

## The Crab-Eating Macaques (*Macaca fascicularis*) of Angaur Island, Palau, Micronesia<sup>1</sup>

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**Key Words.** Crab-eating macaque · Ecology · Behavior · Adaption · Genetic isolation

**Abstract.** Crab-eating macaques on Angaur are an exotic fauna introduced to the island in the early 1900's. The present population of 480-600 animals reportedly are descendents of a pair of monkeys brought to the island by German phosphate miners. During a 10-week period, June to August, 1973, we spent a total of 253:30 hours in the field locating and studying monkeys. Of this total, 75:30 hours are direct observation time. This article discusses aspects of the ecology, social behavior, and problems of adaptation of the Angaur crab-eating macaques.

### Introduction

#### Distribution

Crab-eating macaques, *Macaca fascicularis* (= *M. irus*), range throughout Southeast Asia. From the northern border of India they range into Burma, Thailand, Vietnam, Cambodia, Malaysia, the island state of Singapore, and the Philippine and Indonesian archipelago [FIEDLER, 1956]. The range should now be extended to include the recently introduced population inhabiting the Palauan Islands of Angaur and possibly Babeldaob, Koror, and Guam (Fig. 1). Because of the wide distribution and varying ecotones, crab-eating macaques display considerable morphological variation. (It is still unclear whether this variation is expressed in behavior and social organization.) 21 sub-species have been noted [NAPIER and NAPIER, 1967]; however, CHASEN [1940] raises doubts of the utility of the subdivisions. Perhaps what some

<sup>1</sup> This study was conducted with funds provided by a grant-in-aid from the Ohio State University Graduate School through funds provided by a National Institutes of Health General research support grant.

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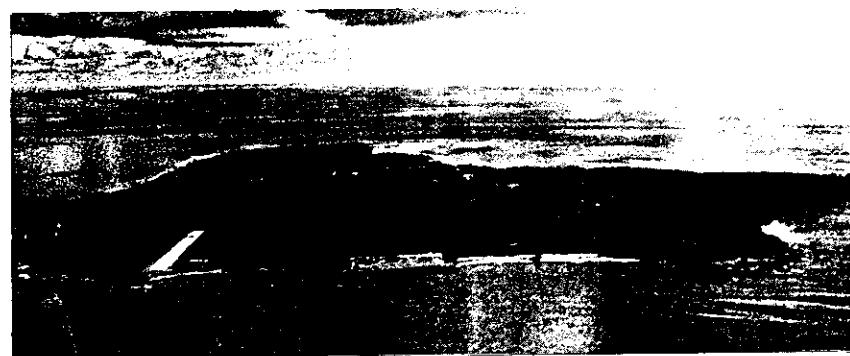


Fig. 1. An aerial view of Angaur Island, Palau (photo: DAVID R. MOORE). Note the landing strip in the left hand portion of the picture. The US Coast Guard Station is in the front middle of the picture.

now consider subspecific variation, often on the basis of limited data, may demonstrate population variability. Variability is generally towards slightly smaller body sizes and 'warmer' hair colors from north to south [CHASEN, 1940].

Two common names are often used to refer to *M. fascicularis*: long-tailed macaque and crab-eating macaque. Tail lengths of both sexes are generally greater than the body length [FOODEN, 1971]. HARRISON [1964] suggests the long tail is an adaptation to arboreal life, and aids in balancing during quadrupedal arboreal locomotion. Crab-eating macaque refers to coastal populations which reportedly dig, catch, and eat crabs on sandy beaches. Although this study witnessed no actual crab-eating behavior, FURUYA [1965] reports crab eating among a captive group.

#### Physical Description

FURUYA [1965] remarks that *M. fascicularis* from the Malay Peninsula have a brownish pelage and that the top hair (hair on top of the head) lacks the characteristic 'sharpening' found among Indochina peninsular forms. *M. fascicularis* from the Indochina Peninsula has a grayish-brown hair coat. From these characteristics monkeys on Angaur may be descendents of monkeys introduced from the Indochina Peninsula, perhaps from Indonesia as previously suggested. Angaur macaques have a brownish-gray to brownish-gold hair color with hair tufts, at least in younger animals, shaped into crests (Figs. 2, 3).

SHIREK-ELLEFSON's [1967] study describes the physical appearance of the



Fig. 2. Infant crab-eating macaque from Angaur (photo: DAVID R. MOORE).

Singapore Botanic Garden animals. These animals weighed 3.2–9.1 kg, with males weighing two to three times as much as the females. Both sexes possess long tails. The exposed skin of the head and face is dark purple to black, the eyelids and area above the eyelids are unpigmented, appearing white. The contrast in coloration is striking and important in communication. Pelage is brownish-gold, the stomach hair, hair beneath the tail, and the back of the hind limbs is white. The hair cap approaches a black coloration and is often darker than the rest of the body hair. Hair caps are 'nondescript', although some are pointed and streaked with darkly colored longitudinal stripes. Females have brushes of white whiskers framing the lower half of the face, males have white and black whiskers.

*M. fascicularis* on Angaur show some variations from the above. Whether these variations are indicative of the ancestral stock or are restricted to this genetically isolated population is unknown. Hair color of the Angaur monkeys is a brownish-gold hue, sometimes tending to darker shades. Except for the long tails, morphologically they are quite similar to rhesus macaques. Older animals exhibit lightening of the hair color, probably associated with age. Eyelids are lighter than the rest of the face, which is variously pigmented according to age. Stomach hair is lightly colored, as is the hair beneath the tail and on the back of the hind limbs, providing protective coloration when animals are arboreal. Although some animals exhibited facial hair, we are reluctant to describe these as whiskers, as SHIREK-ELLEFSON [1967] noted in



Fig. 3. Infant crab-eating macaque from Angaur (photo: DAVID R. MOORE).

Singapore. Younger animals, juveniles in particular, are identifiable by a pointed hair crest. Infants are recognizable by their dark natal coat. A relative age scale of animals is shown in table I.

Some physical abnormalities were noted in adults. One male in the light-house group was missing a right eye and had a healed facial scar. Furthermore, his poorly articulated jaw prevented fully occluding his teeth. The jaw may have been broken or permanently disarticulated. He showed no signs of feeding problems, and seemed well adapted. We assumed the disability was rather old. The 'control' female of the same group was distinguishable by the presence of a tumor on her lower abdomen near the crotch and a polyp on her nose. The tumor was somewhat smaller than a ping-pong ball and projected through the hair. Possibly the tumor indicated parasitic infection; however, we lack confirmatory data. She was also missing a piece of her right ear.

### Ecology

#### Description and Topography

Angaur is a coral platform island, a raised limestone reef, with an area of 830 ha. In its greatest dimension, NNE-SSW, the island is slightly more than 8.8 km. The island is

Table 1. Age determination of Angaur macaques

Age	Distinguishing physical traits
Infant (one)	Natal coat – a paler skin tone, hair is darker than exhibited by older animals. Hair color begins to darken by 5 months.
Infant (two) – based on a captive male estimated to be 8–9 months	Fully developed scrotum and testicles are descended. Eyelids are lighter than the face. Hair color is lighter than among adults. The scrotum is a pink color.
Juveniles	Juveniles have a pointed hair crest distinguishing them from adults, and a reddish facial color when compared with older animals.
Adult females	Multiparous females have pendulous breasts. They vary in weight from 4.5 to 6.8 kg. Body and facial color are distinguishable from younger animals. No sign of whiskers noted by SHIREK-ELLEFSON [1967] and KURLAND [1973]. There is a red coloration of the ano-genital region. <sup>1</sup>
Adult males – including one shot specimen	The scrotum is a rather bright red color. The shot specimen weighed approximately 11 kg. Eyelids have a light blue hue. Body length is about 60 cm; overall length, head-tail, is about 105 cm. No sign of the whiskers noted by SHIREK-ELLEFSON [1967] and KURLAND [1973].

