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Troop Size and Structure in Free-ranging Formosan Macaques (*Macaca cyclopis*) at Mt. Longevity, Taiwan

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Minna J. Hsu and Jin-Fu Lin (2001) Troop size and structure in free-ranging Formosan macaques (*Macaca cyclopis*) at Mt. Longevity, Taiwan. *Zoological Studies* **40**(1): 49-60. Among the 19 extant species of the genus *Macaca* that are found in southern and eastern Asia as well as northwestern Africa, the Formosan macaque is one of the least known. A long-term field study to investigate the population dynamics and social behavior of 7-16 troops of free-ranging Formosan macaques at Mt. Longevity, Taiwan has been conducted since July 1993. Between Dec. 1994 and Dec. 1997, a systematic census was conducted on a biweekly basis to record data on the demography of Formosan macaques. We used focal animal sampling and ad libitum sampling twice per week in respective troops to record data on social behavior including male replacement and fission processes. The maximum density of macaques has been estimated as 26 individuals per km^2 in Oct. 1997. The average troop size was 26.1 ± 9.7 (n = 7) in Jan. 1995 and it reached the highest level of 47.0 ± 21.2 (n = 13) in Aug. 1997. Two cases of fission were observed. The branch troops, Ia and Aa, that were formed as a result of fission had the smallest size with 9 individuals in the beginning, while troop I had the largest size of 86 individuals. Births were recorded mainly between Apr. and June (97%) with a peak in mid-Apr. to mid-May. The annual average overall sex ratio was 1.06 ± 0.28, while the adult sex ratio (adult males to adult females) was 0.53 ± 0.12. The average tenure length of alpha males was 16.8 ± 18.9 mo (n = 34) and ranged from 1 wk to a maximum of 6 yr. The average alpha male tenure in newly formed troops was significantly shorter (p < 0.01) than that in the remaining troops. About 88% of alpha male changes occurred between Oct. and Feb., which paralleled the peak and the end of the mating season, respectively.

Key words: Reproduction, Troop composition, Sex ratio, Male tenure, Fission.

Non-human primates are known to exhibit a wide variety of social and grouping patterns (Eisenberg et al. 1972). Changes in primate troop size and density have reflected short-term alterations in environmental conditions (Eisenberg 1979), epizootics (Collias and Southwick 1952), and natural disasters (Horwich and Johnson 1986). Changes in population structure can also be long-term adaptations to altered environmental conditions such as deforestation and human predatory pressure (Freese et al. 1982). Troop size and composition are the result of demographic processes that take years to develop, and short-term studies of relatively few groups may lead to misconceptions about primate social organization (Crockett 1985). Understanding the adaptive significance of troop size and flexibility on a long-term basis is therefore fundamental for understanding primate social ecology (van Schaik 1999). It is widely believed that predation and inter-troop resource competition as selective pressures favor group living and influence troop composition among non-human primates (Treves and Chapman 1996).

The genus *Macaca* is one of the most wide-spread primate groups in the world, but the Formosan macaque, *M. cyclopis*, is considered to be one of the least known. Among the 19 extant species of the genus *Macaca* that are found in southern and eastern Asia as well as northwestern Africa (Fa and Lindburg 1996), the Formosan macaque is endemic

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to the island of Taiwan (area 36 000 km^2). Much previous research on this species was focused on field surveys and observations to estimate the population status and distribution (Dien 1985, Masui et al. 1986, Tanaka 1986, Kawamura et al. 1991, see Lee and Lin 1991 1995 for review). Although it is distributed in a wide range of elevations (100-3300 m) occupying a variety of habitats (Masui et al. 1986, Lee and Lin 1991 1995), the density is relatively low, at around 0.1 group/km^2 in the southeastern coastal mountains (Masui et al. 1986). Hunting pressure on *M. cyclopis* has been substantial with mass captures for the purpose of exports for medical or experimental use (Masui et al. 1986). Even during 1986-1987, illegal hunting of this species was still reported (Lee and Lin 1995). It is listed in the *IUCN Red List of Threatened Animals* (1996) as well as being protected under Taiwan's *Wildlife Conservation Law* (1989).

The social structure of macaques is generally characterized as often occurring as a large stable multimale-multifemale troop. Masui et al. (1986) reported a sighting of a troop of *Macaca cyclopis* with more than 45 individuals (2 adult males and 13 adult females) in Taitung. However, long-term data on group size and birth for *M. cyclopis* are limited to a single field study of 2 single-male-multifemale troops, with a troop size of 9-16 individuals (Wu and Lin 1992 1993). Variation in grouping patterns has been found recently among species such as *M. fuscata* (Fukuda 1989), *M. nemestrina* (Oi 1990), and *M. sylvanus* (Menard and Vallet 1996). Birth rate and immature survival rate have been differently predicted as a function of group size by models on the evolution of group living in primates (Wittenberger 1980, Wrangham 1980). In an earlier survey of Mt. Longevity, Lin and Wang (1991) found 5 troops with a total of 76 Formosan macaques, but no details on troop composition or birth rate were described. Nevertheless, most troops at Mt. Longevity have a multimale-multifemale structure, and this makes the population interesting for socio-ecological investigations including variations in demographic parameters.

Habituation of animals is often required in order to collect detailed demographic assessment of a non-human primate species. We have been monitoring 7-16 habituated troops of free-ranging Formosan macaques that live in lowland rainforest habitat at Mt. Longevity, southern Taiwan since July 1993. In this paper, we present 3 yr of systematic data on troop structures and dynamics of Formosan macaques. Details are also given on troop size, composition, density, sex ratio, fission, dispersal, and alpha male tenures in order to compare the population and social dynamics data of Formosan macaques with other well-studied species of the genus *Macaca*.

