or lactation to the the times when the richest supply
of food is available (van Schaick & van Noordwijk, 1985).

Although Troops A, B, and C lived adjacent to one another
and their habitats were almost identical, the distribution of
monthly births in Troop C differed markedly from those in Troops
A and B. This difference may be a result of social, rather than
ecological factors. Troop C was different from Troops A and B in
two respects: Troop C frequently formed subgroups and the alpha
and the beta male of the troop reversed their dominance during
the study (Oi, submitted a). Females hanuman langurs come into
estrus when the takeover of a troop is taking place (Sugiyama,
1965). The concentration of births in a period in Troop C might
represent a related phenomenon. An estrous explosion of several
females may have been precipitated by the arrival of a potent
male, who later became the alpha.

Mate Monopolization by Males

As most individuals of both sexes copulated with multiple
partners, the mating system of the study troop can be described
as polygynandrous (Robertson, 1987). Caldecott (1986b) and
Robertson (1987) hypothesized a harem-type breeding unit to
explain the grouping tendency of pigtails from the composition of
groups that they studied. In their model, copulation would occur
exclusively between a certain male and some fixed females. The
present data do not support this model.

18

Pigtail males compete for mating partners. Sexual access by subordinate males to estrous females was restricted by the presence of dominant males. The dominant males interfered with mating interactions by the subordinate males. As a result, two top-ranking males in each troop performed most of the copulations.

Monopoly of copulation by the dominant males was achieved because there were usually only a few females in estrus at one time. The smaller the number of estrous females, the more conspicuous the mate monopolization by the dominant males became. By contrast, as the number of estrous females increased, so the frequency of copulation by the subordinate males and the non-troop males increased, a finding which agrees with the priority of access model (referred in Dunbar, 1988).

Counteracting this monopolistic tendency of the dominant males, females solicited even the lower-ranking males and tended to copulate with as many as males possible. Furthermore, they on some occasions rejected attempts by top-ranking males to copulate. In Troop B, the fact that more sexual solicitations by females were directed at the beta male than the alpha implies female preference for the subordinate male. It could be said that choice of mates by the females drives the tendency towards promiscuity.

In the small area of the baiting sites where individuals crowded together, males could easily monitor the condition of estrous females, and their positions in relation to other males. Thus, dominant males could easily maintain exclusive access to estrous females. In the forest, however, bushes and undergrowth provide cover where subordinate males can copulate surreptitiously,

19

thereby weakening the dominant male's ability to monopolize estrus females.

However, since there are only a few estrous females with conspicuous sexual signs in a troop at any given time, a few dominant males could probably herd them. Thus, the tendency towards monopolization of copulation with the fertile females by a few males is highly probable even outside the baiting site.

The extremely skewed adult sex ratio in pigtails is unique among macaque species (Caldecott, 1986a, 1986b), and might be related to mate monopolization, which is controlled by the pattern of estrus among females. Furthermore, this pattern might affect the spacing and mating strategy of solitary males. Observations of solitaries around a troop were not concentrated in a particular period, and the number of solitaries was comparatively small. Six solitary males appeared at Site I, and three solitaries appeared at Site II. In contrast to this, in Japanese macaques, solitaries were seen visiting a troop and copulating during the restricted mating season. Furthermore, the number of solitaries was two or three times larger than the number of troop males (Yamagiwa, 1985).

Two Different Types of Promiscuity in Macaques

It has been proposed that the number of estrous females in a reproductive unit affects intermale competition and the number of males in the unit (e. g., Emlen and Oring, 1977; Wrangham, 1979, 1980; Berenstein and Wade, 1983). Macaca species have the widest distribution among non-human primates, extending from non-seasonal to seasonal environments. Species living in a seasonal habitat

20

have a shorter breeding season, during which mature females become estrous in synchrony. Thus, the number of estrous females at any given time is relatively larger in a seasonal habitat compared with the same-sized reproductive units in a non-seasonal habitats (Ridley, 1986). My finding of a relationship between the number of estrous females and the tendency towards mate monopolization by males suggests that the mating system should be more promiscuous in species that live in seasonal habitats. Furthermore, such seasonality might also result in a greater proportion of males in a troop. Conversely, in the non-seasonal environment, a clear tendency towards mate monopolization by a few males and smaller numbers of males in a troop could be expected.

Ridley (1986) described a significant relationship in primates between length of breeding period and the nature of reproductive units, i. e., multi-male or single-male. However, he chose only seasonal species of macaques for his analysis. Table 5 shows data for six species of macaques with regard to breeding seasonality, and intra-troop adult sex ratios, taken from the literature. As breeding seasonality is a relative term, species with more than 70% of births concentrated within three months are considered to be seasonal breeders, and all others with almost year-round births are considered to be year-round breeders (Table 5). Macaca nemestrina and M. silenus are considered to be year-round breeders, and M. fuscata, M. sylvanus, M. radiata, and M. sinica are considered to be seasonal breeders. M. fuscata and M. sylvanus live at higher latitudes, and M. radiata and M. sinica live at low latitudes

21

but where the climate changes drastically from a dry period to a rainy period. The mean number of females per male in a troop of year-round breeders is 4.8 (SD=2.1, n=25), which is higher than that for seasonal breeders: 2.1 (SD=1.2, n=64) (Mann-Whitney's U-test, Z=5.9, N_1=64, N_2=25, p<0.01, one-tailed). Most troops of M. silenus, which is a year-round breeder and forms a small troops ($\bar{x}$=11, SD=6.6, n=16), have a single-male multi-female composition (Johnson, 1985; Kumar & Kurup, 1985a). It appears that, in Macaca, large group size, which means large numbers of females, and seasonally restricted estrus of females may provide suitable conditions for the evolution of troops with a multi-male configuration, and to increase the number of troop males. In addition to these requirements, the spatial cohesion of females within a unit group may also be important (van Schaick & van Hooff, 1983; Newton, 1988; Oi, 1988).