<sup>1</sup> It is unlikely that this had any connection with the reproductive cycle. NAWAR and HAFEZ [1972] and ONG [1964] note that no swelling or color variations in tissues surrounding the external genitalia of adult females was observed at any stage of the menstrual cycle. CORNER's [1932] study, however, suggests a color change and swelling of the sexual skin.

located 6°53' and 6°55' north and 134°8' and 134°9' east. Angaur is the southernmost tip of the Palau island chain. Angaur stands alone, outside the lagoon system protecting the rest of the Palau island chain. Approximately 11.3 km of open sea separate Angaur from its nearest neighbor Pelileu, site of intensive action during World War II. Angaur lies 691 km above the equator, 1,175 km southwest of Guam, 1,600 km southeast of Manila, and 805 km north of New Guinea.

Because of its rather isolated location, Angaur is rather difficult to reach. The most direct route is to fly from Honolulu to Guam to Koror. Once in Koror, arrangements must be made to take the Angaur community owned boat to Angaur. Service to Angaur is limited to one round-trip per week on average. The distance from Koror to Angaur, about 64 km, is a 4- to 5-hour journey depending upon weather conditions and whether the trip calls for intermediate stops. Because of the difficulties of obtaining supplies on Angaur, many supplies must be purchased in Koror.

Topographically, Angaur is predominantly jungle with dense forests covering most of the island. Periodically, during intermittent severe typhoons and because of very intense bombing during World War II, the forest cover was obliterated. The greatest relief is in the

northwest corner of the island. Between the lowest sink and highest solution-sharpened ridge the elevation is rarely more than 60 m. The southeastern two thirds of the island, less than 9 m above sea level, is almost a level plain with a broad shallow depression, occupied by a 46-ha inland swamp. The northwestern portion of the island is a bowl-shaped upland consisting of a rim of steep hills, with summit altitudes of 30–45 m, encircling a basin roughly 600 m in diameter, whose floor is no less than 3 m above sea level. The north-central part of the island is a succession of alternating subdued ridges and shallow depressions concentric to the bowl-shaped upland.

The coastline, especially the northern and eastern coasts, is quite forbidding and very jagged. One slip on this terrain can result in extensive abrasions and major cuts. The coastline is steep and dissected, strewn with jutting shelves, boulders, corroded limestone, extensive tidal pools, and bombed out remnants of World War II bunkers and landing craft. It is relatively easy to travel about the island's perimeter because of a bulldozed road which is periodically cleared of the overgrowth. During torrential rains, however, the road becomes flooded. Roads dissect parts of the interior making survey of certain regions rather easy.

The thick, rich rain forest is covered with a multiplicity of climbing vines. Deep, worn limestone craters and extensive bomb craters make interior parts of the island almost inaccessible. The few native trails criss-crossing the interior are passable if one takes a machete. Additional problems of working the interior are presented by mining depressions which may be hidden by thick vegetation, and filled with water seepages from the ocean. One final hazard of the island's interior is the presence of live ammunition, particularly hand grenades, remnants of the war. Caves dot the interior, in which one finds history's remains, evidence of the Angaurese past in the form of abundant pottery sherds [some described in OSBORNE, 1966] and of the contest of World War II in the grisly presence of supplies, ammunition, and occasionally human skeletons.

#### Settlement Patterns

Native settlement patterns may be of some help in understanding the monkeys' distribution. Native settlements are primarily limited to the southern part of the island. The Angaurese cluster into approximately eight old village areas or chieftains. A US Coast Guard Loran Station occupies the northern coast. Its landing strip is used as a primary means of travel across the island's center. Native land utilization is presently limited, although one finds scattered and often isolated farmsteads and numerous taro and tapioca plots. Two large taro swamps yielding extensive food supplies are found in the south. Plantings north of this are mainly sweet manioc. Occasionally one locates areas which are partially cleared for planting of banana, coconut, lemon, papaya, avocado, guava, and betel nut trees. Many low-lying swamps are remnants of once intensive phosphate mining.

#### Native Population

While census figures are not particularly accurate, the population is approximately 400–450 persons, a number which fluctuates seasonally. Currently, most of the population is concentrated within one area and there is little direct competition between the human inhabitants and monkeys.

#### Brief History of the Island's Occupants and their Influence on the Monkey Population

Certain aspects of Angaur's history bear directly upon the monkey population. Historical records indicate that the Spanish were the first Europeans to inhabit the Palau Islands.

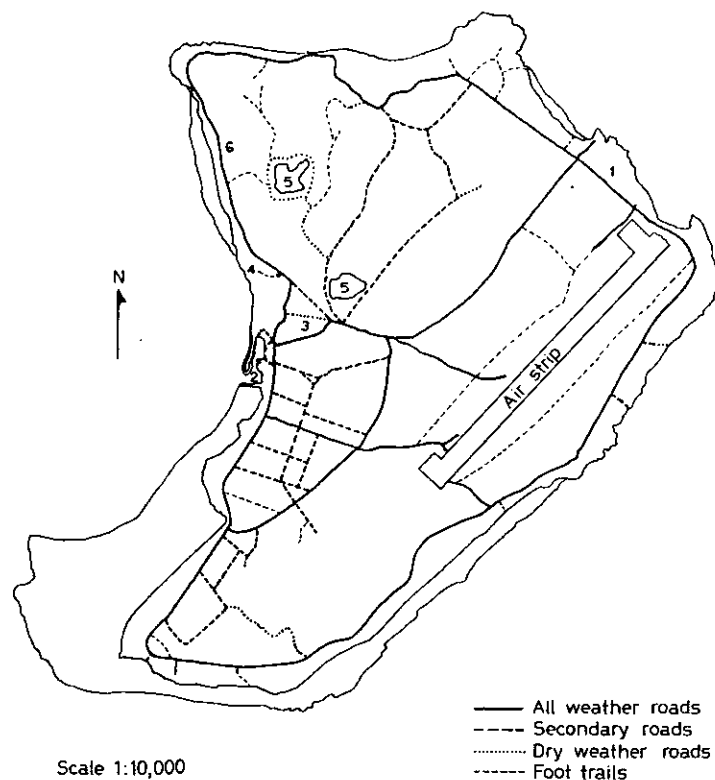


Fig. 4. Map of Angaur Island (original drawing by W. REYNOLDS, redrawn by S. Wolkow). 1 = US Coast Guard; 2 = boat basin; 3 = phosphate works ruins; 4 = old light house; 5 = lakes; 6 = research area.

Although they made no attempt to directly administer the islands, a number of Catholic Missions were established. There is no indication in Spanish reports that monkeys existed on Angaur prior to 1900. The monkeys were apparently introduced during German rule (from 1900 to 1914) by early phosphate miners. One old man said he distinctly remembered that two monkeys were brought by German phosphate mining engineers. He spent almost his entire life on the island and assured us that no animals were subsequently imported.