MATERIALS AND METHODS

Description of Mt. Longevity study site

Mt. Longevity is located in Kaohsiung City adjacent to the Taiwan Strait. It is about 5 km long and 2.5 km wide with a height of 354 m and has an area of about 1116 ha. This mountain is isolated from other nearby mountains and forests due to the development of the city over the last 40-50 yr. The terrain is dominated by uplifted coral reefs, and the total surface area of Mt. Longevity is estimated to be 35 km^2 due to the complex topography (Lin and Wang 1991). We used a topographic field map to calculate the total area used by all macaque troops, which includes several uplifted coral reefs, and undulating hillocks and valleys. The northern part of Mt. Longevity is still a restricted military base, and researchers are not permitted to enter the area. Thus the study area excluding the military area covers about 25 km^2. Due to the long-term effects of water penetration in the hills, strange shapes of stones and steep valleys have been formed, and these combined with natural lowland rainforest habitat provide safe roosting areas for the macaques. The flora of Mt. Longevity includes 209 species in 164 genera and 72 families (Lin and Wang 1991). About 5% of the plants are ferns, which grow in the few wet gorges of the forest floor, or on trees. The dominant tree species include *Ficus septica*, *F. wightiana*, and *F. caulocarpa*, which also constitute a major food source for the macaques. Shrubs of *Severinia buxifolia* and *Lantana camara* and vines of *Bauhinia championii* are widely distributed. Introduced plants include *Acacia confusa*, *Leucaena glauca*, and *Delonix regia*; agricultural fruit trees such as *Euphoria longana*, *Mangifera indica*, and *Annona squamosa* are also found. The habitat and succession of plant communities follow the pattern of distinct wet and dry seasons that is similar to that in the nearby Kenting National Park (Wu and Lin 1992). The dry season begins in Oct. and ends in Apr. (Fig. 1). The average annual rainfall between 1995-1997 was about 1453 ± 576 mm concentrated from May to Sept. as the wet season with monthly averages near or above 100 mm (Fig. 1). Moreover, from Nov. to Feb., the average monthly rain falls below 35 mm. The average monthly temperature was lowest in Feb. (18.6 °C) and highest in July (29.9 °C, Fig. 1).

Census and observation plan

The study area was thoroughly searched for Formosan macaque troops along forest trails, footpaths, and transects using methods described by Hsu and Agoramoorthy (1996). Interviews with local people were conducted during the initial stages of the census to locate monkey troops and to collect preliminary data on the population size since July 1993. The existence of a few troops has been known since Feb. 1989 (Table 1). Some of these troops were also recorded in an earlier survey conducted by Lin and Wang (1991). Systematic census of 7-16 troops was conducted on a biweekly basis between Dec. 1994 and Dec. 1997 (Table 1). The roosting sites of most study troops were marked on a field map (Fig. 2). Identification of individuals was based on their natural marks and body characteristics using video and photographic documentation (US National Research Council 1981). We did not attempt to capture monkeys for marking purposes. Body weights of selected individuals from habituated troops were measured by using peanuts to attract the animal to stand or sit on a body scale.

Individuals were classified into broad age-sex classes based on direct measurement of chronological age with known birth year or based on physical characteristics and body size according to US National Research Council (1981). Chronological ages of individuals born after the onset of our study were known and were estimated for those individuals born earlier. Most females give birth to their first infants at around 5 yr of age. Subadult males were between the ages of 5 and 6 yr, and their secondary sexual characteristics had not fully developed as in adult males. Other individuals aged between 2 and 4 yr were considered to be juveniles. Infants of both sexes were typically nursing, and being cared for by their mothers when less than 1 yr old. We used focal animal sampling and scan sampling (Altmann 1974) to record data on social behavior including male replacement and fission processes twice per week in respective troops.

Data calculation and analysis

The annual growth rate was calculated using troop sizes in consecutive years for each troop when compared with the troop size of the previous year (December). The average annual growth rate was calculated from the annual growth rate for each of the 7 troops identified in the early part of the study for each year from 1994 to 1997. Population density was calculated as the maximum number of monkeys counted within the study period divided by the study area (25 km^2). Solitary males were often associated or interacted with particular troops and were seen mating with some peripheral females during the

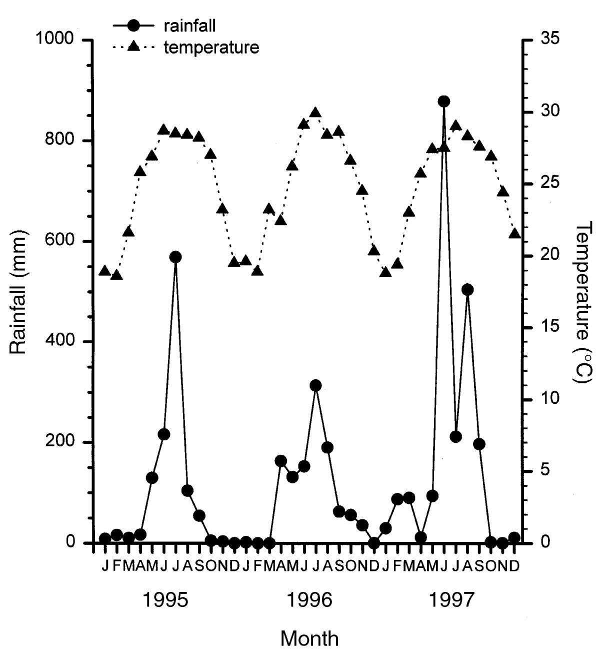

Fig. 1. Chronological data on monthly average temperature and total rainfall in Kaohsiung from 1995 to 1997. Data were provided by the Central Weather Bureau, R.O.C.