The relationship between seasonality of breeding and tendency towards promiscuity is summarized in Table 6. Wild troops of non-seasonal breeders, such as pigtails, show a tendency towards mate monopolization by a few top-ranking males, or troops of single-male composition, like those of the lion-tailed macaques, which is indicative of mate monopolization by a single male. This tendency towards mate monopolization by pigtail males was also reported from a laboratory study (Tokuda et al, 1968). However, the present study shows that the tendency towards mate monopolization changed in accordance with the number of estrous females in the troop at any one time. By contrast, in some wild troops of seasonal breeders there was no correlation between the dominance rank of males and frequency of copulation (Enomoto,

22

1978; Takahata, 1982 for M. fuscata; Simonds (1965) for M. radiata; Taub (1980) for M. sylvanus). However, even such seasonally breeding species show a tendency towards mate monopolization by dominant males, and correlations between dominance rank and frequency of copulation were reported for confined troops (Hanby et al., 1971; Modahl & Eaton, 1977 for M. fuscata; Witt et al., 1981 for M. sylvanus), in which dominant males can easily perceive the behavior of estrus females, and can easily control the behavior of subordinate males. These results indicate that promiscuity in Macaca varies in relation to the conditions, such as the number of estrous females available at one time, and the ease with which subordinate males can be controlled by dominant males.

Promiscuity of M. sylvanus is unique among macaque mating systems. Taub (1980) reported that, in a wild troop, the frequency of copulation was not correlated with the males' dominance rank, both males and females changed their mating partners frequently, and consortships were short (17 minutes on the average). This mating system was sustained by the females' promiscuity and the males' apparent unwillingness to interfere with mating by other males. M. radiata might have the same tendency, in that males appear to be inhibited from interfering with the mating by any other males (Rahaman & Parthasarathy, 1969), and the dominance rank of males is not correlated with the number of copulations (Shively et al., 1982; Caldecott, 1986a). Furthermore, M. radiata and M. sylvanus have other similar behavioral characteristics, for example, tolerance between males is high, males copulate with single-mount ejaculation, length of

23

consortships is short, etc. (Shively et al., 1982; Caldecott, 1986a). These similarities imply that they have the same mating system. The most striking similarity is that both of them are seasonal breeders.

M. fuscata and M. nemestrina males are explicitly competitive, in that dominant males interfere with the mating by subordinate males in any situation. Their promiscuity should be called a superficial promiscuous state and is derived from unilateral female-promiscuity and the inability of dominant males to exert mate monopolization at times when too many females are in estrus. In such a promiscuous state, if dominant males continue a monopolistic strategy with interference of matings by other males, the rate of copulation by the dominant males would decrease, as was suggested from the present study. The decrease in the rate of copulation might be ascribed to excessive time spent guarding many females or interfering with mating by others. In such cases, it would be adaptive to stop such ineffective interference with copulation (Takahata, 1982; Huffman, 1987) and guarding. M. sylvanus practices such a non-exclusive mating strategy, abandoning any interference, but they can also employ an exclusive mating strategy in situations where mate monopoly is possible (Witt et al., 1981). Males of M. fuscata do not practice such a non-exclusive mating strategy.

It might be expected that each phylogenetic species group (Fooden, 1980; Cronin et al., 1980; Delson, 1980; Melnick & Kidd, 1985) would demonstrate one or other of the two strategic repertoires in its mating behavior (exclusive or non-exclusive mating strategy). Only the sylvanus group (M. sylvanus) and the

sinica group (M. sinica, M. radiata, M. assamensis, M. thibetana) include species in which males have a non-exclusive mating strategy. However, M. sinica might be the exception in the sinica group because they are explicitly competitive for mates (Dittus, 1975, 1979). The silenus group (M. silenus, M. nemestrina, M. pagensis, and Sulawesi macaques), and the fascicularis group (M. fascicularis, M. mulatta, M. cyclopis, M. fuscata) include the species with an exclusive strategy. In the case of arctoides group (M. arctoides), the strategy is unknown.

A scenario whereby each species group came to have one or other mating strategy can be deduced from the process of geographic deployment of each species group which has been proposed by some researchers (e. g., Delson, 1980; Eudey, 1980) (Fig. 5). If the multi-male troop of macaques is derived from a single-male troop by the addition of extra males (Eisenburg et al., 1978), the proto-macaques which formed multi-male troops should appear in a seasonal environment, where many females come into estrus simultaneously in a single reproductive unit, and in such a unit group, several males could coexist. The dry areas, where rainy season and dry season change dramatically, and the high-latitude areas, found around the Mediterranean Sea where the oldest fossil macaque was excavated, represent just such a seasonal environment. The mating relationship of this proto-macaque should involve superficial promiscuity, with males being exclusively competitive. This behavioral tendency might be an inheritance from the ancestors of the proto-macaques which dwelled in a tropical, non-seasonal environment and formed

25

single-male troops.