The Japanese period lasted from 1914 until 1945. Their presence directly and indirectly affected the Angaur macaque population. When we first became aware that monkeys existed on Angaur, we were told they were introduced by Japanese. With the help of Mr. GOH ABE (a graduate student in our department) we searched old Japanese literature [i.e. HORII, 1916] from Micronesia and became convinced that monkeys were resident when the Japanese arrived. This was confirmed by a Japanese administrator of Angaur who now resides in Tokyo. He advised that monkeys were long-resident on Angaur when he arrived in the 1930's.

The Japanese apparently killed a number of monkeys for sport, food, and medicinal purposes. However, we are unable to estimate how much predation pressure the Japanese exerted. The Japanese period also affected the monkeys: (1) Intensive phosphate mining greatly altered the middle section of the island by removing a large forest area. (2) Lumber requirements caused the gradual destruction of large forest areas. (3) Some jungle areas were cleared to make room for their 'towns' and they relocated natives to other parts of the island. Because of a reduction of habitation areas by economic destruction, perhaps the monkeys were introduced more often to human populations. Furthermore, intensive farming practiced by the Japanese in localized areas may have affected the monkey population by (a) introducing them to new foods; (b) exposing them to predation; (c) removing potential areas of habitation, and (d) providing garbage areas for foraging [i.e. KURLAND, 1973].

The most devastating effects of the pre-1945 period result from the war. Angaur, as its neighboring island Pelileu, was the scene of large Japanese and subsequently American troop installations and supply depots. For almost 3 months prior to the American invasion, the island sustained saturation bombing. Native tales, and pictures taken by the invasion forces, starkly document the damage done by the bombings. The original forest cover was all but removed and the rain forests were totally decimated. Native informants described the effects of wartime activities on the monkey population, and noted that during the period of intensive bombing the monkeys, as well as native inhabitants, migrated to the so-called 'caves'. Extreme population reduction probably resulted from these attacks.

Two major typhoons have obliterated vast portions of the rain forest, the last time in 1964. After each typhoon the forest returned in full force. It is almost impossible to tell that recently the island's character has been so drastically altered.

At least three times within the last 30 years the Angaurese macaque's environment has been drastically altered, their numbers reduced, and their food supplies depleted, but they survived. This is testimony to the nonhuman primate's ability to adapt to harsh, devastating and overnight changes. (Another instance of remarkable adaptability is found in POIRIER's [1969] study of Nilgiri langurs; further instances are found in JAY [1968].) How these various cataclysms influenced this particular gene pool is not known. Perhaps the current population genetically exhibits the results of genetic drift, the bottleneck effect, or the founder principle. This situation, as POIRIER's [1971] study of St. Kitts green monkeys, provides a situation for investigation of microevolutionary change.

#### *Climate (Fig. 5)*

Precipitation on Angaur is heavy, approximately 350 cm per year is not uncommon. Neither, however, are periods of droughts. Monthly rainfall totals vary from year to year. There are two seasons on Angaur, the wet and the dry season. Although the months of these relative seasons shift somewhat, summer months are usually the wettest and winter months the driest. Torrential downpours are not uncommon during the rainy season. While consecutive days may be cloudy and rainy, it is likely that the rains will come in the evening and early morning hours.

Although the island of Koror is some 64 km north of Angaur, the weather bureau's statement for Koror is basically applicable. Northeast trade winds prevail from December through March and are generally light to moderate. Precipitation, heavy during December and January, declines sharply when the belt of convergence moves south. February through April are among the driest months. During May there is an increasing influence of easterly winds. In June the belt of convergence again moves north bringing heavy rainfall and

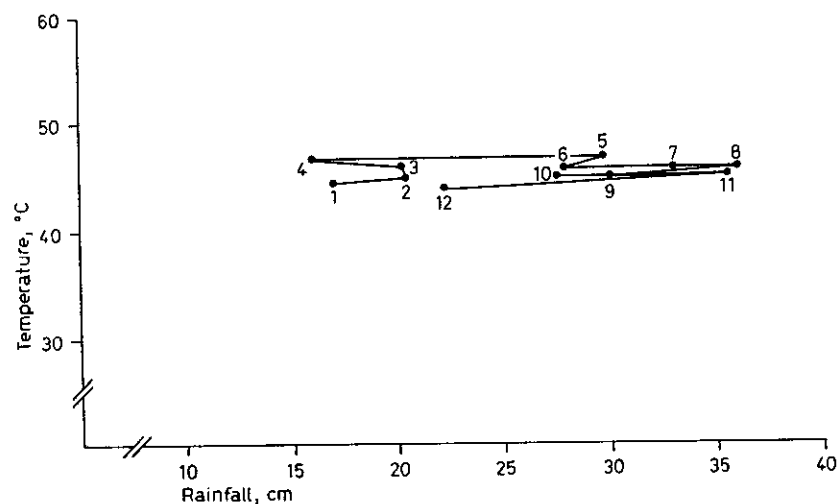


Fig. 5. Average monthly rainfall and temperature, 1963-1965. Months of year numbered consecutively (by S. WOLKOW).

thunderstorms, yielding 2.5 cm of rain within a 15- to 30-min period. The summer months are intermittently windy, cloudy, and rainy.

Temperature ranges on Angaur during a 24-hour period may be 11-14 °C. Throughout the year, however, mean daily temperatures are quite constant, averaging about 47 °C during the day.

### Materials and Methods

One prime objective of this study was to ascertain whether monkeys exist on Angaur in numbers warranting further study. Much of our time was spent surveying to obtain a clear picture of the island's monkey population and distribution. Our second objective was to gather comparative behavioral data. We were particularly interested in discerning how this population adapted to its relatively new econiche.

The two observers spent 253:30 h in the field (table II). We spent 75:30 h in direct observational contact, e.g. 1 h of observational time for each 3.3 h in the field ( $x = 1.8$  h observation/day in field). Much of the time was joint observations. We cross-checked our data and found considerable inter-observer reliability. This method allowed one to observe and take cursive notes while the other photographed. (Photography proved quite difficult because of obstructing vegetation and fluctuating light conditions.) We also separated for part of the study, maximizing our observational effectiveness.

According to SHIREK-ELLEFSON's data [1967], crab-eaters show two marked activity cycles, one in the morning and one in the later afternoon, presumably corresponding to cooler times of the day. The morning peak of the Singapore Botanic Garden animals begins about 0900 and lasts for 1-2½ h, the afternoon peak begins between 1400 and 1600 h and lasts until about dusk. Reference to table III indicates an approximation of the Angaur

Table II. Distribution of field time<sup>1</sup>

	Hours spent in field	Hours of observation
Joint field time	183:10	54:50
Field time (POIRIER)	35:50	10:45
Field time (SMITH)	34:30	9:55
	253:30	75:30

<sup>1</sup> A total of 253:30 h were spent during 42 days in the field searching for monkeys. Of the total time spent in the field, 75:30 h were in direct observational contact with the monkeys. On an average, we were able to obtain 1 h of observational time for each 3.3 h spent in the field. On a daily average, this is 1.8 h of observation for each day spent in the field.

Most of the observational sightings were made by the authors jointly, the distribution of hours in the field and hours of observation, both jointly and alone, are given.