Table 1. Troop size of Formosan macaques during 1st contact, initial census (December 1994), and final census (December 1997) at Mt. Longevity, Taiwan

Troop	First contact		Dec. 1994	Dec. 1997
name	Data	Size	Size	Size
A	February 1989		24	35
B	February 1991		28	47
C	February 1989		32	50
D	February 1994		11	29
E	February 1992		10	22
F	February 1989		33	64
K	February 1991		33	64
G	04 Feb. 1995	47		69
Aa	14 May 1997	9		9
I	03 Dec. 1995	72		84
J	19 Nov. 1995	28		39
Ia	03 Feb. 1996	9		29
M	01 Jan. 1997	27		31
N	15 Oct. 1995	17		32
O	27 Sept. 1997	39		39
Q	01 Jan. 1996	19		
Total			171	643
Avg.			24.42	42.87
SE			10.05	20.10

breeding season. Therefore they were included within a troop size count to get a better estimation of adult sex ratio (adult males/adult females) instead of being calculated separately. The average adult sex ratio was calculated monthly for all available social troops. The overall sex ratio for each troop was calculated monthly as the number of males (adult, subadult, juvenile, and infants combined) divided by the number of females within a troop during the monthly census period. The annual overall sex ratio for each troop was the average of overall sex ratio calculated each year for 1995, 1996, and 1997.

Then we calculated the mean annual overall sex ratio for each troop, and we used this data set to get an average of the entire population during the study period. The tenure length of an alpha male was calculated as the duration of time that a male maintained this status in a troop.

All statistical analyses were conducted with Statistical Analysis System software (SAS Institute 1989). All mean values are presented as ± 1 standard error. The significance of troop size and the number of adult females on the rate of troop growth was tested using analysis of variance (ANOVA). Pearson correlation coefficients were used to test the relations of average troop growth to the average number of adult females and average troop size (with or without infants). Various regression analyses were conducted to obtain the best model to estimate the rate of troop growth. Spearman rank correlation coefficients were calculated for troop size without infants, number of adult females, and numbers of births and deaths of each troop. The effects of troop size (without infants) and number of adult females on dependent variables, such as the number of surviving infants, number of births, birth rate, and infant mortality, were tested using General Linear Models. The nonparametric Wilcoxon test was used to compare average tenure length of alpha males in newly formed troops to that of troops with longer histories (> 2 yr).

RESULTS

Density and troop size

Troop sizes of *Macaca cyclopis* at Mt. Longevity had a wide range from 9 to 86 with a maximum average troop size of around 47 individuals in Aug. 1997 (SE 21.2, *n* = 13). The troop size increased during our study period (Table 1; Fig. 3) and the maximum

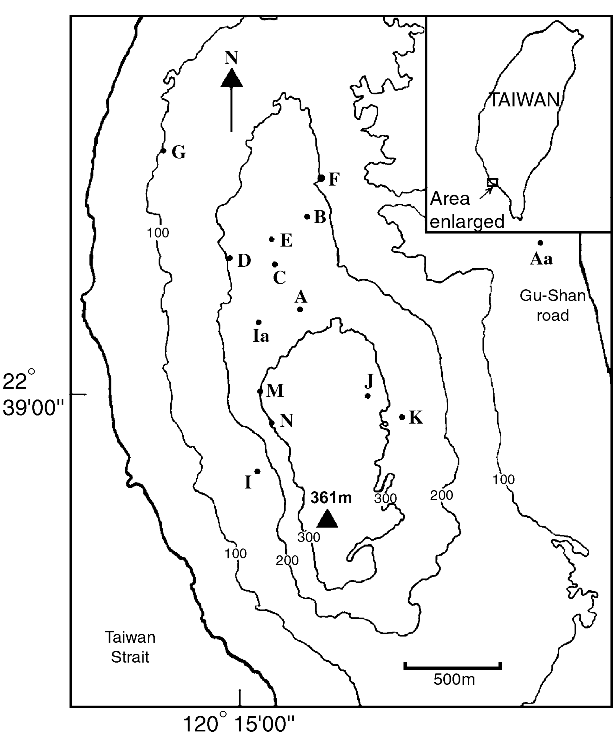

Fig. 2. Map of Mt. Longevity study site indicating the roosting sites of Formosan macaque study troops (A-N) between 1995 to 1997.

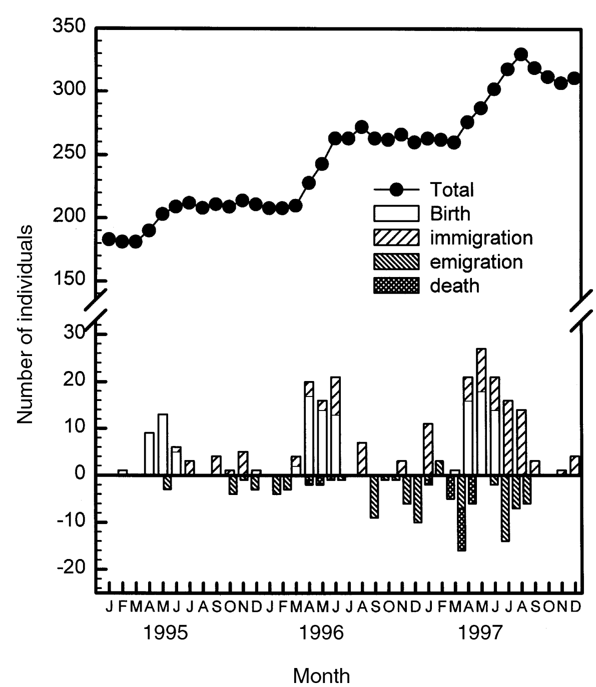

Fig. 3. Changes in number of individuals of 7 troops (A, B, C, D, E, F, and K) of Formosan macaque, *Macaca cyclopis*, at Mt. Longevity, Taiwan from 1995 to 1997. Number of individuals who died or who emigrated out of these troops are presented as negative values on the Y-axis.

