

The *Macaca fascicularis* at Padangtegal, Bali, Indonesia.

Authors

A. Fuentes¹, A.L.T. Rompis², I.G.A. Arta Putra², N. L. Watiniasih², I. N. Suartha², I.G. Soma², I.N. Wandia², I.D.K. Harya Putra², and R. Stephenson³

Abstract

Baseline data from studies on semi-free ranging, food enhanced populations are important to our investigations of primate behavior, especially as sympatry between human and non-human populations increases. Currently there are few multi-year data sets for such primate groups. Here we report preliminary results from a five-year study on the semi-free ranging, food enhanced population of long-tailed macaques (*Macaca fascicularis*) at Padangtegal, Ubud, Bali, Indonesia. At the site there are three groups totaling 122-204 individuals between 1998 and 2002. We compiled 2378 hours of behavioral data and conducted population assessments for 46 months of demographic data.

Activity patterns of *Macaca fascicularis* groups in this population are generally similar to other *M. fascicularis* populations. General activity patterns are similar for adult females and males in this population, with females engaging in more affiliation and holding of infants, and males resting solitarily more than females. Consumption of provisioned foodstuffs made up the majority of feeding observations. Variable male tenure and male migration were observed. Infant deaths resulting from female infant taking were observed. The demographic history of this population suggests that population growth may be curbed by epidemics.

Keywords: *Macaca fascicularis*, demography, activity patterns, semi-free ranging

Introduction

Macaca fascicularis is one of the most broadly distributed primate species. They range from Bangladesh, Thailand and Vietnam in the North (18° latitude North) to the Southeastern reaches of the Indonesian Archipelago (12° latitude South) between 95° and 125° longitude, and are found across habitats, ecozones and island groups. They have been introduced by humans to Islands in the Indian Ocean and in Micronesia. Given the recent primatological overviews demonstrating behavioral flexibility, range diversity and adaptation (Dolhinow and Fuentes

¹ Dept of Anthropology, University of Notre Dame

² Pusat Kajian Primata, Universitas Udayana

³ Dept. of Anthropology, University of Guam

1999, Strier 2002) *Macaca fascicularis* may be an excellent species to examine adaptation to a particularly wide array of habitats and environmental variables especially where human impact is a core component of the landscape.

Within the long-tailed macaque (*Macaca fascicularis*) there are between 10 and 21 recognized subspecies, dramatic variation in facial hair patterns, and body size varies from 2.5-7.0 Kg for females and 4.7-14k for males (Fooden 1995, Napier and Napier 1967, Rowe 1996).

Despite their well documented occurrence and utilization of primary tropical rainforest (up to 2000m elevation), the long-tailed macaques appear to prefer riverine habitats, coastal forests, swamp or mixed forests and secondary forest habitats (Crockett and Wilson 1980). This ability to thrive in a variety of environmental types probably played a role in this group's evolutionary success throughout Southeast Asia. Especially during the last 5-8,000 years of human (agricultural) induced environmental change.

To date long-tailed macaques have been the focus of numerous studies concerning free ranging behavior, social organization and ecology (e.g. Aldrich-Blake 1980, Angst 1975, Crockett and Wilson 1980, de Ruiter et al. 1994, Koyama et.al. 1981, van Noordwijk 1985, Wheatley 1980), post-conflict interactions in captive groups (Aureli et.al. 1989, Aureli and van Schaik 1991, Cords 1988, 1992, Cords and Aureli 1993, Das et.al. 1997), post-conflict behavior in a free ranging group (Aureli 1992), a few studies that focus on aggression amongst females in non-captive situations (eg. Wheatley 1991), object manipulation (Fuentes 1992, Wheatley 1988), and human-nonhuman primate interactions (Wheatley, Harya Putra and Gondar 1996, Wheatley and Harya Putra 1994).

The island of Bali is approximately 5632 km² and has a rich history of volcanic activity and thus some of the most fertile soils in the world. There are approximately 247 rivers all cascading down slope from the central volcanic range. During both the wet and dry seasons moisture accumulates above the volcanoes in the center of the islands providing a nearly year-round supply for the rivers that course rapidly down towards the sea, creating deep ravines and ready access to water for the south central portion of the island. Bali's landscape can be currently described as a highly human modified environment, where nearly all land in south central Bali is human villages, rice agriculture and rivers with deep ravines. The fertile soils combined with nearly one thousand years of highly successful wet rice agriculture has facilitated some of the highest human densities in the world for a primarily rural population (avg. 482/Km², range 259-1104/Km²) (Mantra 1995). Currently, three primate species are indigenous to the island: *Macaca fascicularis*, *Trachypithecus auratus* and *Homo sapiens*.

Although numerous studies of have been conducted on *Macaca fascicularis* the large population of these macaques on the island of Bali (*M.f. submordax* or *M.f. mordax*, Fooden 1995) remains poorly documented. Previous to this study the majority of information on the Balinese macaques comes from published studies at the Padangtegal (Ubud) monkey forest by Bruce Wheatley and colleagues (Wheatley 1999, 1991, 1988, Wheatley, Harya Putra and Gondar 1996, Wheatley and Harya Putra 1994). Aside from these only a few researchers conducted behavioral or physiological studies at monkey forests in Bali (Angst 1975, Dolhinow, Fuentes and MacKinnon 1995, Kawamoto, Ischak, and Supriatna 1984, Koyama, Asnana, and Ansir 1981, Fuentes 1992, Fuentes et al. 2000). Additionally, since the mid-1990's Balinese and other Indonesian

researchers have undertaken various projects related to the macaques in Bali, most of which are currently unpublished (Suaryana et al. 2001).

Bali provides a valuable opportunity to examine an island population of nonhuman primates that has co-existed with large human populations and substantial habitat alteration for at least 1000 years. Here we report on the findings of a five year study of the three groups of *Macaca fascicularis* at Padangtegal, Bali, Indonesia.