Table III. Approximation of the daily cycle of the Angaur macaques<sup>1</sup>

Hours of the day	Observations <sup>2</sup>	Time in the field <sup>3</sup>
0700-0800	16	30
0800-0900	13	33
0900-1000	19	33
1000-1100	19	32
1100-1200	13	25
1200-1300	5	9
1300-1400	10	17
1400-1500	18	31
1500-1600	13	39
1600-1700	10	25

<sup>1</sup> The table attempts to approximate times when the study of the Angaur macaques was most promising. Although the authors feel that the table reflects the times of most activity, a number of variables are present: (1) the table reflects the distribution of hours which the observers spent in the field; (2) the table reflects the times of greatest activity of the monkeys, times of resting, grooming, and other leisurely activities are probably not fully represented as the forest canopy obviated observations of silent monkeys; (3) the table reflects the weather to some degree, for rainy days greatly hampered our activities and slightly reduced the animals' activity.

<sup>2</sup> Number of times we actually saw monkeys during the time period.

<sup>3</sup> Number of times we were actually in the field during the particular time period.

macaque's daily cycle, and suggests activity peaks between 0900 and 1100 h and in the afternoon between 1400 and 1500 h. Our data are incomplete, however.

Field equipment was minimal. Each investigator carried a pair of binoculars, a 7 × 35 and 7 × 50 wide-angle lens. Photographs were made with a Nikon F equipped with a 200-mm telephoto lens and a Mamiya-Sekor 1000 DTL with a 90–230 mm zoom. Because of the high humidity and heat, and lack of storage facilities, it was difficult to prevent film spoilage. We carried a pedometer (lost in one of the taro swamps), and a stopwatch. All our work was done by foot. Although we varied the routine, the field day usually began by 0700 and lasted until 1130 or 1200 h, and resumed again from 1330 or 1400 to 1630 h. (Because of the lack of transportation, we missed a lot of good observation time. However, this was unavoidable.) Daylight lasted from 0545 to 1830 h. Hand-written field notes were elaborated and indexed each evening. An integral part of the study involved questioning natives about their relations with the monkeys. To supplement field observations, we briefly observed a young captive animal, and photographed and described a freshly killed adult male.

To habituate animals to our presence, we made frequent use of a bombed pre-World War II Japanese lighthouse. This structure stood about 25 m above the forest canopy in the middle of the home range of the lighthouse group. Many hours were spent atop the lighthouse accommodating animals to our presence. Even though we could not see them we were positive they were observing us. Soon they began to tolerate our presence. By the end of the study, many animals in this group, especially one distinctive adult female and the youngsters, tolerated our presence from distances of approximately 4.5–6 m. (Unfortunately, we were not as lucky with many of the other troops.) Because of their tolerance, most behavioral data are derived from this group, comprised of approximately 40–50 members.

Observational conditions were difficult<sup>3</sup>. Once we entered the rainforest, the thick vegetation made prolonged observation impossible, as it did tracking the animals. Nevertheless, we were able to record some behavioral interactions. Observations from atop the lighthouse, or from the road, were only slightly better. In these instances we only saw animals when they chose to show themselves<sup>4</sup>.

### Comparative Data

FURUYA [1961/62, 1965, 1971], GOUSTARD [1961, 1963], KURLAND [1973] and SHIREK-ELLEFSON [1967] have all studied crab-eaters; however, no long-term naturalistic investigations were undertaken until the work of ANGST [1973, in press] in Java and Bali. Dr. D. LINDBURG [personal commun.] and some of his students conducted a recently completed study in Indonesia.

In addition to the above, some data, especially on distribution of *M. fascicularis*, can be found in BANKS [1949], BERNSTEIN [1967], CHASEN [1940], CHIVERS [1970], DAVIS [1962], FOODEN [1971], HARRISON [1964], MCCLURE

<sup>3</sup> ANGST [in press], KURLAND [1973], and LINDBURG [personal commun.] also report considerable difficulty observing forest-dwelling *M. fascicularis*.

<sup>4</sup> ALDRICH-BLAKE [1970], CHALMERS [1968a, b], POIRIER [1971], and STRUHSACKER [1969], among others, have discussed the observational problems inherent in forest studies.

[1964], MEDWAY [1969], and SOUTHWICK and CADIGAN [1972]. BERKSON [1970, 1973] describes the maternal-infant behavior of blind crab-eating macaque infants. CHIANG [1967] reports on tool use among crab-eating macaques, CORNER [1932] and NAWAR and HAFEZ [1972] on the reproductive cycle, FADY [1969] reports on play behavior, GAUTIER-HION and GAUTIER [1971] on swimming behavior, and KARRER [1970] on tail use.

### Reactions to the Observers

Initially, the monkeys were neither particularly wary nor particularly cooperative allowing observation. After habituation they slowly became accustomed to our presence; at the end of the study the lighthouse group tolerated our presence within 10–15 m while they were arboreal. Several behavioral patterns characterizing the animals' reactions to our presence are discussed below.

(1) The animals most often seen were youngsters. This pattern also characterizes other primates. Youngsters are often the most curious.

(2) For the lighthouse group an adult female, rather than an adult male, seems to perform the role of group protector against possible external threat. This female usually signalled our arrival to the group, using what we labelled the 'threat-warning bark'. We are unable to say anything about the consistency of this behavior among females for other troops; however, we noted that adult females were often among animals threatening or watching the observers.

(3) The possibility of sentinel behavior was also noted. Whenever a group fled after contacting the observers, one animal remained behind to watch the intruders, while remaining group members silently and imperceptibly slipped away. The remaining animal frequently emitted threat-warning barks, while moving in a wide perimeter about the intruders. The distance to which the 'sentinel' animal approached the intruders varied with the situation. Vocalizations continued long after the observers left.

KURLAND [1973] describes a similar pattern for Indonesian crab-eaters, though in KURLAND's study an adult male performed the vigilance role, emitting the 'kra' call. As the male calls, the rest of the troop moves off and the male continues to call and move towards the stimulus. After calling for 5 min or so, the male quietly moves in the direction the troop appears to have gone. All animals then remain quiet. During the interaction the male succeeds in leading the intruder away from the bulk of the troop, all the while keeping himself between the intruder and the troop.

Sentinel behavior has been noted for other primates: POIRIER [1971] notes sentinel behavior among St. Kitts green monkeys, ALTMANN and ALTMANN [1970] for yellow baboons, MAXIM and BUETTNER-JANUSCH [1963] for cynocephalus baboons, and CROOK and ALDRICH-BLAKE [1968] and HALL [1960] note it for anubis baboons. In these instances the 'sentinel animal' is a male. On Angaur the 'sentinel' role in at least one group is assumed by a female. There is the further possibility that on Angaur older juveniles act as sentinels for others of the juvenile subgroup.

(4) In some cases, the animals' reaction to our presence seemed to be influenced by where we met them. Animals were more excited by our presence when on the ground than when they were arboreal, and we could approach more closely when they were arboreal than terrestrial. Occasionally, however, they fled on the ground, especially when surprised by our appearance (which was not unusual), separated from us by physical obstructions, or simply far away. The animals were not constantly vigilant and we sometimes surprised them. They scattered and uttered harsh threat and warning calls. There was no evidence of panic diarrhea on these occasions, however. The lighthouse group was particularly calm when we met them within what seems to be one of their core areas. When in this forest area, the animals would approach within 4.5 m and showed no signs of disturbance.

(5) Reactions to us were also influenced by whether the animals saw us first, or whether they met us as we awaited their arrival.

(6) One of the most typical reactions to our presence, during the early stages of habituation, was continued vocalization, lasting for 30 min or more. Then suddenly there was silence. We learned quickly that silence signalled the animals' retreat. The encounter ended, and it was unlikely that we would meet the animals again for some time. Both retreat and silence were sudden with no forewarning. What signalled movement, which animal or animals moved first, is unknown.