density was estimated as 26 individuals/km^2 in Oct. 1997. The maximum number of individuals recorded was 652 among 15 troops in Oct. 1997. Their troop composition and age class distribution are shown in table 2. Initially, our study troops included 7 troops (171 individuals, Table 1) in Dec. 1994, and later 9 new troops were found and habituated including 2 troops (Aa and Ia) that formed as a result of fission from troops A and I (Table 1). Two of our study troops changed their original home ranges and disappeared from our study site, one temporarily while the other never reappeared. Troop Q disappeared on 26 June 1996 and was never seen again, while troop N disappeared on 9 June 1996 but reappeared on 5 Oct. 1997.

The average size of 7 troops of Formosan macaques in Dec. 1994 was 24.4 ± 10.1 (Table 1), and it reached the highest at 47.1 ± 16.9 in Aug. 1997 but decreased again to 44.4 ± 16.5 in Dec. 1997 (Fig. 4). The average annual growth rate of these 7 troops was 24.4% per year. This annual growth rate actually decreased from 29.0% (± 16.7 SE) in 1994/1995 to 25.4% (± 9.0 SE) in 1995/1996 to 18.7% (± 16.9 SE) in 1996/1997. In addition, the average annual growth rates of troops D and E with smaller troop sizes were higher than those of the other 5 medium- to large-sized troops (Fig. 5). In 11 troops that had been monitored for more than 2 yr (Table 1), the average annual growth rates were negatively correlated with average number of adult females ($r = -0.68$, $p < 0.05$) and average troop sizes excluding infants ($r = -0.61$, $p < 0.05$). This trend remained even when we excluded troops A and I (that underwent fission) from the analysis. However, the best regression model ($R^2 = 0.466$, $F_{1,9} = 7.86$, $p < 0.05$)

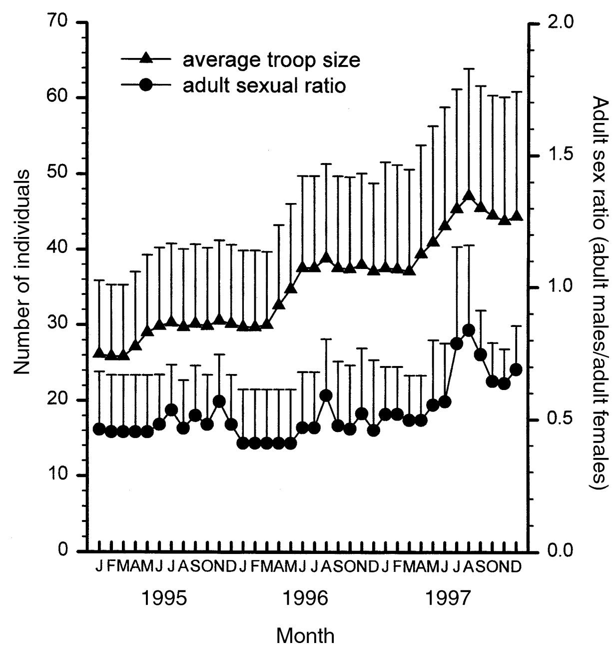

Fig. 4. Recorded changes of average troop size and operational sex ratio of 7 troops (A, B, C, D, E, F, and K) of Formosan macaque, *Macaca cyclopis*, at Mt. Longevity, Taiwan from 1995 to 1997. Vertical bars indicate the standard errors of the means.

Table 2. Troop composition and adult sex ratio of Formosan macaques recorded during the October 1997 census at Mt. Longevity, Taiwan

Troop	Adult sex	Adult		Sub-adult	Juvenile		Infant		Total
name	ratio	male	female	male	male	female	male	female	
A	0.88	7	8	2	6	7	5	1	36
B	0.83	10	12	3	8	8	4	2	47
C	0.54	7	13	8	8	9	3	3	51
D	0.57	4	7	2	4	5	5	2	29
E	0.57	4	7	0	2	6	1	3	23
F	0.54	7	13	9	14	13	3	4	63
G	0.27	4	15	8	16	13	8	4	68
Aa	0.60	3	5	0	3	0	0	0	11
I	0.29	5	17	4	21	18	9	6	80
J	0.60	6	10	3	14	3	3	3	42
K	0.60	9	15	5	13	9	8	4	63
Ia	0.71	5	7	0	10	3	4	1	30
M	0.63	5	8	4	7	4	4	3	35
N	0.83	5	6	4	8	7	3	2	35
O	0.80	8	10	6	8	7	0	0	39
Total		89	153	58	142	112	60	38	652
Avg.	0.62	5.93	10.20	3.87	9.47	7.47	4.00	2.53	43.47
SE	0.18	2.02	3.75	2.92	5.24	4.58	2.73	1.64	18.62

for estimating the annual growth rate (%) was 46.6 – (2.2114 × the number of adult females).