Methods

The study site of Padangtegal Wanara Wana is located in the villages of Padangtegal and Ubud in the Gianyar regency of South-Central Bali, Indonesia (Map 1). The site consists of approximately 7 ha of mixed forest and a temple complex (three temples and various shrines/statues), and is bordered by two towns, rice fields, a road, and two rivers. One of the rivers marks the eastern edge of the forest and forms a ravine that extends southward out of the forest and is fringed by riparian growth for at least 2 kilometers away from the site. One hundred and sixteen species of tree/shrub/liana are found at the site with the top three genera being; *Artocarpus*, *Cocos* and *Ficus* (Kriswiyanti and Watiniasih 1999). The forest is described as secondary forest with a broken canopy and has a maximum height of 35m. The ground level consists of tree litter, dirt, and stone paths. Humans regularly use the site. Local Balinese use the temples at the site for ceremonies and use the paths through the forest to move between village areas. Between 40,000-110,000 domestic and international tourists visited the site annually between 1998-2002.

From 1998-2002 we collected behavioral data on the Padangtegal population for between six to ten weeks per year during the months of June-August (Dry season for this part of Bali). Data on area use, activity budgets, and specific social behaviors were collected 1999-2002, with the 1998 field season being devoted to initial behavioral observations, range use patterns and establishment of the methodology for the subsequent years. Nine to 23 observers annually collected group composition, diet, ranging, and general activity data across the 1999-2002 study periods resulting in 1,568 hours of behavioral activity data. Dominance ranks for adult males and females were calculated annually from approach-retreat interactions (displacements), the results of aggressive contests and priority of access to resources (provisioned food and favored resting sites). Over 500 hours of additional data from affiliated projects related to diet, copulatory behavior, object rubbing, temple licking, intestinal parasites, and wounding patterns were also collected and their results are reported elsewhere (Arta Putra et al. 2001, Emel, Fuentes and Suaryana 2001, Fraver et al. 2001, Kriswiyanti and Watiniasih 1999, Louden, Fuentes, and Welch 2002, Suartha, Watiniasih, and Fuentes 2002, Suaryana, Arta Putra, and Fuentes 2000, Truce and Fuentes 2002, Velucci, Fuentes and Suaryana 2000, Welch, Louden, and Fuentes 2001). In addition to the behavioral data, Universities Udayana Pusta Kajian Primata staff and members of the Padangtegal Wanara Wana management staff collected 46 months of general demographic data between 1998 and 2002.

Observers were trained in age/sex class recognition of the macaques and utilized a modified behavioral checklist. Individually known adult macaques were assigned sex and number indicators (M1 for male number 1, for example) which remained consistent across the data collection periods. Females were termed Adult when they reached approximately 3.5 years old

(85-90% adult body size). Males were initially added to the identified individuals list at age 5 (~80% adult body size) but termed sub-adult until approximately age 6-7 (full canine eruption and testicular size). General behaviors were recorded on customized record sheets during twenty minute focal follows, at one minute intervals, using the naked eye and binoculars to facilitate observation (a scan sample method with a modified behavior repertoire was used, Altmann 1974, Dolhinow 1978). Only identified individuals who had more than three hours of follows per six-week observation period were included in behavioral data analysis. All data collectors were tested as exceeding 90% inter-observer reliability in data recording with project PIs before initiating sample collection. Video and still image records were made of adult animals and specific behaviors at the Padangtegal site annually between 1999 and 2002.

Results

Demographic patterns:

Table 1 shows the population changes from 1986, 1990-1992 (from Wheatley 1999) and from 1998-2002 (this study). The data since 1998 include changes in group size. Although Wheatley (1999) provides group sizes they are not included in table 1 due to the unclear relationship between Wheatley's groups 1, 2 and 3 and the current groups 1, 2 and 3. Because of methodological inconsistencies in reporting of deaths between August 1998 and June 1999 data on deaths are not given for either 1998 or 1999.

The population at Padangtegal has undergone a 40% increase in size between 1998 and 2002, with 80% of this growth occurring since 2000 (Table 1). This increase in population size has not been equally distributed across the three groups in the population. The smallest group, group

1, increased by 35.5% between 1998 and 2002, and underwent a transition from a one-adult male group to a multi-adult male group (1 adult to three adult males). Group 2, the largest group, has increased by 65%, and group three (the largest group in 1998) has only increased by 10.5%.

Table 2 shows the age and sex class distribution for the total population for 1986, 1990-1992 and 1998-2002. During the 1990-1992 period the number of adult males increased by 27%, adult females by 31%, and immatures by 25%. During the 1998-2002 period adult males increased by 34%, adult females by 46%, and immatures by 37%.

Table 2 includes the newborn, “black infants,” and nursing “brown” infants for the period 1986, 1990-1992 as these are how the data were reported by Wheatley (1999). The table 2 entries for this study (1998-2002) contain only those infants born during the May-August period as we have observed that some individuals nurse for more than one year and pelage changes can vary somewhat between individuals. Since 1998 we have observed two birth/mating peaks annually in the population, with a small number of births occurring outside of these peaks. We observed 16 neonates born during May-August of 2000, 19 in 2001, and 23 during the same period in 2002 (Table 2). Females who have recently given birth are observed copulating (within less than a month of parturition) suggesting a post-partum false estrus period. Interbirth intervals ranged between 16-36 months. A majority of the adult females in the population gave birth to infants during the 1998-2002 period, with some giving birth to as many as three offspring. One female successfully gave birth to a set of twins (who have survived past the age of 2 years). Wheatley et al. (1996) report an extremely high infant mortality rate (~90%) in 1990 at this site, however our observations suggest that the current rate averages less than 30% for the period 1998-2002.

Between 1998 and 2000 at least 10 young males disappeared from the site. We assume that they attempted emigration. At least one adult male is known to have emigrated from the site during this time as well. Between 2000 and 2002 only three subadult males were confirmed to have left the population. We have observed three immigration attempts by males from outside of population, two of which were successful. We have also observed three inter-group transfers by males and 1 by a female at the site.