(7) Upon meeting a group, juveniles would often lie prone on a branch and observe us. This posture was not typical of inter-animal encounters and seemed to have been reserved for our presence. Juveniles often did this while hiding behind a clump of leaves, their heads darting in and out for a glimpse of our whereabouts. Pressing the body against a branch may be a means whereby the animal makes itself less conspicuous.

(8) Towards the end of our study in August, the animals of the lighthouse group became wary of our presence and began to change their movement patterns. We encountered them in previously untravelled areas. Perhaps they were extending their home range. During this time we noted a possible

consort relationship between an adult male and an adult female. We also noted some bisexual adult mounting, possibly a number of cases of removing ejaculate from the penis and vaginal areas, and a tendency towards more intragroup and intergroup antagonism. Although information is scanty, it suggests that the animals were entering a stage of sexual excitement.

We have noted in some detail the animals' reactions to us for these reveal several characteristics about the Angaur macaques. We were most impressed by the role of the adult female in threatening us. We were also impressed by the possibility of sentinel behavior and the differential use of the terrestrial vs. arboreal settings during times of stress.

ANGST [in press] notes that when he encountered troops they avoided calling; however, one animal may alarm-call. Many of the groups encountered moved silently away, offering evidence of social facilitation in the silent flight pattern. ANGST notes that when one animal stops alarm-calling, another begins. The vocalizing animal remained hidden and the calls continued after the observer left. In most particulars, ANGST's data fit our observations. Although we found that a number of animals often alarm-called (which we called a threat/warning bark) at our presence, we can confirm the interesting pattern of one animal calling, stopping, and another beginning.

### *Population Dynamics*

Table IV compares the population data from Angaur with those from other published studies of *M. fascicularis*. Group sizes on Angaur closely approximate troops which ANGST [in press] studied in Java, Indonesia – one of the most likely homelands of the Angaur population. Our island survey recognized seven different troops. However, it is our impression that others exist in the rather impenetrable forest areas. Utilizing a trail survey method developed by MITTERMEIER [1973], we estimated the total population to be approximately 480–600 animals.

Because of many observational problems, we were unable to get a clear picture of troop compositions; however, we can confirm that these are multiple adult male multiple adult female groups. The sociometric sex ratio is unknown, although our notes indicate that there are more adult females than adult males in the groups. One striking characteristic of these groups is the very large number of young animals, particularly juveniles.<sup>5</sup> We first assumed that sightings of young animals were based on their greater visibility; how-

<sup>5</sup> This is in marked contrast to SOUTHWICK and CADIGAN's [1972] data.

Table IV. *Macaca fascicularis*: comparative troop sizes and composition

Source	Location	Troop size	Socionomic sex ratio, etc.
This study	Angaur, Palau	40–50 as an average; 1 group may contain 75 or more animals	multiple males and females; large juvenile subgroups; peripheral animals
ANGST	Java: forest groups temple groups	48.5 average 47.3 average	2–9 adult males; females outnumber males 1:2.5; peripheral and semi-solitary males no peripherals
BERNSTEIN (4 troops)	Malaysia	14, 15, 20, 70 ( $\pm 20$ animals) plus a group of 18 with 2 pigtail hybrids	
FOODEN (9 troops)	Thailand	7–100 with a mean of 35.3	
FURUYA	Mangrove forest – Malaysia	30 (one troop)	2:1
	Penang Waterfall Garden	72	5.6:1 to 2:1
	Singapore Botanic Garden	45, 45, 38, 13	solitary and peripheral animals present
KURT and SINGA [in ANGST] (14 troops)	Sumatra	6–20 with a mean of 16	
KURLAND (12 troops)	Indonesian Borneo	10–30 with a mean of 18.2	no peripheral or solitary
MEDWAY	Malaysia and Singapore	8–40 plus	
SHIREK-ELLEFSON (one troop)	Singapore Botanic Garden	59	3.7:1, no peripherals means for ages and sexes:
SOUTHWICK and CADIGAN (9 troops)	Malaysia	7–44 with a mean of 24.0	adult males, 3.4 adult females, 8.4 infants, 4.2 juveniles, 7.8

ever, it became apparent that the large number of young animals was a reality of troop compositions. Although we cannot explain this, we offer the following possibilities.

(1) Because younger animals are more active, and form subgroups, they are seen and counted more often. While this is a fact, it still does not explain their numbers.

(2) Many animals were probably killed during the last (1964) typhoon, either directly or indirectly because of lack of food. Survivors might have been the progenitors of a subsequent population explosion.<sup>6</sup> A rather wide open niche, free from interspecific competition, could lead to rapid growth. Thus, the population structure reflects a higher proportion of young animals for a number of generations.

(3) The Angaur macaques may be experiencing very high birth rates. With no natural predators, and perhaps a lack of disease, these animals might be experiencing a period of abnormally rapid growth.

Whatever the cause of the large number of young animals, it is rather certain that the current population, as the original, are descendents of a limited number of progenitors. This population may have passed through a 'bottleneck' within the last 10–15 years. Perhaps some of the subtle, but observable, phenotypic differences in different groups result from this process.

Our data allows an estimate of average group size. Our first impression was that groups were comprised of 20–25 animals. However, as groups became habituated to our presence, troop size estimates were revised upwards. We estimate an average group size of 40–50 animals based on counts of the lighthouse group. The largest group contained approximately 75 animals. (Native reports place group sizes at about 100, but this seems to be exaggerated.) Since these animals move along specific travel routes, and primarily in single file, we were able to get rather accurate data.<sup>7</sup>

<sup>6</sup> Possibilities 2 and 3 are suggested by the situation on Barro Colorado where the animals experienced rapid population growth after being decimated possibly by a yellow fever epidemic. Whatever the cause, the population level in 1951 of 239 animals in 30 groups rose sharply until by 1959 the population was 814 animals in 44 groups. Within 8 years the Barro Colorado population increased 3.4 times [SOUTHWICK, 1963].

<sup>7</sup> ANGST [in press] notes the following on the problem of obtaining good troop counts. 'On the other hand I must add, that for my part I found it impossible to count a forest group completely, except when a group crossed a large open area. I could imagine that some of the low numbers quoted are affected by missing a part of the group'. This, we suppose, is because groups do not move as a unit, but are widely spaced and are rather slow in their movement patterns when undisturbed. KURLAND [1973] similarly reports wide spacing of troop animals.

The question must be raised, although we are unable to provide a satisfactory answer, as to what mechanisms influence population growth. Again, reference to table IV indicates that the figures for troop size on Angaur compare favorably with those of ANGST, FOODEN, FURUYA, MEDWAY, SOUTHWICK and CADIGAN, and SHIREK-ELLEFSON. The animals on Angaur are virtually predator-free, disease vectors must be minimal (although we have suggestive evidence of parasitic infestation in the form of tumors), and the food supply is ample. The two most obvious population control mechanisms are seasonality of food supply and biological controls. Although food is seasonally plentiful, during the dry season it may be limited. It is during this season that the monkeys apparently utilize cultigens.<sup>8</sup> Perhaps the seasonality of food stuffs is one mechanism of population control.

Another mechanism of control could be species-specific troop sizes. FURUYA's [1965, 1971] data on the introduced Kijima Island population suggest that troop fission is an element of *M. fascicularis* social life.