Troop Aa was the smallest with 9 individuals in Dec. 1997 (Table 1), while troop I reached a record high of 86 individuals in Aug. 1997. All troops had a multi-male structure with the exception of the initial troop formation of Ia and Aa. These 2 new troops had single males associated with adult females during the initial stages, but became multi-male troops after 7 and 16 wk, respectively.

Infant birth and survival

Births were recorded between Feb. and June annually, and 85% of the births occurred within 2 mo (Apr. 15 to June 15, Fig. 3). Most successful matings with sperm ejaculation were observed from Sept. until the following Feb., which indicated a distinct mating season. The total birth rate over 3 birth seasons was 0.7 infants per adult female per year. Birth rates increased from 0.5 infants per adult female per year in 1995 to 0.7 in 1996 and 0.8 in 1997 if all adult females in all troops were combined. However, the infant birth rate (birth per adult females) did not change significantly ($F_{1,11}$ = 1.774, $p > 0.20$) with troop size excluding infants (Fig. 6A) and also did not correlate with the number of adult females ($F_{1,11}$ = 1.078, $p > 0.32$). A total of 235 births were recorded during 1995-1997, of which 2 pairs were twins. Both sets of twins survived for over 3 yr and were still alive at the time of writing. Most infants (97%) were born between Apr. and June with the exception of 1 in Feb. and 5 in Mar.. Thirty-nine females were observed to deliver their 1st infants when they were about 4 yr old.

The number of surviving infants was correlated with the number of births (Spearman correlation coefficient, $r = 0.89$, $p < 0.001$), and the number of adult females and troop size without infants ($p < 0.001$). The number of infant deaths, however, did not correlate with any of these variables. The average mortality rate for infants within 6 mo of birth was 22.58% (± 2.95 SE) in 1996-1997. When troop Aa was excluded from the data set, the average infant mortality did not correlate linearly with average troop size (excluding infants) for 12 troops ($F_{1,10}$ = 0.07, $p > 0.79$, Fig. 6B). The percentage of infants within a troop was relatively constant and did not correlate with troop size ($p > 0.05$) when troop Aa was excluded. Troop Aa was small and newly formed from fission, and in that troop, two infants had died before

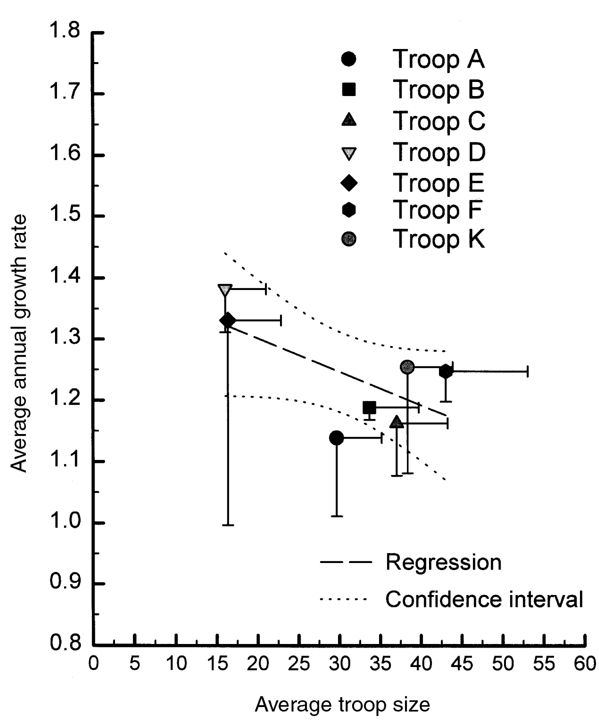

Fig. 5. The relationship of average troop sizes of 7 troops (from Dec. 1994 to Dec. 1997) and average annual growth rates. Error bars indicate the standard errors of the averages.

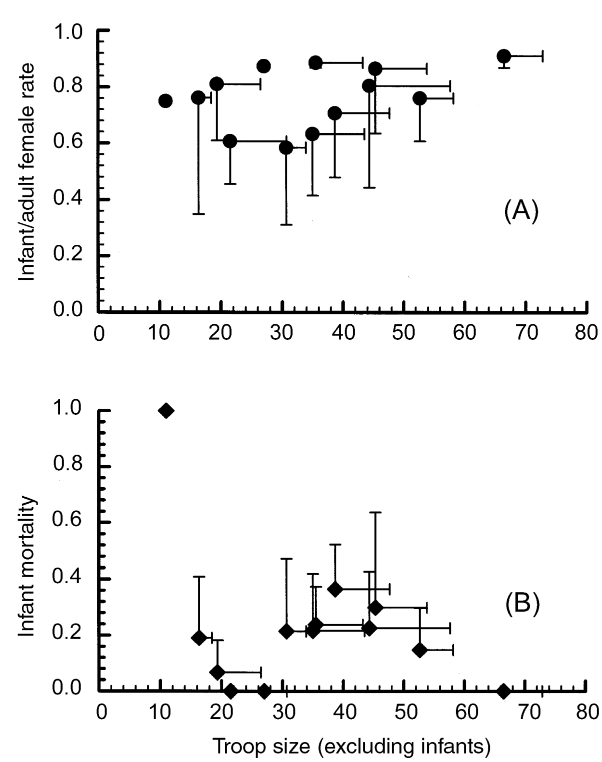

Fig. 6. Relationships between troop sizes of 13 troops (from troops A to M in Table 2) and infants per adult female (A) and infant mortality (B) among Formosan macaques. Data are shown as the mean ± SE.

Sept. 1997 (Table 2).