Range use:

Macaques at the Padangtegal site use approximately 24.3 ha of area (Map 2), including the temple and temple forest proper (Map 3). Each group uses all areas within the ~7 ha temple and temple forest (Map 3) (100% overlap in areas used over the five-year observation period).

However, groups are rarely in the same area at the same time. Groups 2 and 3 consistently displace group 1 (the smallest group) within the temple forest area. Groups 2 and 3 had variable dominance interactions across the five year study, with group 2 displacing group 3 in over 70% of observed inter-group displacements since 2000. Over 90% of the inter-group displacements occurred at the central area (Garuda area on Map 3) of the temple forest (main tourist location) or the plaza area on the west side of the main temple (secondary tourist area). Temple staff provided provisions for the macaques at both locations. Other inter-group displacements took place in the forest area just south of the main temple and in the graveyard in the eastern portion of the temple forest.

Outside of the temple forest area Group 1 uses the roadside forest and the riparian growth up to 200m away from the eastern forest edge (main road). Group 2 uses the southern rice fields and

the Northwestern rice fields and riparian forest up to 300m away from the temple forest proper. Group 3 uses areas Southwestern, west and northwest of the forest proper. Although area usage varied across years and seasons, group 1 has a range averaging approximately 7.2 ha, group 2 has a range of approximately 11 ha, and group 3 ranges across 17 ha.

Activity patterns:

Across the four study periods where standard activity data are available (1999-2002) adult male and adult female macaques exhibited similar behavioral patterns. Figure 1 shows the per-scan frequency of thirteen activity categories as a mean values across 1999-2002 for the combined categories of adult males and adult females (individual data will be reported elsewhere).

Females huddle (including sit in contact) with other individuals more frequently ($\chi^2=12.4$, $df=1$, $p<.05$) and have infants on ventrum more frequently ($\chi^2=25.26$, $df=1$, $p<.05$) than do males.

While males rest nearly twice as frequently as females ($\chi^2=5.88$, $df=1$, $p<.05$). Interestingly, both males and females in this population engage in object manipulation at the same frequency as they exhibit aggression. Also, for both sexes the frequencies of play behavior and copulations are nearly identical. When compared with other *Macaca fascicularis* sites in Southeast Asia at the general activity budgets of the Padangtegal macaques fit well within the species normative range (Table 3).

Dietary Patterns:

We examined a record of 11,761 feeding instances (1999-2001) during the months of June-August for feeding patterns. During these months the macaques at this site receive nearly 70% of their diet from provisioning (Table 4). Monitoring during other times of the year indicate that

the percentage of provisioned food drops to ~50% during February-May and October-November as the overall human traffic at the site is dramatically reduced. The temple management committee staff provisions the three macaque groups with sweet potatoes, papaya leaves and various fruits and vegetables. Tourists visiting the site primarily provide bananas and peanuts. It is clear that ongoing study is needed to effectively document the annual dietary variation in these macaques. It is also clear from monitoring the appearance of the individuals that they are quite well-fed and healthy.

The “other” category in table 4 consists of temple offerings, chicken eggs provided by temple staff, a few types of pre-packaged food provided by tourists, and vertebrate animals (primarily infant squirrels, infant rats and adult frogs). All the macaques in this population have sporadic access to rice, a variety of flowers, cakes, chicken, and a variety of fruits as these are frequent contents of offerings placed at the temples by the local Balinese. However, amounts of offerings vary dramatically across ceremony and time and access to offerings is generally mediated by dominance rank of the macaques. Once a year the temple staff provides numerous eggs to the macaques as part of a festival honoring the monkeys. Occasionally, throughout the year temple staff will provide an egg or two to adult males as well. Although only 17 instances of vertebrate consumption were observed, it was predominantly immature individuals (between 2-4 years of age) who consumed vertebrate prey (15 of 17 instances). Therefore, distribution of the nutritional content of offerings and other items in the “other” category is not equal across age/sex classes and individuals.

Dominance:

As with *Macaca fascicularis* across Southeast Asia, Balinese macaque males and females each have separate hierarchies. Top ranked males' tenure ranged from 8 to >40 months, and males have been observed changing groups within the monkey forest populations in which they live (Loudon, Fuentes, Welch 2002, and in review). Rank and copulatory success are loosely correlated in group 2 but not in group 3 at the Padangtegal site (Welch, Loudon and Fuentes 2001). Preliminary data analyses suggest that adult males may practice both aggression and affiliative strategies to gain access to females (Loudon, Fuentes and Welch 2002, Welch, Loudon and Fuentes 2001). Although high intensity fighting occurs amongst adults, often with substantial wounding, the conflicts rarely result in death (Suartha, Watiniasih, and Fuentes 2002). During the period 1998-2002 only two adult males and two adult females died from wounds inflicted by other macaques or from injuries resulting from falls during aggressive arboreal chases. However, it is not clear how many of the immature deaths resulted from wounds inflicted by other macaques.

Infanticide:

No infanticide by adult males were observed at Padangtegal between 1998-2002. None were reported by Wheatley (1999) for the 1986, 1990-1992 period either. Two cases of female infanticide were observed. Females were frequently observed taking infants and holding them away from their mother for between 3 minutes and four days. In the majority of these cases the female taking the infant held it, groomed it, allowed other females to touch and inspect it, and on occasion allowed the infant to suckle. In a few cases females were observed to act aggressively towards infants they had taken. In one case (during July 2000) an infant received a lethal head wound (bite) from an adult female while the infant was being held by a different adult female

that was not its mother. The infant was subsequently returned to its mother and died within 24 hours. The other observed infant death resulted from a female refusing to allow her newborn to nurse. The infant died three days after birth. We also suspect that at least two additional infant deaths were related to females taking infants from their mothers, but cannot rule out infant illness or congenital disorders. We did not observe males interceding once an infant taking female was in possession of an infant, although interventions that successfully protected an infant from being taken may not have been recognized as such.