#### *Juvenile Subgroups*

A major characteristic of the Angaur macaque's social organization is the presence of juvenile subgroups. Regular assemblages of animals within a group having a recognizable affinity from day to day were designated subgroups [SOUTHWICK *et al.*, 1955]. Subgroups are social aggregates of individuals of similar age and apparently bisexually organized. On Angaur the juvenile subgroup is an assemblage which fed, moved, and played together. The presence of the subgroup is particularly noticeable during movement, when juveniles cluster at the front or middle of the travel group. While we recognized a very clearly demarcated juvenile subgroup, we have no information that animals of other age classes closely associated with one another.

#### *Solitary or Peripheral Animals*

Data as to the possibility of solitary or peripheral animals are particularly difficult to analyze because of the wide troop spread, long intervals in movement, and observational difficulties. However, a number of sightings led us to suggest the possibility of peripheral or solitary animals, mostly adult males. On a number of occasions we encountered lone adults and were unable to locate other animals in their vicinity. Indirect proof that these animals were alone comes from the fact that when we encountered them they did not issue

<sup>8</sup> And as ANGST [1973] reports from Java, during the dry season when foods are diminished and locally abundant, intertroop contact is more common.

the threat/warning bark commonly emitted by troop-living animals. FURUYA [1965], ANGST [1973], and HERR [noted in KURLAND, 1973] also report the existence of solitary animals. However, BERNSTEIN [1967] and KURLAND [1973] report that they occur neither in Malaysia nor in Indonesia.

#### *Birth Peaks*

Although our data are scanty, they are suggestive. Natives reported that the macaques bear their young once a year during March and possibly in February and April. Observations of multiple youngsters within the same groups strongly suggest that most were born at approximately the same time. (In July we examined one captive male specimen which we judged to be about 6 months old. This would place his birth in January. The owner of the monkey said the animal was 8 months old, placing its birth in November.) Whatever the case, our evidence suggests the possibility that infants are born early during the dry period lasting from the end of January until April.<sup>9</sup> In June heavy rains again appear; at this time youngsters born 2-3 months earlier could consume solid foods.

Weather data (table V, fig. 5) present an unclear picture as to possible climatic factors impinging upon the birth cycle. The birth peak or peaks may be related to the monsoon seasons, but there is no clear evidence of any relationship between births and such subsidiary effects as temperature fluctuation, humidity, cloud cover, or wind velocity. However, we suggest a relationship between birth peaks and the monsoons, influencing seasonal fruiting and flowering. The monkeys' favorite foods are the Palauan apple and wild cherry which fruits during June and July. Thus, youngsters would be weaned when preferred foods are available. Potentially, youngsters weaned during the dry season would encounter reduced food sources. There may be increased intertroop antagonism during the dry season, thus exposing infants to possible injury. Also, if crop raiding occurs during the dry season, there is increased likelihood of human predation.

KURLAND's [1973, p. 248] observations tend to support this viewpoint. He notes that flooding and windstorms may be cyclic as a result of the seasonal rains. 'If this is the case, periodic floods and wind storms might be determinants of vegetative and fruiting seasonality, and of secondary growth succession. Consequently, primate feeding strategies and even population dynamics may have evolved, in part, under such regularly occurring density-independent factors.'

<sup>9</sup> PENG *et al.* [1973] noted a mean gestation period of 167 days for 146 pregnancies.

Table V. Humidity and wind velocity<sup>1</sup>

Month	Relative humidity <sup>2</sup> , %		Wind velocity <sup>3</sup>	
	mean high	mean low	mean speed	direction
January	90	77	8.5	NE
February	90	75	8.7	ENE
March	90	75	8.3	NE
April	91	75	7.11	ENE
May	92	78	6.3	E
June	93	79	5.9	E
July	91	79	6.9	NW
August	91	78	6.5	SW
September	89	78	6.9	W
October	91	77	7.4	W
November	92	77	6.6	NE
December	91	77	7.6	ENE

<sup>1</sup> Although these data were collected on Koror, they are approximate for the situation which obtains on Angaur.

<sup>2</sup> Mean highs and lows for 1972.

<sup>3</sup> Mean speed and direction, 1972.

Comparative data on *M. fascicularis* birth peaks are found in ANGST [in press], SHIREK-ELLEFSON [1967], and FURUYA [1965]. ANGST reports that in Indonesia infants are born during the rainy season from December to May. Mating occurs during the summer months, but it is not a conspicuous behavioral pattern. SHIREK-ELLEFSON reports a bimodal birth peak among crab-eating macaques in Singapore. The first peak occurs in January and February, the second in July and August. The bimodal birth peak produces infant clusters facilitating classification into age categories. FURUYA notes that in Malaysia births occur throughout the year and suggests there is no definite birth season. There is no mention of the situation among the transplanted Kijima island animals.

Based upon rather scanty evidence, crab-eating macaques appear to have either a birth season or birth peaks [LANCASTER and LEE, 1965]. It is unclear what natural factors stimulate this phenomenon. In fact, the information appears to be contradictory; ANGST's Indonesian animals bore infants during the rainy season, and the Angaur macaques seem to give birth during the dry season. However, in all three studies reporting possible birth peaks the months of December through February occur as strong possibilities.

### Interspecific Competition

The Angaur macaque population is relatively predator-free. Our observations suggest no natural predators, and the major force limiting population growth seems to be food availability and natural calamities. We observed no instances of interspecific behavioral interaction initiated by the monkeys. Although a number of avian forms exist on the island, we have no evidence of any interactions with them.

Dogs seem not to bother the monkeys, and the monkeys simply stay out of reach. In Koror a juvenile from Angaur was agitated by the presence of a crocodile caged next to it. Although two crocodiles live on Angaur, we have no evidence that they prey upon the macaques, and feel that it is unlikely.

The major possible threat to the monkeys' existence seems to be from the human population. In terms of human harassment, however, most natives on Angaur seem to leave the monkeys alone. Since firearms and ammunition are tightly controlled, monkeys are seldom hunted. The traps set in the taro patches meet with minimal success. Some of the Coast Guard personnel occasionally hunt monkeys for sport. Overall, we estimate that human predation has a minor impact upon the current population.

When we began investigating the possibilities of working on Angaur we were repeatedly told of efforts to eradicate the monkeys. The justification was that the monkeys were eating or otherwise destroying some of the taro and tapioca plots, main food sources of the Angaurese.<sup>10</sup> We were asked to help collect data which would assist in this eradication program. Being extremely hesitant to do this, we spent time investigating reports of intense human-monkey competition for food. Our brief study concluded that there was little substance to reports of extensive cultigen damage. Interviews established that the natives had no desire to rid the island of the monkeys. Instead, there was the expressed desire to preserve them and only to prevent crop damage, which seems negligible during most of the year. Based on our findings, thoughts of an eradication program now seem to have been dropped.

<sup>10</sup> The monkeys are considered to be such pests that the export of female monkeys from the island is strictly forbidden. Nevertheless, there are confirmed reports of a few animals (males and females) living in the inaccessible forests of Babeldaob where they are predation-free. There are also reports of a few crab-eating monkeys roaming free on Pelileu, Koror, and on Guam.