Sex ratio

The average overall sex ratio was approximately 1:1 (1.06 ± 0.28, n = 16, range 0.63 to 1.67), and the average adult sex ratio was close to 0.53 (± 0.12, n = 16, range 0.30 to 0.71). Solitary adult males accounted for 5% of the entire population, and they were seen interacting with social troops especially during mating season (between Sept. and Jan.) which slightly increased the adult sex ratio (Fig. 3).

The proportions of adult females in troops did not significantly decrease ($p > 0.05$) when troops' sizes increased from 20 to 85. However, the smallest troop, Aa, had the highest percentage of adult females (45.5%), while the largest troop, I, had the lowest percentage of adult females (21.3%, Table 2).

Troop fission

Two cases of fission were observed during 1996-1997.

Case 1. On 3 Dec. 1995 troop I had 72 individuals, and its home range was on the west slope of Mt. Longevity where visitors seldom hike. On 3 Feb. 1996, the gamma male (AM1) was found with 3 low-ranking adult females and 5 juveniles from troop I, and it was later named as a new troop (Ia). Three of the juveniles (2 males and 1 female) were 1 yr old, and the other 2 males were 2 yr old. The adult sex ratio (adult males to adult females) of troop I before fission was 0.21, and it changed to 0.19 after fission, whereas the adult sex ratio of the newly formed troop Ia was 0.33. Troop Ia was a 1-male troop for 7 wk before becoming a multi-male troop. Five months later, another 3 low-ranking adult females with 2 newborn infants emigrated from troop I to the newly formed troop Ia. Two more juvenile males joined the troop on 21 Sept. 1996. Even 1 yr after the formation of troop Ia (on 7 Feb. 1997), an adult female along with a juvenile male from troop I was observed to immigrate into troop Ia. During the same period of time, three adult solitary males also immigrated on separate occasions into troop I. Thus the adult sex ratio of troop I increased to 0.42, which was very similar to the ratio of troop Ia (0.43).

Case 2. Prior to fission in Apr. 1997, troop A had 42 individuals including 12 adult females. Three low-ranking adult females were seen 200 m away from the main troop A on 16 Apr. 1997. Three weeks later, an adult female with a 2-d-old infant accompanied by 3 male juveniles joined the trio. Although 2 peripheral males (AM1 and AM2) from troop A followed the 4 females, none was accepted as a leader since the alpha female (AF1) led the others. She also repelled the 2 males when they approached her. On 23 Aug. 1997, two other adult males (AM3 and AM4) were seen with the females. A week later, AM3 was established as the alpha male of the newly formed troop Aa.

Dispersal of males and females

Males stayed in their natal troops until 5 to 6 yr of age (n = 54) and dispersed either to become solitary or to immigrate into other troops. However, most juvenile males (3 to 4 yr old) usually moved gradually from the core area to the peripheral part of their natal troops. We did not observe any natal troop males engaging in true sexual mating with adult females in their natal troops. In the majority of the observed inter-male encounters (n = 31), solitary adult male invaders fought with the dominant male leader of social troops to access estrous females, often resulting in injuries. On the other hand, subadult males and old adult males (n = 39 in 11 troops) did not engage in aggressive encounters with alpha males in social troops. Subadult males and newly immigrated adult males were frequently observed in the peripheral part of social troops forming coalitions that ranged from 2-14 individuals. However, alpha males usually displaced these males and forced them to the periphery of the troops. The average tenure length of alpha males was 16.8 ± 18.9 mo (n = 34) with a range from 1 wk to a maximum of 6 yr. Average alpha male tenure (3.1 mo, n = 7) in troops that were newly formed as a result of fission, was significantly shorter ($p < 0.01$) than average tenure (20.4 mo, n = 27) in the rest of the troops. About 88% of changes of alpha males occurred during the peak of the mating season. The majority of adult females stayed in their natal troops, with the exception of troop fission. Sometimes subordinate females were mobile between main troops and newly formed troops. In one case, an adult female was observed to move between main troop A and new troop Aa on 4 occasions before her disappearance from the study area. Although female transfer is rare compared to male transfer in Formosan macaques, six solitary adult females successfully immigrated into other troops during our study.

DISCUSSION

Wild troops of Formosan macaques have been in existence in Mt. Longevity for many centuries, and the earliest record was cited on a 17th century Dutch colonial map with the name *Apenberg*, meaning Apes Hill (Lin and Wang 1991). Most of Mt. Longevity has been a restricted military base since the Japanese occupation of Taiwan for more than half a century and has only been partially opened to the public since 1989. The protection of the natural forests at Mt. Longevity by the military has left the majority of the flora little disturbed over the years. The forest also provides sufficient food resources for the monkeys, and in addition, some troops with home ranges close to trails irregularly receive some food items from visitors. In an earlier survey of Mt. Longevity, Lin and Wang (1991) found 5 groups of Formosan macaques ranging from 12 to 19 individuals per group, and they were named as troops A, B, C, F, and K in our study. These troops and troop E were habituated earlier than the rest of the troops. The other troops were afraid of humans when we first encountered them. Hunting pressure is thought to be the major cause for small troop size and low density of *Macaca cyclopis* in the wild (Masui et al. 1986, Wu and Lin 1992) before hunting was banned in 1989. The newly added study troops, solitary male immigration into social troops, and the reduction of hunting pressure were contributing factors for the increase in population size of monkeys at Mt. Longevity.