Object manipulation:

Object manipulation is common in the population at Padangtegal and has been observed at other macaque sites in Bali (Alas Kedaton, Uluwatu, Pulaki, Sangeh, and Bedugal) (Central Bali) where the macaques also have frequent interaction with humans (Fuentes, Southern and Suaryana in press). Object manipulation observed includes stone play, stone use in food acquisition, use of leaves to groom other individuals, multi-object rubbing, and food washing.

All age/sex classes were observed to manipulate objects, with Sub-adult Males and Immatures being the only class to manipulate objects more than expected. Nonfood items were manipulated significantly more often than food items. There was no significant difference between manipulated food items being eaten or not eaten. Approximately 82% of all items manipulated were not eaten (Truce and Fuentes 2002a).

There were significant differences in the frequency of manipulation styles between the age/sex classes and between food and non-food items. Non-food items were rubbed on the ground and

pounded more often than food items, while food items were rubbed between the actor's hands more often than non-food items (Truce and Fuentes 2002).

Discussion

The results from this five-year project can be compared to data reported by Wheatley (1999) from his research on this population between 1986 and 1992 to provide an overview of the longest study of semi-free ranging *Macaca fascicularis* groups at one site.

Demographics

Ranging patterns reported by Wheatley (1999) for the three groups suggest that his groups 1-3 maybe the same as groups 1-3 in this study, however given the lack of monitoring during 1993-1997 we cannot be sure of this. If these are the same groups as Wheatley's then between 1992 and 1998 group one decreased in size by 41%, group 2 decreased by 4.5%, and group 3 increased in size by 173% (Wheatley 1999, this study). This may suggest that groups 1 and 2 were impacted most severely by the streptococcus outbreak in 1994 which caused high mortality in many macaques groups in central Bali (see table 1). However, local temple officials and villagers have stated that group 3 suffered significant losses as well. The demographic patterns between 1992 and 1998 at this site remain unclear.

Wheatley (1999) also reports a relatively cohesive all male group from 1990-1992 at Padangtegal. We observed frequent play groups composed of juvenile and sub-adult males from either group 2 or group 3. Occasionally young males from both groups formed a play group in the space between groups. However, these play groups were temporary lasting from a few

minutes to multiple hours. There was no evidence of any permanent or temporally cohesive male groups. It is possible that the increase in overall population has created substantial peer clusters within each group and led to the reduction in inter-group play by immatures.

In 1999 a new management program was initiated which included removal of plastic and other wastes from the forest, anti-erosion control, reclamation and re-forestation of fields bordering the forest, and occasional medical care for injured or sick individual macaques. It is clear that this change in management style combined with the increased diversity, amount, and regularity of provisioning and increased tourist presence (and feeding) has resulted in the population increasing in size at dramatic rate.

The number of new infants in the May-August birth peak (table 2) is increasing annually. These births make up approximately half the annual births. If this rate of increase continues we predict expansion of the ranges of the groups and more conflict within the population and between the macaques and humans in the surrounding towns.

As the diet of this population is heavily provisioned, the death rate is fairly low and infant mortality appears low as well, population growth appears to be primarily curbed by epidemics (at least in the period between 1986 and 2002). This suggests that pathogen environment may be significant selective force on these macaques. A significant role for epidemics/disease has also been proposed for the semi-free ranging population of macaques (*Macaca sylvanus*) in Gibraltar (Fa and Lind 1996) and a large population of Chimpanzees in Tanzania (Nishida et al. 2003).

Immigration/emigration

Koyama et al. (1981) report the immigration of two adult males into this population. Wheatley did not observe any immigration and we observed three attempts of which two were successful. We also noted 13 emigrations by sub adult males and one by an adult male. This suggests that there is potential gene flow between populations of macaques in south-central Bali. Elsewhere we propose a model for the appearance and maintenance of gene flow across many of the macaque groups despite high human density on the island of Bali (Fuentes, Southern and Suaryana, in press).

Range use and intergroup dominance

Wheatley reports his group 1 dominant to group 2 and group 2 dominant to group 3 in 1986-1990, however by 1992 group 2 regularly displaced both groups 1 and 3 from preferred sites (Wheatley 1999). This reflects the current situation (1999-2002) with group 2 frequently displacing the other groups. In 1998 groups 2 and 3 displaced each other equally. This further suggests the possibility that the Wheatley's and our groups may be the same.

The pattern of inter-group dominance suggests that group size is a key factor in achieving access to desired areas (see table 2). As reported by Wheatley (1999) we also observed single males, or a few young males, from one group (usually group 2) displacing entire other groups. However, in inter-group conflicts where a number of individuals were involved adult females and adult males (usually high ranking) appeared at the forefront of the displacement activities.

The locus of inter-group dominance activities remains similar across the two studies with both Wheatley (1999) and this study reporting the majority of inter-group displacements occurring in areas where the majority of provisioning occurred.

Activity patterns and feeding/provisioning

General activity patterns in the Padangtegal population are generally similar to other *M. fascicularis* groups in Asia (both free and semi-free ranging). However, using such broad categories as “feed,” “range,” and “other” creates only a very generalized picture and thus these similarities between other reported studies and the macaques at Padangtegal may overlook substantial differences within the categories of feed and travel (and of course, other). At Padangtegal male and female activity patterns are similar for the behaviors recorded except that females engage in friendly affiliative contact with other individuals and hold infants more often than do males. Males, alternatively, rest significantly more frequently than females. Given the basic distribution of individuals in a macaque group and the relative adult sex ratios it is not surprising that females are more frequently in contact with other individuals than are males. Figure 1 shows that males were involved in grooming more than females and females fed more frequently than males, but the differences are not significant.

Interactions with humans are a daily part of the behavioral repertoire and human-made structures constitute a substantial segment of the environment of these macaques. This is not uncommon for populations of *M. fascicularis* or *M. mullata* (Agaramirasee 1989, Wolfe 2002) and therefore documenting the basic activities of such populations is important for understanding the range of macaque potential behavioral patterns.