Species groups which are descended from the proto-macaque and have intruded into tropical Asia should have retained the tendency for males to be exclusively competitive for mates in the non-seasonal environments there (proto and extant silenus group). The proto fascicularis group speciated in tropical Asia and deployed recently into higher-latitude zones in a relatively short time (Delson, 180; Eudey, 1980; Fooden, 1980), and the males of this group existing today have retained the tendency to be exclusively competitive for mates, which evolved in the non-seasonal environments of the tropics, even at higher-latitudes in seasonal environments, because their intrusion into the new habitat occurred rapidly and relatively recently (time delay of adaptation).

Meanwhile, M. sylvanus (and possibly M. radiata) has been living in a seasonal environment and has developed a promiscuous mating system in which males have a non-exclusive mating strategy. The oldest fossil macaques are regarded as subspecies of M. sylvanus and have been excavated from Pliocene strata around the Mediterranean Sea. The climate of Western Europe has been warm temperate zone or cool temperate zone, at least since the Pliocene era (Dorf, 1964). The faunal assemblage excavated with fossil macaques in Europe suggests that "macaque originally may have adapted to seasonal or decidious or even tree savanna" (Eudey, 1980). In the process of adaptation to such seasonal environments, the males of this species may have developed a non-exclusive mating strategy whereby they gain access to mates without wasteful sexual interference to other males.

26

ACKNOWLEDGMENTS

REFERENCES

Berenstain, L. & T. D. Wade, 1983. Intrasexual selection and male mating strategies in baboons and macaques. Int. J. Primatol., 4: 201-235.

Bernstein, I. S. 1967. A field study of the pigtail monkey (Macaca nemestrina). Primates, 8: 217-228.

Bullock, D. W., C. A. Paris & R. W. Goy, 1972. Sexual behaviour, swelling of the sex skin and plasma progesterone in the pigtail macaque. J. Reprod. Fert., 31: 225-236.

Caldecott, J. O., 1986a. Mating patterns, societies and the ecogeography of macaques. Anim. Behav., 34: 208-220.

Caldecott, J. O., 1986b. An Ecological and Behavioural Study of the Pig-Tailed Macaque. Contributions to Primatology 21, F.S. Szalay (ed.), Karger, Basel.

Cronin, J. E., R. Cann, & V. M. Sarich, 1980. Molecular evolution and systematics of the genus Macaca. In: The Macaques, D. G. Lindburg (ed.), Van Nostrand Reinhold, New York, pp. 31-51.

Deag, J. M. and J. H. Crook, 1971. Social behaviour and 'agonistic buffering' in the wild Barbary macaque, Macaca sylvana L. Folia primatol., 15: 183-200.

Delson, E., 1980. Fossil macaques, phyletic relationships and a senario of deployment; In: The Macaques, D. G. Lindburg (ed,), Van Nostrand Reinhold, New York, pp. 10-30.

Dittus, W. P. J., 1975. Population dynamics of the toque monkey, Macaca sinica. In: Socioecology and Psychology of Primates. R. H. Tuttle (ed.), Mouton, The Hague, pp.125-151.

Dittus, W. P. J., 1977. The social regulation of population density and age-sex distribution in the toque monkey. Behaviour 63: 281-322.

Dittus, W. P. J., 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. Behaviour, 69: 265-302.

Dorf, E., 1964. The use of fossil plants in palaeoclimatic interpretations. In: Problems in Palaeoclimatology, A. E.

M. Nairin (ed.), Wiley-Interscience, London, pp. 13-31.

Dunbar, R. I. M., 1976. Some aspects of research design and their implication in the observational study of behaviour. Behaviour, 58: 78-98.

Dunbar, R. I. M., 1988. Primate Social Systems, Crook Helm, London & Sydney.

Eisenberg, J. F., N. A. Muckenhirn, & R. Rudran, 1972. The relation between ecology and social structure in primates. Science, 176: 863-874.

Emlen, S. T. & L. W. Oring, 1977. Ecology, sexual selection, the evolution of mating systems. Science, 197: 215-223.

Enomoto, T., 1978. On social preference in sexual behavior of Japanese monkeys (Macaca fuscata). J. Human Evol., 7: 283-293.

Eudey, A. A., 1980. Pleistocene glacial phenomena and the evolution of Asian macaques, In: The Macaques, D. G. Lindburg (ed.), Van Nostrand Reinhold, New York, pp. 52-83.

Fooden,J.(1975): Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). Fieldiana (Zool.), 67: 1-169.

Fooden,J.(1980): Classification and distribution of living macaques (Macaca Lacépède, 1799). In: The Macaques, D. G. Lindburg (ed.), Van Nostrand Reinhold, New York, pp. 1-9.

Furuichi, T., 1983. Dominant-subordinate relationships in the social life of Japanese macaques. Iden, 37: 3-9. (in Japanese)

Hadidian, J. & I. S. Bernstein, 1979. Female reproductive cycles and birth data from an Old World monkey colony.