The widely variable range of troop size recorded in this study is consistent with other macaque species such as *M. nemestrina* (Caldecott 1986), *M. sylvanus* (Menard and Vallet 1996), *M. mulatta* (Southwick and Siddiqi 1988), and *M. fascicularis* (Kyes 1993). The average troop size in this study is comparable to a previous report of a troop of 45^+ individuals (Masui et al. 1986). Although it was reported that troop size could exceed 100 (Lee and Lin 1995), the authors were unable to verify is large a size. However, a social troop of *M. cyclopis* seldom exceeds 80 individuals and is not as large as reported for the provisioned troops of rhesus macaques on Cayo Santiago (Berman et al. 1997) and in Kowloon (Burton and Chen 1996) or for Japanese macaques (Furuya 1969).

The ratios of infants to adult females (crude birth rate) appeared to be constant regardless of troop size (excluding infants). This situation differed with Japanese macaques (Takahata et al. 1998a) and lion-tailed macaques (Kumar 1995). We found that a relatively larger troop (larger than 60 excluding infants) had an advantage in inter-troop competition with a higher percentage of winning troop interactions (Lin and Hsu unpubl. observ.). Nevertheless, in a small-sized troop, in which few separate matrilineal groups of females occur, intra-troop competition between different matrilineal females may be reduced, but their infants might be extremely vulnerable during the alpha male changes and inter-troop interactions.

Troop size of *Macaca cyclopis* on Mt. Longevity did not continue to grow, and some underwent fission even though their troop size was less than 50. Two new troops were formed in this study as a result of fission. Similar cases of fission have been observed among *M. fuscata* (Furuya 1969, Maruhashi and Takasaki 1996), *M. mulatta* (Rawlins and Kessler 1986), *M. sylvanus* (Menard and Vallet 1996), *M. sinica* (Dittus 1988), *M. silenus* (Kumar 1995), and *M. cyclopis* (Wu and Lin 1992). However, troop sizes before fission in *M. cyclopis* were much smaller than those reported for *M. fuscata* (100-650, Furuya 1969). We observed relatively low-ranking females splitting from main troops to form new troops. Furthermore, low-ranking adult females were seen joining one of the newly formed troops even several months after the establishment of the troop. This suggests that intra-troop competition among females for resources or position might have been the proximate cause of troop fission (Wrangham 1980). In addition, sexual advantage in attaining 2nd rank may have been the incentive for a male to form the new troop, Ia. The costs and benefits of troop fission may vary between individuals, and the phenomenon needs future quantitative analysis.

Although troop sizes of *M. cyclopis* at Mt. Longevity ranged widely from 9 to 86, the average troop size did not change much whether calculated either from the original 7 troops or from 13 troops in Aug. 1997. In both cases, the maximum average troop size was around 47 individuals. Although the average troop size of these 7 troops increased from 24.4 (1994) to 42.9 (1997), the average annual growth rates actually decreased from 29.0% (1995) to 18.7% (1997). An annual troop size increase of 25.2% was previously reported for this species at Kenting (Wu and Lin 1992), which is close to our findings at Mt. Longevity. The annual growth rates of small-sized but socially stable troops, such as troops D and E in our study, were higher than those of large-sized troops. The rate of growth of a troop is a decreasing function of the number of adult females in the troop. This indicates that annual grow rates of large-sized troops decrease possibly through lower immigration, higher emigration (including fission), or higher mortality of juveniles and/or infants. The 2 troops at Kenting reported by Wu and Lin (1992) were relatively small with 9 to 16 individuals, which are closer to the smallest troop size recorded during this study. Unfortunately, the high growth rate shown at Kenting was not sustained; these 2 troops disappeared from their home ranges after incidents of illegal hunting.

Hunting pressure and intra-troop competition appears to play major roles in limiting troop size and population size increases in *M. cyclopis* at Mt. Longevity. The threat of illegal hunting still continues despite the fact that this species has enjoyed legal protected status for over a decade. About 5% of our study individuals managed to escape from hunters' traps with severe wounds or broken limbs (unpubl. data).

The effects of food provisioning on birth rate, growth rate, and troop size in our study are not significant. Although the Japanese macaque birth rate was high in provisioned troops (0.54-0.59) compared to that of wild troops (0.27-0.35, Sugiyama and Ohsawa 1982, Koyama et al. 1992, Takahata et al. 1998b), we found that the birth rate was constant across all troops regardless of human provisioning and interaction. About 50% of troops (8 troops) receive food from people on an irregular basis (usually on weekends and holidays), but it is difficult to access the exact amount of food provided by tourists. Other troops still remain wild with minimal contact with tourists. Troop I, the largest group with 72 individuals was wild and was not habituated when we first made contact in 1995. Even after fission in 1996, troop I remains the largest known troop with minimal contact with people.

The birth rate (0.67 infants per adult female per year) and overall annual growth rate (24.4%) in our study were actually less than those of non-provisioned troops reported previously in a similar ecoregion (0.8 and 25.2%, prospectively, Wu and Lin 1992). Masui et al. (1986) indicated that the ratio of infants to adult females (0.77) in a group of Formosan macaques was slightly higher than that of wild Japanese macaques (Takasaki and Masui 1984). Therefore, the birth rate of Formosan macaques is more similar to that of the rhesus macaque (0.82, Wolfe 1986) than the wild or provisioned Japanese macaque (0.27-0.59, Sugiyama and Ohsawa 1982, Wolfe 1986, Takahata et al. 1998b).