Wheatley (1999) reports that between 39 and 81% of this population's diet came from provisioning during 1990-1992. As provisioning was less consistent and less diverse during that period, it is probable that the mean percentage of provisioned food in the diet of all groups in this population is above 50%, and probably closer to the 70% reported here. There are a number of potential food items growing in the forest (Kriswiyanti and Watiniasih 1999) and the macaques appear to exploit invertebrates more consistently (7.5% of diet) between 1998-2002 than in the previous study (1-9% for 1986,1990-1992) (Wheatley 1999). Given the high rate of provisioning, the current relatively diverse composition of the provisioned food and the lack of mortality tied to obesity or other diet based-health issues we propose that this population is not under nutritional stress. In fact, the abundance of foodstuffs and the relative protection offered by the temple forest most likely are combining to produce the rapid population growth observed between 1998 and 2002.

Infanticide:

Although male infanticide has been inferred in two groups of long-tailed macaques (van Schaik 2000) no infanticide by males has been observed or inferred at Padangtegal either by Wheatley (1999) or during this study. However, infant deaths did result from female infant taking. This has been reported for two Balinese macaque populations (Padangtegal and Sangeh, Wheatley 1991, 1999, this study). Wheatley (1991, 1999) and Wheatley, Gondar and Harya Putra (1996), report infant injuries resulting in deaths occurred during inter-group aggression at the Padangtegal site between 1986 and 1992. While we have observed frequent inter-group aggression we have not recorded a consistent association between these conflicts and infant

injury at Padangtegal between 1998-2002. Wheatley (1999) also reports four observations of infant taking resulting in infant death. He refers to this behavior as “kidnapping.” Wheatley (1999) suggests that this is an example of reproductive competition between females, with higher ranking females taking and killing the infants of competing lower ranking females. However, Wheatley clearly stresses that the infant deaths in these cases probably did not result from “intent to kill” but rather from higher ranking females’ attempts to harass lower ranking females (Wheatley 1999:93). While infants are frequently held by females other than their mothers, we suggest it still remains unclear why in a few instances this results in the death of an infant. The two cases we observed are substantially different from each other precluding any single explanatory hypothesis. A possible by-product of infant taking is the potential for successful adoption. Between 1998 and 2002 we observed the successful adoption of 2 infants younger than 6 months whose mothers died.

Object manipulation:

While early reports suggested that the majority of manipulation behavior may be a form of food acquisition (Wheatley 1988, 1999), recent research suggests that food preparation may account for only a relatively small fraction of the object manipulation observed at monkey forest sites (Fuentes 1992, Truce and Fuentes 2002). In fact, preliminary research suggests that variation in, and overall rates of, object manipulation may be tied to the levels of macaque-human interaction, provisioning, and specific structural factors associated with monkey forests and their proximity to human villages (Fuentes 1992, Truce and Fuentes 2002).

Relevance of studying a human impacted semi-free ranging population

As the overall range of many free-ranging primates continues to diminish, understanding the patterns of interaction between nonhuman primates and sympatric humans will facilitate future management issues, disease research, and behavioral investigations (Chapman and Peres 2001, Fuentes and Wolfe 2002, Kautz et al. 2003). Studying the macaques at Padangtegal can contribute to the overall attempt to understand the *Macaca mulatta-fascicularis* group's relative success in South and Southeast Asia where they exhibit a multi-millennia pattern of overlap with human settlements and use areas.

Specifically documenting the pattern of demographic changes across time in the Padangtegal population might allow us to better understand how to facilitate management procedures that will maintain a healthy macaque population and minimize the potential negative impacts (be they pathogen transmission, crop raiding, or other elements) to the human populations. Also, by examining behavioral patterns such as object manipulation and infant taking we might be able to gain insight into the range of potential behavioral expression when macaques are relieved of specific selective stressors such as food and predation stress.

Conclusions:

Given the results of research at the Padangtegal site few general conclusions can be made:

- 1) Activity patterns of *Macaca fascicularis* groups in this population are generally similar to other *M. fascicularis* populations.
- 2) General activity patterns are similar for adult females and males in this population, with females engaging in more affiliation and holding of infants, and males resting more than females.

- 3) The diet of these macaques is heavily provisioned and thus this population may be free from nutrition stress and therefore exhibit behaviors that otherwise may be suppressed by increased foraging requirements (such as increased object manipulation).
- 5) The demographic history suggests that population growth is may be curbed by epidemics and therefore pathogen environment may be a significant selective force on semi-free ranging populations of macaques (or at least on this population). .
- 6) Interactions with humans and existence within a human modified habitat are integral aspects of the behavioral repertoire of these macaques and a “natural” component of their environment worthy of investigation and documentation.

Acknowledgments

In memoriam of Dr. Komang Gde Suaryana, a pioneer of Balinese Primatology.

This project has been conducted under research permission from Lembaga Ilmu Pengatahuan Indonesia (LIPI), the Provincial Government of Bali and the Regency of Gianyar, and the Padangtegal Wanara Wana Management Committee. We wish to extend special thanks to the Rector of Universitas Udayana, the Governor of Bali, the Directorate of Social and Political Affairs, Pak Selamat and the Padangtegal Wanara Wana Management Committee and the Wanara Wana staff. We also thank Central Washington University, Dr. Hiro Kurashina, the University of Guam, Universitas Udayana Pusat Kajian Primata, and the student team members and faculty of the Balinese Macaque Project field school 1998-2002. Partial support for this

study came from the Central Washington University Office of International Studies and Programs and Office of Graduate Studies.