## Econiche Utilization

The Angaur monkeys are primarily forest-dwelling animals which make occasional use of coastal areas and cultivated plots. Most of the inhabited forest environment is secondary forest, the total primary forest has long been destroyed. LINDBURG [personal commun.] notes that Indonesian groups were strongly oriented to riverine growth. At night they slept in riverine trees and seldom foraged more than 1,000 m from the river. Based on their study of primate distributions in Malaysia, SOUTHWICK and CADIGAN [1972] note that of 33 crab-eating groups, 12 inhabited secondary forests, 20 inhabited urban forests (parks and recreation areas in close contact with humans), and only one group inhabited primary forests. Both KURLAND [1973] and MEDWAY [1969] report that of all Southeast Asian primates, crab-eating macaques consistently and easily utilize the secondary forest. These data compare favorably with surveys conducted by MCCLURE [1964] and CHIVERS [1970]. Coupled with FURUYA's [1961/62, 1965] and SHIREK-ELLEFSON's [1967] data, it is clear that crab-eating macaques are very adaptable creatures, which seem to have an affinity for secondary and low-lying forest areas and appear to adapt well to human habitation. Crab-eating macaques seem particularly well adapted to meet the challenges of human population expansion, specifically the destruction of primary forest econiches. KURLAND [1973] notes a preference for feeding in human garbage dumps, regardless of inherent danger. On Angaur the animals have adjusted to numerous devastating destructions of the environment, and have not only survived but increased in number. Furthermore, they seem to have adjusted well to human harassment.

## Feeding and Drinking Behavior

Table VI is only a partial inventory of the Angaur macaque's diet. In the short time on Angaur we obtained a small sampling of the foods which the monkeys consumed, and therefore relied heavily upon a knowledgeable informant.<sup>11</sup> We never observed nor do we have any first-hand information suggesting that the monkeys eat crabs; however, native reports suggest they do. Furthermore, FURUYA's [1965] captive group on Kijima Island was fed crabs. Our evidence suggests that the monkeys eat primarily vegetable foods;

<sup>11</sup> Our examinations of fecal remains were limited by the dearth of fecal material. We did recognize seeds of the wild cherry (*Muntingia calabra*) or mulberry (*Morinda citrifolia*) in such remains, however.

Table VI. Angaur macaque food list<sup>1</sup>

Scientific nomen	English common nomen	Part
<i>Pandanus kororensis</i>	pandanus	stalk
<i>Saccharum officinarum</i>	sugar cane	stalk
<i>Zea mays</i>	corn	
<i>Areca catechu</i>	betel-nut palm	
<i>Cocos nucifera</i>	coconut palm	
<i>Colocasia esculenta</i>	true taro	stalk
<i>Cyrtosperma chamissonis</i>	giant taro	stalk
<i>Ananas comosus</i>	pineapple	
<i>Dracaena multiflora</i> (lily family)		
<i>Dioscorea alata</i>	true yam	
<i>Dioscorea bulbifera</i>	bitter yam	
<i>Musa</i> spp.	banana	fruit
<i>Alpinia pubiflora</i> (Zinger family)		
<i>Casuarina equisetifolia</i>	common ironwood	
<i>Artocarpus altilis</i>	breadfruit	fruit
<i>Ficus</i> spp.		
<i>Ficus microcarpa</i>	banyan	
<i>Annona muricata</i>	soursop	fruit
<i>Horsfieldia amklaal</i> (nutmeg family)		
<i>Raphanus sativus</i>	tapioca	stalk
<i>Erythrina variegata</i>	Indian coral tree	flower
<i>Inocarpus fagiferus</i>	Tahitian chestnut	nuts
<i>Ormosia calavensis</i>	necklace, bead tree	nuts
<i>Pithecellobium dulce</i>	opiuma	bear
<i>Citrus reticulata</i>	mandarin	fruit
<i>Codiaeum variegatum</i>	croton	bark
<i>Macaranga carolinensis</i>	macaranga	fruit
<i>Manihot esculenta</i>	cassava	
<i>Sapium indicum</i>		
<i>Spondias pinnata</i>	amra	fruit
<i>Salacia naumannii</i> (Hippocratea family)		fruit
<i>Nephelium lappaceum</i>	rambutan	fruit
<i>Colubrina asiatica</i> (buckthorn family)		fruit
<i>Muntingia calabra</i>	panama cherry	cherry
<i>Hibiscus rosa-sinensis</i>	red hibiscus	flower
<i>Hibiscus tiliaceus</i>	hau	flower
<i>Ceiba pentandra</i>	kapok	fruit
<i>Melochia compacta</i>	melochia	fruit
<i>Pangium edule</i>	pangi, payan	fruit
<i>Wikstroemia elliptica</i> (Akia family)		fruit
<i>Barringtonia racemosa</i> (Barringtonia family)		fruit
<i>Terminalia catappa</i>	tropical almond	nut

Table VI (continued)

Scientific nomen	English common nomen	Part consumed
<i>Eugenia javanica</i>	wax apple	fruit
<i>Eugenia</i> spp.		fruit
<i>Psidium guajava</i>	guava	fruit
<i>Polyscias nodosa</i> (Panax family)		fruit
<i>Tournefortia argentea</i>	tree heliotrope	fruit
<i>Premna obtusifolia</i> (verbena family)		fruit
<i>Ixora casei</i> (coffee family)	ixora	flower
<i>Morinda citrifolia</i>	Indian mulberry	fruit
<i>Randia cochinchinensis</i> (coffee family)		fruit
<i>Citrullis vulgaris</i>	watermelon	

<sup>1</sup> The list is a partial inventory of the Angaur macaque's diet. It was compiled from personal observations and from conversations with a knowledgeable local informant. The scientific terminology is from a key prepared by DEMEI O. OTOBED, Chief Entomologist of the Biology Laboratory, Koror.

This list presents 52 plant varieties consumed by the Angaur macaques. Where it is known (e. g. has been observed by us or reported to us) the diet consists of the fruits of 24 plants, the flowers of 4 plants, the stalks, roots, or bark of 6 plants, and the beans and/or nuts of 4 plants.

In addition to the plant foods consumed, the Angaur macaques have also been said to eat dead crabs, termites, lizards, dragon flies, and grasshoppers.

however, termites, dragonflies, and grasshoppers may also be consumed. Insect larvae attached beneath leaf surfaces were probably consumed as a by-product of eating the leaves themselves. Although numerous bee's nests and spider webs with insects trapped in them were noted, we have no recorded instances of the monkeys actually tampering with these. Our study supports KURLAND's [1973] findings that these are opportunistic omnivores who are also terminal-branch-end feeders, despite the apparent lack of specific morphological and locomotor adaptations often accompanying such feeding behavior as found, for example, in gibbons. The crab-eating macaque appears to have behaviorally adapted to this situation. It is not certain whether their feeding at the terminal ends of branches modifies tree growth as OPPENHEIMER and LANG [1969] report for *Cebus capucinus*.

The Angaur macaques live in a relatively rich food environment with trees and shrubs providing most of the food supply. Although seasonal variation in food supply is likely, unless a prolonged drought occurred, theoretical

food limitations do not seem severe. It is during the dry season that the animals apparently destroy some cultigens, especially taro (*Colocasia esculenta*) for food.

Our study suggests that the monkeys fed primarily in the forest. Although intensive surveys of the tidal pools and the beaches were conducted, no signs were located that the monkeys frequented the area for food. The only evidence of the animals' visiting the coastline is one instance of dry fecal remains on rocks overlooking a beach. The jagged coastline provides an immensely rich, easily obtainable source of ocean foods, for example crustaceans, in numerous tidal pools dotting the pock-marked limestone. Numerous coastline rock depressions offer an excellent collecting area for fresh water and might occasionally be visited for that purpose.