29

<u>Primates</u>, 20: 429-442

Hanby, J. P., L. T. Robertson & C. H. Phoenix, 1971. The sexual behavior of a confined troop of Japanese macaques. <u>Folia primat</u>., 16: 123-143

Huffman, M. A., 1987. Consort intrusion and female mate choice in Japanese macaques (<u>Macaca fuscata</u>). <u>Ethology</u> 75: 221-234.

Izawa, K., 1972. Japanese monkeys living in the Okoppe Basin of the Shimokita Peninsula: The second report of the winter follow-up survey after the aerial spraying of herbicide. <u>Primates</u>, 13: 201-212.

Izawa, K., 1978., Ecological study of Japanese snow monkey in Hakusan National Park-Troop movement and intertroop relationships in snowy season. II. <u>An</u>. <u>Rep</u>. <u>Hakusan Nature Conserv</u>. <u>Cent</u>., 4: 93-109. (in Japanese)

Johnson, T. J. M., 1985. Lion-tailed macaque behavior in the wild. In: <u>The Lion-tailed Macaque: Status and Conservation</u>, Monographs in Primatology vol.7, P. G. Heltne (ed.), Alan R. Liss Inc., New York, pp. 41-63.

Kawai, M., S. Azuma, & K. Yoshiba, 1967. Ecological studies of reproduction in Japanese monkeys (<u>Macaca fuscata</u>). I. Problems of the birth season. <u>Primates</u>, 8: 35-74.

Koyama, N. & P. B. Shekar, 1981. Geographic distribution of the rhesus and the bonnet monkeys in west central India. <u>J</u>. <u>Bombay Nat</u>. <u>Hist</u>. <u>Soc</u>. 78: 240-255.

Kuehn, R. E., G. D. Jensen, & R. K. Morill, 1965. Breeding <u>Macaca nemestrina</u>: a program of birth engineering. <u>Folia Primatol</u>., 3: 251-262.

Kumar, A. & G. U. Kurup, 1985a. Inter-troop interaction in

30

the lion-tailed macaques, Macaca silenus. In: The lion-tailed
Macaques: Status and Conservation. Monograph in Primatology,
vol.7, P. G. Heltne (ed.), Alan R. Liss Inc., New York pp.
91-101.

Kumar, A. & G. U. Kurup, 1985b. Sexual behavior of the
lion-tailed macaque, Macaca silenus. In: The lion-tailed
Macaques: Status and Conservation. Monograph in Primatology,
vol.7, P. G. Heltne (ed.) Alan R. Liss, Inc. New York, pp.
109-130.

Maruhashi, T., 1980. Feeding behavior and diet of the Japanese
monkey (Macaca fuscata yakui) in Yakushima Island, Japan.
Primates, 21: 141-160.

Maruhashi, T., 1982. An ecological study of troop fission of
Japanese monkey (Macaca fuscata yakui) in Yakushima Island,
Japan. Primates, 23: 317-337.

Mehlman, P., 1986. Male intergroup mobility in a wild population
of the Barbary macaque (Macaca sylvanus), Ghomaran Rif
Mountains, Morocco. Amer. J. Primat. 10: 67-81.

Melnick D. J. & K. K. Kidd., 1985. Genetic and evolutionary
relationships among Asian macaques. Int. J. Primatol. 6:
123-160.

Modahl, K. B. & G. G. Eaton, 1977. Display behaviour in a
confined group of Japanese macaques (Macaca fuscata). Anim.
Behav. 25: 525-535.

Nadler, R. D. & L. A. Rosenblum, 1973. Sexual behaviour
during successive ejaculations in bonnet and pigtail macaques.
Am. J. Phys. Anthrop. 38: 217-220.

Newton, P. N., 1988. The variable social organization of

hanuman langur (<u>Presbytis</u> <u>entellus</u>), infanticide, and the monopolization of females. <u>Int</u>. <u>J.</u> <u>Primatol</u>. 9: 59-77.

Nozaki, M. & K. Ohsima, 1987. Seasonal changes of the gonadotropic function in the female Japanese monkey. In: <u>Seasonal</u> <u>Effects</u> <u>on</u> <u>Reproduction</u>. <u>Infection</u> <u>and</u> <u>Psychoses</u> <u>Progess</u> <u>in</u> <u>Biometerorology, vol. 5</u>, T. Miura (ed.), SPB Academic Publishing, The Hague, The Netherlands. pp. 41-49.

Oi, T., 1988. Sociological study on the troop fission of wild Japanese monkeys (<u>Macaca</u> <u>fuscata</u> <u>yakui</u>) on Yakushima Island. <u>Primates</u>, 29: 1-19.

Oi, T., submitted a. Population organization of wild pig-tailed macaques (<u>Macaca</u> <u>nemestrina</u> <u>nemestrina</u>) in West Sumatra.

Oi, T., submitted b. Social behavior of wild pig-tailed macaques (<u>Macaca</u> <u>nemestrina</u> <u>nemestrina</u>) in West Sumatra.

Rahaman, H. & M. D. Parthasarathy, 1969. Studies on the social behaviour of bonnet monkeys. <u>Primates</u>, 10: 149-162.

Ridley, M., 1986. The number of males in a primate troop. <u>Anim</u>. <u>Behav</u>., 34: 1848-1858.