Bibliography:

Angst, W. (1975) Basic data and concepts on the social organization of *Macaca fascicularis* in Rosenblum, L.A. (ed) *Primate Behavior: developments in field and laboratory research* Academic Press pp.325-388

Arta Putra, I.G.A., Fuentes, A., Suaryana, K.G., and Rompis, A.L.T. (2001) Perilaku makan monyet ekor panjang (*Macaca fascicularis*) di Wanara Wana, Padangtegal, Ubud, Bali. in *Konservasi Satwa Primata: Tinjauan ekologi, sosial ekonomi dan medis dalam pengembangan ilmu pengetahuan dan teknologi*. Universitas Gadjah Mada Press, Yogyakarta pp. 132-140

Aureli, F. (1992) Post-conflict behavior among wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* 31:329-337

Aureli, F., van Schaik, C.P. and van Hooff, J.A.R.A.M. (1989) Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *Am. J. Primatol.*, 19:39-51

Chapman, C.A. and Peres, C.A. (2001) Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology*, 10:16-33

Crockett, C.M. and Wilson, W.L. (1980) The ecological separation of *Macaca nemistrina* and *Macaca fascicularis* in Sumatra in Lindburg, D.G. (ed) *The Macaques: studies in ecology, behavior and evolution* Van Nostrand Reinhold pp.148-181

Cords, M. (1988) Resolution of aggressive conflicts by immature long-tailed macaques (*Macaca fascicularis*). *Anim. Behav.* 36:1124-1135

Cords, M. (1992) Post-conflict reunions and reconciliation in long-tailed macaques. *Anim. Behav.* 44:57-61

Cords, M. and Aureli, F. (1993) Patterns of reconciliation among juvenile long-tail macaques. In Pereira, M.E. and Fairbanks, L.A. (eds) *Juvenile Primates: life history, development, and behavior*. Oxford University Press pp.271-284

Das, M., Penke, Z. and van Hooff, J.A.R.A.M. (1997) Affiliation between aggressors and third parties following conflicts in long-tailed macaques (*Macaca fascicularis*). *Int. Jour. Primatol.* 18(2):159-181

Delson, E. (1980) Fossil macaques, phyletic relationships and a scenario of deployment in Lindburg, D.G. (ed) *The Macaques: studies in ecology, behavior and evolution* Van Nostrand Reinhold pp.10-30

de Ruiter JR, van Hooff JARAM, Scheffrahn W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behav* 129:203-224

Dolhinow, P, Fuentes, A. and MacKinnon, K (1995) The four faces of irus: behavioral variability in Balinese *Macaca fascicularis*. *Abstract Am. Jour. Phys. Anth.* Supplement 20:84

G. Emel, A. Fuentes and K.G. Suaryana (2001) Visual monitoring by *Macaca fascicularis* at Padangtegai, Bali, Indonesia. *American Journal of Physical Anthropology Supp.* 32:62

Eudey, A.A. (1980) Pleistocene glacial phenomena and the evolution of Asian macaques in Lindburg, D.G. (ed) *The Macaques: studies in ecology, behavior and evolution* Van Nostrand Reinhold pp.52-83

Fa, J.E. and Lind, R. (1996) Population management and viability of the Gibraltar Barbary Macaques. In J.E. Fa and D.J. Lindburg eds. *Evolution and Ecology of Macaque Societies*. Cambridge Press pp.235-262

Fooden, J. (1995) Systematic review of Southeast Asian long-tailed macaques, *Macaca fascicularis* (Raffles, [1821]). *Fieldiana, Zoology Series No. 81*. Field Museum of Chicago Publication

J.B. Frayer, G. Emel, A. Fuentes, K.G. Suaryana, and I.D.K. Harya Putra (2001)

An ongoing study of the female copulation call in long-tailed macaques (*Macaca fascicularis*) *American Journal of Physical Anthropology* Supp. 32:65

Fuentes, A. (1992) Object rubbing in Balinese macaques (*Macaca fascicularis*).

Laboratory Primate Newsletter 31(2):14-15

Fuentes, A., Southern, M. and Suaryana, K.G.(in review) Monkey forests and human landscapes: is extensive sympatry sustainable for *Homo sapiens* and *Macaca fascicularis* in Bali? in J.

Patterson ed. *Commensalism and Conflict: The primate-human interface* American Society of Primatology Publications

Fuentes, A., Suaryana, K.G., Arta Putra, I.G.A., Harya Putra, I.D.K., and Rompis, A.L.T. (2001) The behavioral ecology and distribution of long-tailed macaques (*Macaca fascicularis*) in Bali, Indonesia. *American Journal of Physical Anthropology* Supplement 31

Fuentes, A., Harya Putra, I.D.K., Suaryana, K.G., Rompis, A., Artha Putra, I.G.A., Wandia, N., Soma, G., and Watiniasih, N.L. (2000) The Balinese Macaque Project: background and stage one field school report *Jurnal Primatologi Indonesia* 3(1):29-34

Fuentes, A. and Wolfe, L.D. (2002) *Primates Face to face: the conservation implications of human-nohuman primate interconnections*. Cambridge University Press, Cambridge.

Gygax, L., Harley, N. and Kummer, H. (1997) A Matrilineal Overthrow with Destructive

Consequences in *Macaca fascicularis* *Primates* 38(2):149-158

Kautz, K.G., Gulibert, L. and Wheatley, B.P. (2003) Connecting local and international, exploring the pressing *Mongkii* issues of Ngeaur, Belau (Anguar, Republic of Palau). Global Processes, Local Impact: Session Proceedings, 10th Annual Pacific Science InterCongress. University of Guam Richard Flores Taitano Micronesian Area Research Center and The Pacific Science Association. Pp: 79-86

Kawamoto, Y., Ischak, T.B.M., and Supriatna, J (1984) Genetic variation within and between troops of the Crab-eating macaque (*Macaca fascicularis*) on Sumatra, Java, Bali, Lombok and Sumbawa, Indonesia. *Primates* 25(2):131-159

Koyama, N., Asnan, A. and Natsir, N. (1981) Socio-ecological study of the crab-eating macaques (*Macaca fascicularis*) in Indonesia. *Kyoto University Overseas Research Report of Studies on Indonesia Macaque*, 1-10

Kriswiyanti, E. and Watiniasih, N.L.