Macaca mulatta is considered the possible ancestor for the island species such as *M. cyclopis* and *M. fuscata* (Hoelzer and Melnick 1996). We found striking similarities in the breeding patterns of these species. Seasonality in breeding in our study is consistent with a previous field report (Wu and Lin 1992) and captive study (Petto et al. 1995) for *M. cyclopis*, as well as for *M. mulatta* (Lindburg 1987) and *M. fuscata* (Kawai et al. 1967, Nigi 1976). Moreover, a laboratory study on *M. cyclopis* reported that when male-female pairs were kept isolated (not in a social troop), they were able to breed throughout the year (Peng et al. 1973a,b). But when several individual females were kept in a social group, they showed a distinct seasonal breeding pattern that was similar to the wild situation (Petto et al. 1995). This suggests that social factors may play a crucial role in the breeding seasonality of *M. cyclopis*, but this needs to be confirmed by further physiological and behavioral studies. Our study indicates that synchronization of birth is more restricted to a narrow range as 97% of births occurred between Apr. and June, whereas Wu and Lin (1992) reported that 75% occurred in this period of time. Although the seasonality of birth reached a peak in mid-Apr. to mid-May for *M. cyclopis*, mounting and mating were observed throughout the mating season. The ages of females who delivered their first infants at 4 and 5 yr old coincided with previous reports for this species, both in captivity (Peng et al. 1973a,b) and in the wild (Wu and Lin 1992). This was similar to results for *M. mulatta* (Rawlins and Kessler 1986, Wolfe 1986), but 1-2 yr earlier than for wild *M. fuscata* (Takahata et al. 1998b).

We found that the annual average overall sex ratio was roughly balanced when all troops were combined, but the adult sex ratio within social troops was frequently not balanced. This was mainly due to male-male competition resulting in the eviction of other adult males entering some social troops. All troops in our study had a multi-male troop structure with 2 exceptions in which new troops were formed as a result of fission, and they had either a single adult male (troop Ia) or no adult male (troop Aa) for a short period of time. However, these troops were not socially stable and became vulnerable to male invasions. This was indicated by the shorter tenure length of alpha males in newly formed troops than those of troops with longer histories (> 2 yr). It is also interesting to note that the adult sex ratio of main troop I was similar to that of the branch troop Ia after a year. On average, no sexual advantage for either males or females accrued to 1 particular group.

Solitary adult males were often seen around social troops prior to immigration into social troops. But they often engaged in aggressive interactions during the mating season (Sept. to Feb.) with troop alpha males and received severe injuries. Similarly, wounding and death of males during troop takeovers have been reported among Tibetan macaques (Zhao 1996). Moreover, subadult males and old adult males were seen to be peripheralized by the dominant alpha male, and the peripheralized low-ranking males often formed coalitions within a social troop, similar to that observed in *M. mulatta* (Southwick et al. 1965), *M. radiata* (Sugiyama 1971), and *M. fuscata* (Imanishi 1957), respectively. Age at natal dispersal was usually at about 5 yr, which is similar to that of *M. fuscata* (Sprague et. al. 1998).

Although a previous study found a range of alpha male tenure length of 5-28$^+$ mo for 2 social troops (Wu and Lin 1992), we have recorded a wide range that varied from 1 wk to 6 yr with an average of 16.8 mo. Most alpha male changes occurred during mating seasons, an indication of severe competition among dominant males (the troop alpha male versus intruders). Thus troop alpha male takeovers in Formosan macaques are influenced by seasonal breeding in order to access sexually receptive females. Similarly, alpha male changes and the appearance of extra-troop males were reported to be higher during mating seasons in species such as *M. fuscata* (Fukuda 1982, Sprague 1992), *M. mulatta* (Neville 1968, Drickamer and Vessy 1973), and *M. sylvanus* (Mehlman 1986). On the other hand, female Formosan macaques remained in their natal troops in most cases with a few exceptions, and thus *M. cyclopis* is considered to be female-bonded which is similar to other species in the genus *Macaca*.

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壽山之臺灣獼猴 (*Macaca cyclopis*) 社群大小與結構

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獼猴屬 (*Macaca*) 主要分布於亞洲東部與南部及非洲的西北部。世界上獼猴屬現存的 19 種物種中，臺灣獼猴 (*M. cyclopis*) 最不為人知。壽山自由活動之臺灣獼猴社群動態和社會行為的長期野外研究，始於 1993 年 7 月。我們經由個體辨識，來確認猴群成員組成變化以及行為。從 1994 年 12 月至 1997 年 12 月，每月至少二次，以有系統的方式，來調查社群成員的數目變動。在相關的社群中，每週至少二次使用焦點取樣及隨機取樣的方式，來記錄其社會行為，包括雄猴首領替代及分群的過程。依壽山表面面積計算，壽山臺灣獼猴的密度最高可達每平方公里 26 隻。平均社群大小在 1995 年 1 月為 26.1 ± 9.7 隻 (n = 7)，平均社群大小在 1997 年 8 月最高，可達 47.0 ± 21.2 隻(n = 13)。研究期間曾觀察到二次分群。最小的社群為剛分出之小旁支社群 Ia 與 Aa ，僅有 9 名個體；最大的社群為社群 I ，曾達 86 名個體。每年嬰猴出生的日期都很集中，主要從 4 月到 6 月(97 %)，且在 4 月中至 5 月中到達高峰。社群平均性比接近一對一，但成年雄猴數目僅約為成年雌猴數目之半。平均首領任期長度為 16.8 ± 18.9 月(n = 34)，任期長度從一週到最長六年。平均首領任期長度在新形成的社群中，顯著比其他的社群平均首領任期長度短。大約 88% 首領任期的替換發生於每年 10 月至翌年 2 月間，即從交配季節的高峰至季末。

關鍵詞：生殖，社群組成，性比，雄性任期，分群。

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