Robertson, J. M. Y., 1987. On the evolution of pig-tailed macaque societies. Ph. D. thesis, University of Cambridge.

van Shaick, C. P. & K. A. R. A. M. van Hooff, 1983. On the ultimate causes of primate social systems. <u>Behaviour</u>, 85: 91-117.

van Shaick, C. P. & M. A. van Noordwijk, 1985. Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (<u>Macaca</u> <u>fascicularis</u>). <u>J.</u> <u>Zool</u>., <u>Lond</u>., 206: 533-549.

Shively, C., S. Clarke, N. King, S. Schapiro, & G. Mitchell,

1982. Patterns of sexual behavior in male macaques. Am. J. Primatol. 2: 373-384.

Simonds, P. E., 1965. The bonnet macaque in South India. In: Primate Behavior, I. De Vore (ed.), Holt, Rinehart and Winston, New York, pp.175-196.

Sugiyama, Y. 1965. On the social change of hanuman langurs (Presbytes entellus) in their natural condition. Primates, 6: 381-418.

Sugiyama, Y. 1968. The ecology of the lion-tailed macaque (Macaca silenus Linnaeus)- a pilot study. J. Bombay Nat. Hist. Soc., 65: 283-292.

Sugiyama, Y. 1971. Characteristics of the social life of bonnet macaques (Macaca radiata). Primates, 12: 247-266.

Takahata, Y. 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. Primates, 21: 303-329.

Takahata, Y. 1982. The socio-sexual behavior of Japanese monkeys. Z. Tierpsychol. 59: 89-108.

Taub, D. M., 1980. Female choice and mating strategies among wild Barbary macaques (Macaca sylvanus L.). In: The Macaques, D. G. Lindburg (ed.), Van Nostrand Reinhold, New York, pp. 287-344.

Taub, D. M., 1982. Sexual behavior of wild Barbary macaque males (Macaca sylvanus). Am. J. Primatol. 2: 109-113.

Tokuda, K., R. C. Simons, & G. D. Jensen, 1968. Sexual behavior in a captive group of pigtailed monkeys (Macaca nemestrina). Primates, 9: 283-294.

Vandenbergh, J. G., and S. Vessey, 1968. Seasonal breeding of free-ranging rhesus monkeys and related ecological factors.

J. Reprod. Fert., 14: 71-79.

Watanabe, K., 1978. Some social alterations in the early periods following the commencement of provisioning in Japanese monkeys (*Macaca fuscata*). *Jap. J. Ecol.*, 28: 35-41.

Whiten, A. & T. J. Rumsey, 1973. 'Agonistic buffering' in the wild Barbary macaque, *Macaca sylvana* L. *Primates*, 14: 421-425.

Witt, R., C. Schmidt, & J. Schmitt, 1981: Social rank and Darwinian fitness in a multimale group of Barbary macaques (*Macaca sylvanus* Linnaeus, 1758). *Folia Primatol*. 36: 201-211.

Wrangham, R. W., 1979. On the evolution of ape social systems. *Soc. Sci. Inf.* 18: 335-368.

Wrangham, R. W., 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75: 262-300.

Yamada, M., 1966; Five natural troops of Japanese monkeys in Shodoshima Island (I)-distribution and social organization-. *Primates*, 7: 315-362.

Yamagiwa, J., 1985. Socio-sexual factors of troop fission in wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 26: 105-120.

Yamagiwa, J., 1986. Social structure of Yaku monkey and male mating strategy. In: *Japanese Monkeys on Yaku-Island*. T. Maruhashi, J. Yamagiwa, T. Furuichi, pp. 60-125. (in Japanese)

Yotsumoto, N., 1976. The daily activity in a troop of wild Japanese monkey. *Primates*, 17: 183-204.

Table 1. Sizes and age-sex composition of troops

Troop name	AdM	AdlM	AdF	AdlF	J	I	Total
Troop A	3	5	22	2	27	15	74
Troop B	3	4	14	1	18	9	49
Troop C	4	4	26	2	34	11	81

AdM: adult male; AdlM: adolescent male; AdF: adult female; AdlF: adolescent female; J: juvenile; I: infant

Table 2.   Phase of sexual swelling and incidence of sexual behavior.

Sexual behavior	Phase of sexual swelling				
	Tumescent	Full swell	Detumescent	Undiscerned	Total
Sexual solicitation by males	14(13)	85(79)	8(7)	1(1)	108(100)
Sexual solicitation by females	43(15)	205(74)	24(9)	6(2)	278(100)
Copulation	27(11)	196(79)	21(8)	5(2)	249(100)

The numbers in the parentheses indicate percent distribution of incidence of each behavior.