Louden, J.E., Fuentes, A. and Welch, A.R. (2002) Shifting status: four years of adult male hierarchy in *Macaca fascicularis* at Padangtegal, Ubud, Bali, Indonesia. *American Journal of Physical Anthropology*, Supp. 30:103-104

Louden, J.E., Welch, A.R. and Fuentes, A. (in revision) Agonism and affiliation: adult male sexual strategies across one mating period in three groups of long-tailed macaques (*Macaca fascicularis*) *American Journal of Primatology*

Napier, J.R. and Napier, P.H. (1967) *A handbook of Living Primates*. Academic Press, New York

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K.D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J.C., Nakamura, M., Norikoshi¹ K., Sakamaki, T., Turner, L., Uehara, S., and Zamma, K. (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology* 59(3):99-121

Rowe, N. (1996) *A Pictorial Guide to the Living Primates*. Pogonias Press

Sartono, S. (1973) On Pleistocene Migration Routes of Vertebrate Fauna In Southeast Asia. *Geol. Soc. Malaysia Bulletin* 6:273-286.

Suartha, I.N., Watiniasih, N.L., and Fuentes, A. (2002) Kesembuhan luka monyet ekor panjang di obyek wisata Wanarawana Padangtegal. *Jurnal Veteriner* 3(2):50-54

Suaryana, K.G., Fuentes, A., Arta Putra, I.G.A., Harya Putra, I.D.K., and Rompis, A.L.T. (2001) Ekologi dan distribusi monyet ekor panjang (*Macaca fascicularis*) di Bali. in *Konservasi Satwa*

Primata: Tinjauan ekologi, sosial ekonomi dan medis dalam pengembangan ilmu pengetahuan dan teknologi. Universitas Gadjah Mada Press, Yogyakarta pp. 120-131

Suaryana, K.G., Arta Putra, I.G.A., and Fuentes, A. (2000) Parasite of the long-tailed macaque (*Macaca fascicularis*) and its potential risk to human health. The International Seminar on Soil transmitted Helminthiasis, Denpasar, Bali, Indonesia

Truce, W. and Fuentes, A. (2002) Object manipulation in a population of semi-free ranging *Macaca fascicularis* in Bali, Indonesia. *American Journal of Physical Anthropology*, Supp. 34:157

van Noordwijk, M.A. (1985) The Socioecology of sumatran long-tailed macaques (*Macaca fascicularis*) II. The behavior of individual. Proefschrift Drukkerij Elinkwijk- Utrecht

van Noordwijk, M.A. and van Schaik, C. P. (2001) Career moves: transfer and rank challenge decisions by male long-tailed macaques. *Behaviour* 138:359-395

van Schaik, C. P. (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In *Infanticide by males and its implications*. C.P. van Schaik and C. H. Janson eds. Cambridge University Press. Pp.27-60

Vellucci, S.M., Fuentes, A., Suaryana, K.G., and Harya Putra I.D.K. (2000) Sex differences Balinese macaque (*Macaca fascicularis*) temple licking: Requirement of lactation or taste for salt? *American Journal of Physical Anthropology*, Supp. 30:310

Welch, A.E., Loudon, J.E. and Fuentes, A. (2001) Male sexual strategies in a semi-free ranging group of long-tailed macaques (*Macaca fascicularis*). *American Journal of Physical Anthropology* Supplement 32:163

Wheatley, B.P. (1980) Feeding and ranging of East Bornean *Macaca fascicularis* in Lindburg, D.G. (ed) *The Macacques: studies in ecology, behavior and evolution* Van Nostrand Reinhold pp. 215-246

Wheatley, B.P. (1988) Cultural behavior and extractive foraging in *Macaca fascicularis*. *Current Anthropology*, 29:516-519

Wheatley, B.P. (1991) The role of females in inter-troop encounters and infanticide among Balinese *Macaca fascicularis* in Ehara et. al. (eds) *Primate Today* Elsevier Science Publishers pp.169-172

Wheatley, B.P. (1999) *The Sacred Monkeys of Bali*. Waveland Press, Inc.

Wheatley, B.P., Harya Putra, D.K., and Gondar, M.K. (1996) A comparison of wild and food enhanced long-tailed macaques (*Macaca fascicularis*). In Fa, J.E. and Lindberg, D.G. (eds.)

Evolution and Ecology of Macaque Societies. Cambridge University Press, Cambridge. Pp. 182-206

Wheatley, B.P. and Harya Putra, D.K. (1994) Bitring the hand that feeds you: monkeys and tourists in Balinese monkey forests *Tropical Biodiversity* 2(2):317-327

Wheatley, B.P., Fuentes, A., and Harya Putra, D.K. (1993) The Primates of Bali. *Asian Primates* 3(1-2):1-2

Whitten, A.J. (1995) Natural areas and nature of inland Bali. In *Bali: Balancing environment, economy and culture*. S. Martopo and B. Mitchell Eds. Department of Geography Publication series, University of Waterloo pp.237-261

Whitten, A.J., Soeriaatmadja, R.E., and Affif, S. (1996) *The Ecology of Java and Bali*. Periplus Editions, Singapore.