Table 3. Mating partner
(a). Troop A

Male/Female	Cw	Ef	Mr	Mi	Dn	Mo	Em	Mm	Up	Uu	Hr	Ww	Rt	Li	La	Li	Pi	Me	Ma	Bt	Ys	Ad	AF	YF	Tot.
NU(AdM)	8	1	2	0	0	0	0	0	1	0	0	0	2	2	0	1	1	0	0	8	0	0	3	2	31
NS(AdM)	3	2	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	1	15
NR(AdM)	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	4	8
DO(AdM)	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
KR(AdM)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KM(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2
IK(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KA(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
AK(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IN(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MN(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UI(Ad1M)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7
Total	13	3	8	0	0	0	1	1	1	0	0	0	4	5	0	1	1	0	0	12	0	0	3	13	66

(b). Troop B

Male/Female	St	Hn	Kg	Ks	Ab	Kn	Tr	Yt	Po	Na	Nl	Ng	Tk	Gl	Mg	Total
AM(AdM)	1	6	0	0	4	27	0	0	0	13	6	0	29	0	0	86
RS(AdM)	0	1	0	0	3	15	0	0	0	16	7	0	14	0	0	56
ID(AdM)	0	2	0	0	0	2	0	0	0	0	4	0	0	0	0	8
JN(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
SR(Ad1M)	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
HG(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PT(Ad1M)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BK(Ad1M)	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
Total	1	9	3	0	7	47	0	0	0	29	17	0	44	0	0	157

AF: unidentified adult females; YF: unidentified adolescent females;
UI: unidentified individuals. DO, KR, MN: males that temporally
stayed with the troop. BK: a solitary male.
Individuals are arranged from top to bottom or from left to right almost
according to their dominance rank order.
Underlined females had swollen sexual skin during the study period.

Table 4. The number of estrous females on each observation day
and the number of copulations by males of each dominance rank.

Dominance rank of males	Number of estrous females				
	1	2	3	4≧	Total
1	37(67%)	40(63%)	15(46%)	5(26%)	97(57%)
2	16(29%)	12(19%)	13(39%)	6(32%)	47(28%)
3	2(4%)	4(6%)	1(3%)	4(21%)	11(6%)
4≧ (n=17)	0(0%)	8(12%)	4(12%)	4(21%)	16(9%)
Total	55(100%)	64(100%)	33(100%)	19(100%)	171(100%)

The data from Troop A and Troop B have been combined.

Table 5. The breeding seasonality and adult sex ratio in
unisolated troops of wild macaques.

Species	Seasonality	References	Adult sex ratio	Reference
M. nemestrina	year-round	1)	6.6(n=8)	1)
M. silenus	year-round	5)	3.6(SD=1.2, n=17)	2),3),4)
M. sylvanus	restricted	9)	1.7(SD=0.75, n=14)	6),7),8),9)
M. radiata	restricted	11)	1.5(SD=0.66, n=22	10),12),13)
M. sinica	restricted	14),15)	2.4(SD=0.83, n=6)	14),15),16)
M. fuscata	restricted	17)	2.8(SD=1.5, n=22)	18)

1)This study, Caldecott (1986b); 2)Sugiyama (1968); 3)Johnson (1985);
4)Kumar & Kurup (1985a); 5)Kumar & Kurup (1985b); 6)Deag & Crook
(1971); 7)Whiten & Rumsey (1973); 8)Taub (1980); 9)Mehlman (1986);
10)Simonds (1965); 11)Rahaman & Parthasarathy (1969); 12)Sugiyama
(1971); 13)Koyama & Sheakar (1981); 14)Dittus(1975); 15)Dittus
(1977); 16)Dittus (1979); 17) Kawai et al. (1967); 18)Yamada (1966),
Yotumoto (1976), Watanabe (1978), Izawa (1972, 1978),; Maruhashi
(1980, 1982), Furuichi (1983), Oi (1988).

Table 6. Breeding seasonality and promiscuity in macaque societies.

Species	Breeding seasonality	Information for correlation between social rank and mating activity of males	
		Free-ranging troops	Confined troops
M. nemestrina	year-round	yes (1)	yes (2)
M. silenus	year-round	many one-male troop (3)	?
M. fuscata	restricted	no (4)	yes (5)
M. sinica	restricted	males are competitive when acquiring mating partners (6)	?
M. radiata	restricted	no (7)	no (8)
M. sylvanus	restricted	no (9)	yes (10)

(1) This study; (2) Tokuda et al. (1968); (3) Johnson (1985), Kumar & Kurup (1985); (4) Enomoto (1978), Takahata (1982); (5) Hanby et al. (1971), Modahl & Eaton (1977); (6) Dittus (1975, 1979); (7) Simonds (1960); (8) Shively et al., 1982; (9) Taub (1980); (10) Witt et al. (1981)

FIGURE LEGENDS

Figure 1. Distribution of live births from May, 1986 to February, 1987.
Seven births from May through the middle of July were estimated by the developmental stage of body size and behavior of the babies.

Figure 2. Distribution of estrous females from March, 1986 to February, 1987.
The numbers from March 1986 to July 1986 were estimated (see text).

Figure 3. Distribution of the numbers of estrous females on each observation day.

Figure 4. Rates of (a) sexual solicitation by males (MSR'), (b) sexual solicitation by females (FSR'), and (c) copulation (CPR') for each male dominance rank according to the number of temporal estrous females (NFD).
Data from Troop A and Troop B have been combined. Vertical intervals indicate standard errors.

Figure 5. Possible process of deployment into seasonal and non-seasonal environments of each species group of Macaca.
Males of the species groups with asterisks have a non-exclusive mating strategy, while males of the other species groups do not.

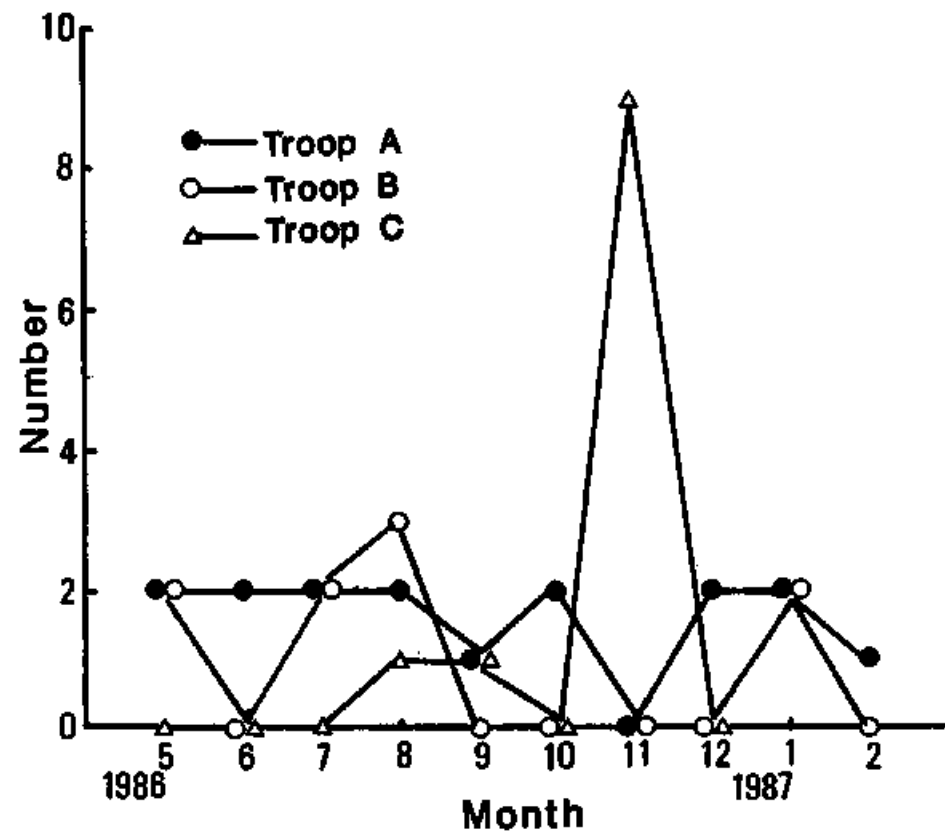The present distribution of the _fascicularis_ group extends into both environments.
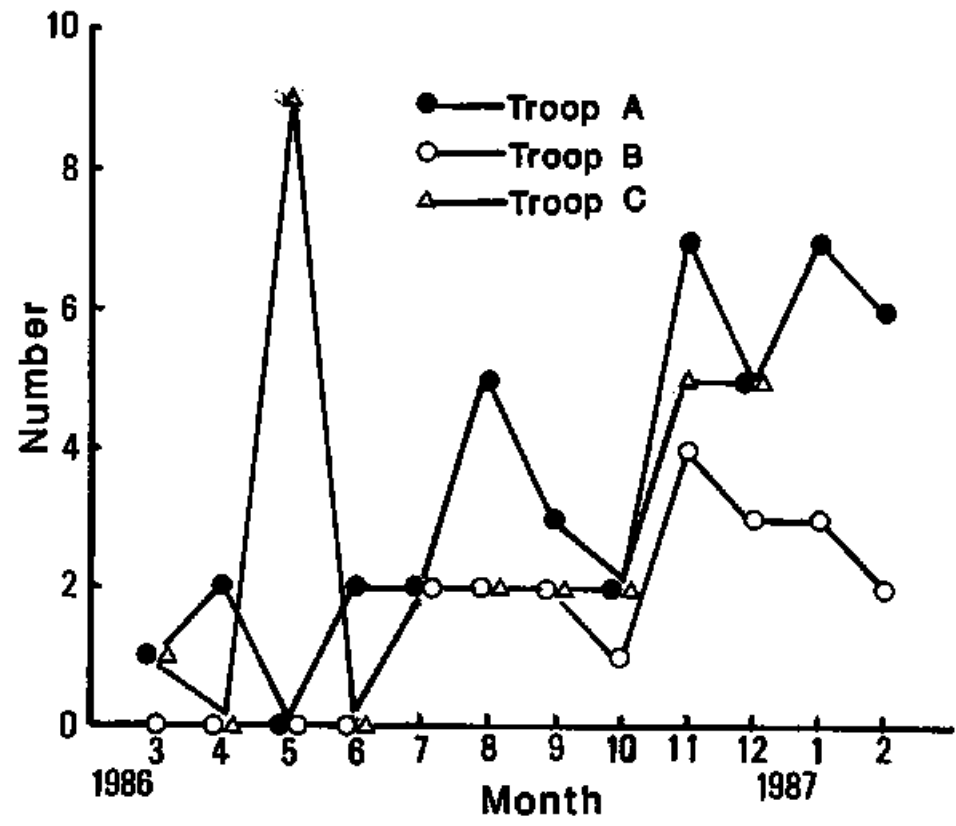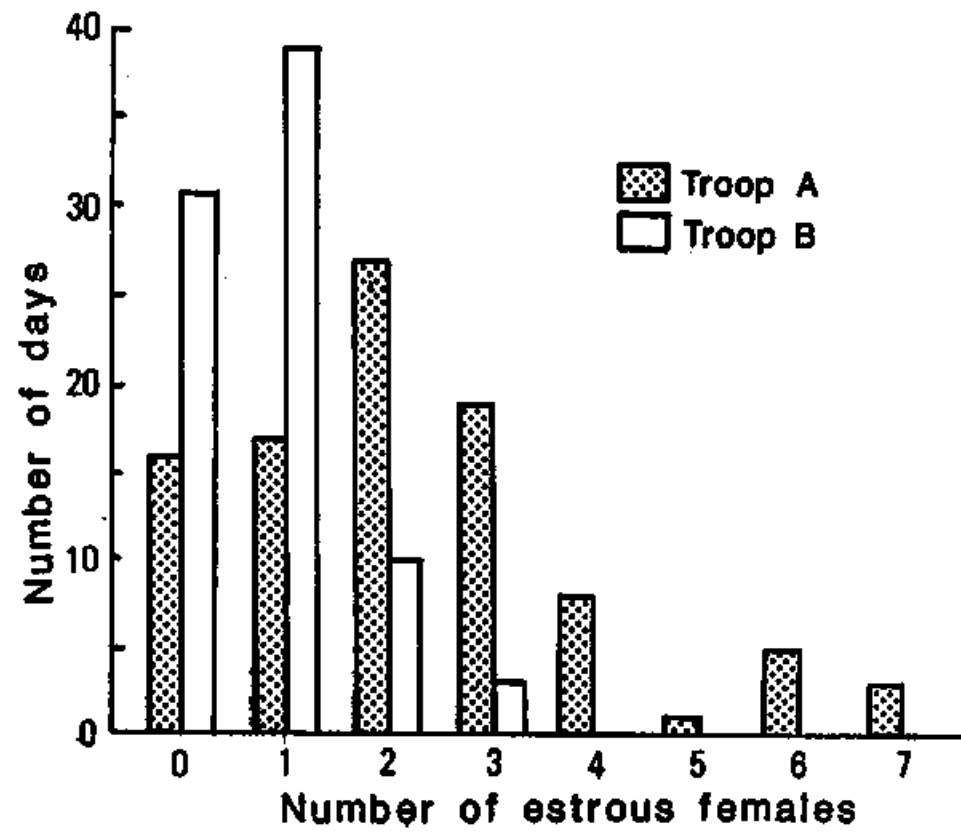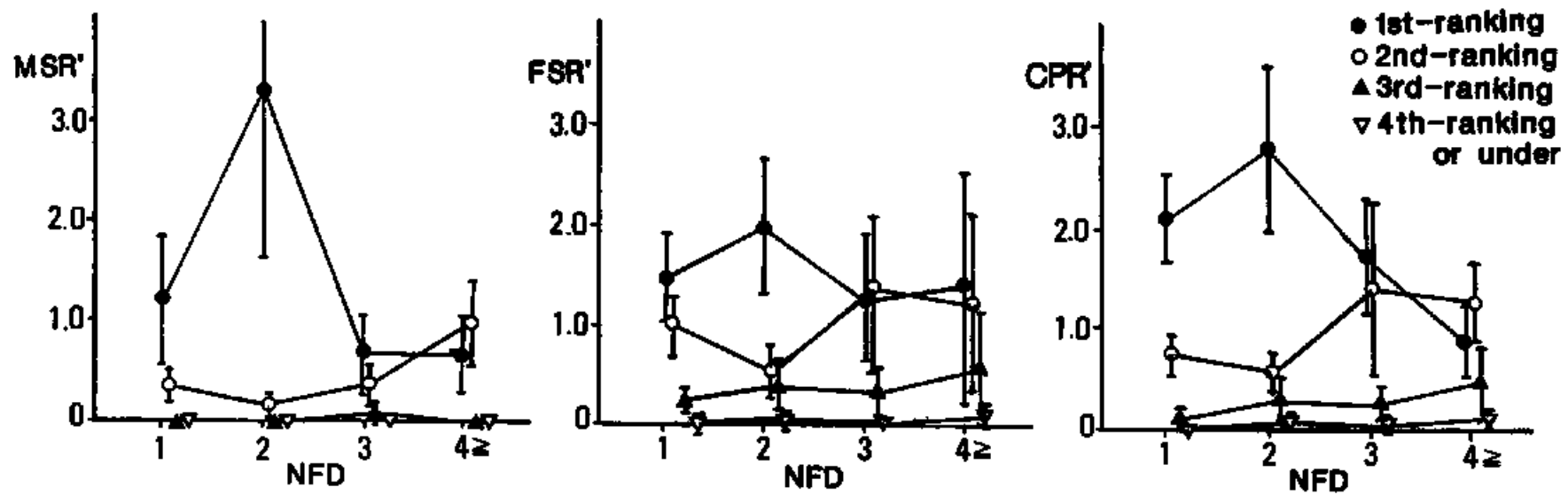
Fig. 1

Fig. 2

Fig 3

Fig. 4

sylvanus
group*

sinica
group*

seasonal
environment

proto-macaque

fascicularis
group

ancestor of
proto-macaque

non-seasonal
environment

silenus
group

time

Fig. 5