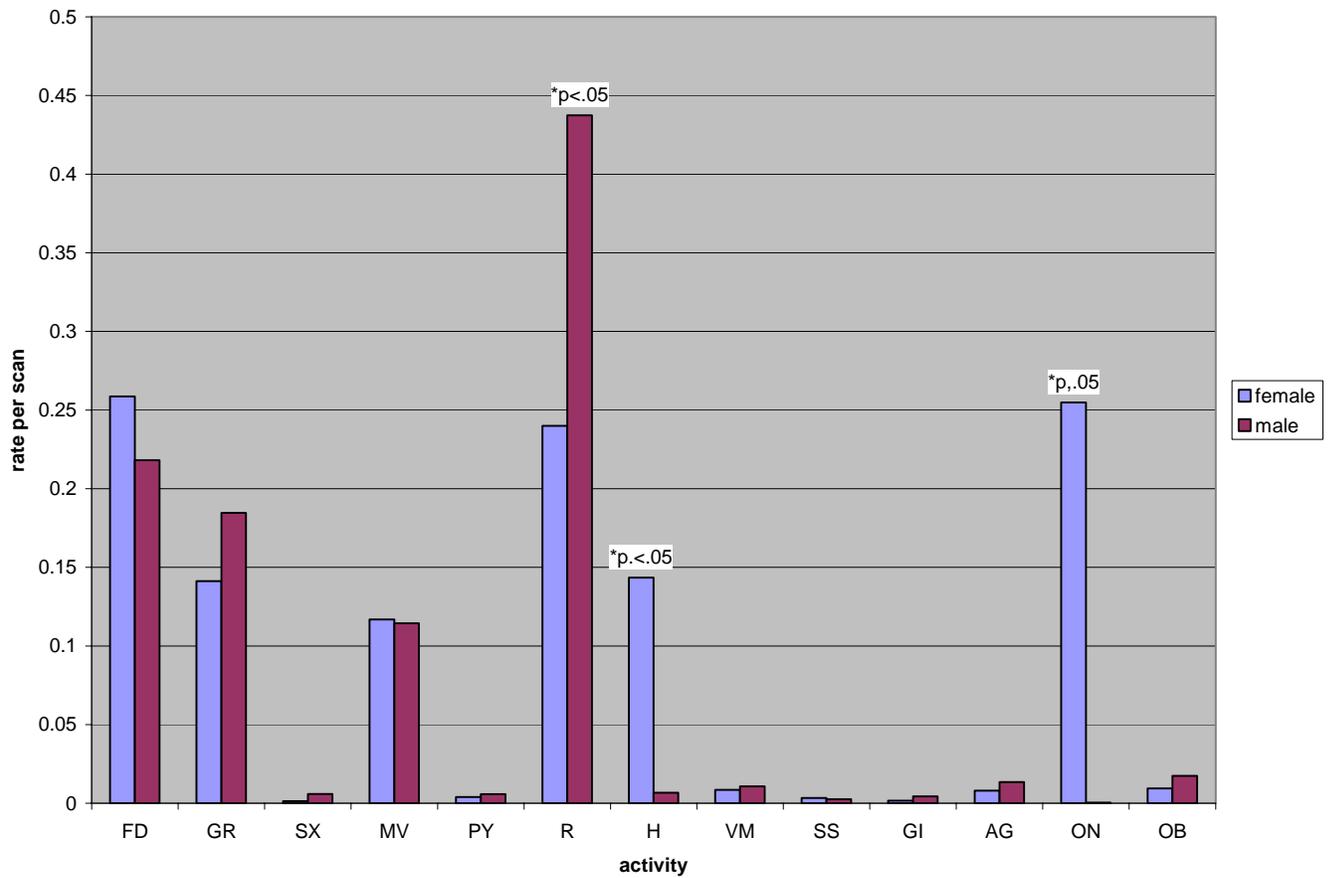


Figure 1. Adult Male and Adult Female mean activity patterns 1999-2002

FD: Feed, GR: Groom, SX: Sex, MV, Move, PY: Play, R: Rest, H: Huddle, VM: Visual monitor
 SS: Sexual solicit, GI: Genital inspect, AG: Aggression, ON: On ventrum, OB: Object
 manipulate

Table 1 Population Size History at Padangtegal

| year | group 1 | group 2 | group 3 | total population | Deaths recorded (August-August) | Population increase |
|-------|---------|---------|------------------------------|------------------|---------------------------------|---------------------|
| 1986* | | | | 69 | | |
| 1990* | | | | 97 | | |
| 1991* | | | | 122 | | 20.5% |
| 1992* | | | | 133 | | 8.3% |
| 1994 | | | Streptococcus outbreak | 10-20% mortality | | |
| | | | 1993-1997 no population data | | | |
| 1998 | 20 | 45 | 57 | 122 | | |
| 1999 | 22 | 49 | 54 | 125 | | 2.4% |
| 2000 | 24 | 62 | 53 | 139 | 5 | 10% |
| 2001 | 28 | 75 | 58 | 161 | 15 | 13.7% |
| 2002 | 31 | 100 | 63 | 204 | 7 | 21% |

* 1986-1992 data from Wheatley 1999

Table 2 Demography: Age and Sex make-up of population at Padangtegal

| year | Adult males | Adult females | Immatures | Infants born during major birth peak (May-August) | Observed deaths June-August |
|-------------|--------------------|----------------------|------------------|--|---------------------------------------|
| 1986* | 5 | 26 | 38 | 2 (11 total infants nursing) | |
| 1990* | 8 | 29 | 60 | 3 (15 total infants nursing) | |
| 1991* | 11 | 35 | 76 | 7 (19 total infants nursing) | |
| 1992* | 11 | 42 | 80 | 3 (19 total infants nursing) | |
| 1998 | 14 | 43 | 65 | 7 | 1 |
| 1999 | 11 | 48 | 66 | 16 | 2 |
| 2000 | 10 | 55 | 74 | 15 | 3(2 inf, one ad M7) |
| 2001 | 10 | 60 | 91** | 19 | 3 (3 inf) |
| 2002 | 21 | 80 | 103 | 23 | 5 (3 inf, one ad male, one ad female) |

* 1986-1992 data from Wheatley 1999

** includes 12 older sub adult males

Table 3. Comparison of Activity Budgets for *Macaca fascicularis*

| | Feed | Travel | Other |
|--------------------|-------------|---------------|--------------|
| Bali (Padangtegal) | 23% | 12% | 58% |
| Sumatra | 15% | 26% | 59% |
| Mauritius | 32% | 4% | 64% |
| Malaysia | 35% | 20% | 45% |
| Kalimantan | 13% | 45% | 42% |
| Bangladesh | 39% | 9% | 53% |

Table 4 Diet During Padangtegal Dry Season (June-August) 1999-2001

(11,761 feeding instances)

| | Provisioned | Non-provisioned |
|-------------------|--------------------|------------------------|
| sweet potato | 28.9% | |
| banana | 21.9% | |
| peanuts | 12.4% | |
| papaya leaves | 5.7% | |
| coconut | 1% | 2.8% |
| invertebrates | | 7.5% |
| forest vegetation | | 9% |
| other | | 10.3% |