As should be obvious, the tidal pools are only potential food sources during low tides. Their potentiality as a food source would be limited to certain times of the months, and then only when low tide occurred during the day-light hours. If the tidal pool inhabitants form any part of the total food supply, it is most likely that this occurs during the dry season when the forest's resources are depleted. Possibly both the cultigens and the tidal pools are important as food sources only during specific times of the year, and may be only contingency food sources. It should be noted that feeding in the tidal pools potentially exposes the animals to more danger than staying within the safe confines of the forests and the trees.

Some specific notes on feeding behavior follow.

(1) The monkeys concentrated feeding on certain foods when they were in season. During the June-August period we suggest that minimally 50% of their food consisted of the fruits of the Palauan apple tree (*Eugenia*), wild cherry (*Muntingia*), or the mulberry (*Morinda*). Undoubtedly, Angaur macaques are seasonal feeders and the concentration of various seasonally fruiting plants affects their movement within the home range. We noted minimal daily movement of any of the troops. Much of the movement seemed to be correlated with travel routes to and from Palauan apple and/or cherry trees. Thus, our impressions as to home range extent, home range utilization, and movement patterns may be skewed. A similar conclusion is suggested by KURLAND's [1973] study. It is also likely that the animals have shifting core areas within the home range related to concentrations of food sources.

(2) The monkeys employed hand-to-mouth or mouth-to-food source feeding techniques, possibly determined by the type of food being eaten. The back side of the hand, and occasionally the palm, was employed to push food from the buccal pouch into the mouth [also KURLAND, 1973].

(3) We observed a number of instances of food carrying, either in the mouth or in the hand. When mouth-carried, food is often tightly compressed between the incisor teeth. We witnessed no terrestrial bipedalism in order to carry food as is quite common of rhesus macaques, for example. Most often younger animals were noticed carrying food, which may indicate some slight tension during feeding. Younger animals preferred to feed in each other's company and apart from the adults, perhaps minimizing possible dominance encounters.

(4) Overall, feeding was relatively tension-free. Dominance interactions during feeding were minimal and troop dispersion was rather wide during feeding. In fact, in all aspects of behavior recorded, feeding, resting, and travelling, the Angaur macaque groups are not tightly compressed.

(5) Angaur macaques are rather wasteful of their food sources. We were easily able to ascertain whether a troop was in an area by examining the debris beneath Palauan apple trees. (However, Angaur macaques are less wasteful than is true of langurs, for example.) When the monkeys eat apples they seem to concentrate on the outside, eating around the hollow core and spitting out the skin, often consuming only one half to three fourths of the fruit.

(6) When monkeys feed on such cultigens as potatoes, presumably these are dug or pulled from the ground. It would be interesting to see if there are troop traditions as concerns this behavior. For example, POIRIER [1969] notes that among Nilgiri langurs which regularly raid cultivated fields, animals either pull or dig the plants from the ground. Forest living langur troops were never seen to dig. When feeding on swamp taro they must enter water. Some freshly eaten taro plants were encountered in water approximately 20–25 cm deep, and certainly deeper after a torrential rain fall. Actual locomotory postures are unclear, however, evidence clearly indicates the animals entered the water to consume the plants. GAUTHIER-HION and GAUTIER [1971] report that crab-eating macaques do swim, 'doggy style', across rivers.

(7) No vocalizations seem specifically related to feeding behavior. One sound frequently heard during feeding, transcribed as 'uhmk', was a soft, throaty sound interpreted as a contact call. It may function to maintain contact between various animals spread over the feeding area.

(8) We occasionally witnessed an animal standing bipedally to swat an insect flying overhead. We also observed five instances of animals unrolling leaves and digging into bark apparently in search of insect food. On a few occasions animals were seen to unroll a leaf with their hands and then visually inspect the leaf, for insects we suspect. Animals were often observed ripping leaves off the Pandanus plant (*Pandanus kororensis*) and then either eating

the stalk of the plant or searching the area. We suspect they were searching for insects.

(9) Interestingly, juveniles and yearlings spent much time feeding on, or at least biting, leaf petioles and the bark of various trees. With both the teeth and the hands, bark is stripped from a twig. We are unable to explain why youngsters should consume a disproportionate amount of such food stuffs; however, similar observations have been made on Nilgiri langurs and the St. Kitts green monkeys [POIRIER, 1969, 1971]. Perhaps some of the bark-eating and bark-stripping was solitary play. It is also conceivable that they were sharpening their teeth, or perhaps using the rough bark in a manner similar to human children using teething rings.

(10) Much of the food which eventually ends up in the mouth is first smelled and then visually inspected. This procedure seemed to be more of a habit than an actual selective process, for we never recorded food being rejected as a result.

Apparently, most of the water supply comes from foods which the animals consumed.<sup>12</sup> We never recorded an animal directly drinking from a water source. The only recorded instance of 'drinking' was of one animal licking water from a leaf after a rain. Although animals shook off rain water in much the same manner as a dog, we never observed them licking water from their own or from another's hair.

### *Movement Patterns and Locomotor Behavior*

No specific vocalizations are associated with movement. The animals did not vocalize while travelling over the home range. We recorded no vocalizations as initiators of movement nor as contact calls during movement. We do not know which, if any, animal(s) initiate movement or which head(s) the movement. Furthermore, we were unable to discern any clues indicating movement.

The animals followed definite arboreal pathways; KURLAND's [1973] report agrees. Areas where trees overlapped, limbs cleared of leaves and other obstructions, and springy clumps of branches – all were likely candidates as travel routes. Older, solid branches seemed to be preferred travel routes. Travel over constant routes kept branches well-worn, and recognizable, which

<sup>12</sup> A similar situation is suggested by KURLAND's [1973, p.254] study. He reports the macaques '... were not seen to drink water from pools or the river'.

is highly adaptive for rapid arboreal movement.<sup>13</sup> When travelling over branches the animals usually moved in single file or two abreast. Juveniles moved in a cluster near the front or middle of the group. There is a gradual shifting process whereby one segment catches another and then moves again. Slow movement seems to occur as a gradual shift in the center of activity.

When jumping across distances, animals leap from a solid branch to clumps of younger leafy branches, areas providing a maximal amount of surface and give. Thus they reduce the probability of misjudging a leap and reducing the shock of impact. When spanning distances of approximately 2 m, or more, they jump 'spread-eagle' fashion, the arms and legs are abducted. This is particularly noticeable when approaching the landing surface. Such behavior increases friction with air currents hitting the body, slowing the trajectory rate and providing more body surface for contact with the landing point. The 'spread-eagle' position may be a means of distributing the landing impact to various parts of the body. However, when they do land the hands most often make initial contact. The propulsive force for making leaps comes primarily from hind limb and foot muscles. KURLAND [1973] mentions that they are spectacular jumpers, making leaps of 5 m or more.

The monkeys frequently drop, 'spread-eagle', from higher to lower branches. When descending from a tree they may move rather rapidly head-first. Animals were also observed to slide, buttocks-first, down a tree trunk. Short distances are often spanned with the body with an animal reaching out and grabbing adjoining branches with its hands, the feet holding to the original position. The feet then release and the animal swings forward. This is a favorite locomotor method of younger animals who seem somewhat hesitant to make the longer leaps of the adults and more experienced animals.

When moving either in the trees or on the ground the tail is horizontal to the body. Angaur macaques hold branches with their tails. When hanging by their feet, the tail may be used to hold a branch. They also seem to use the tail as a 'brake' after making leaps, e.g. after landing the tail may be wrapped about a branch. Although the Angaur macaque does not possess a prehensile tail, the tail is not simply a 'useless' appendage. KARRER [1970] reports the tail is 'quasi-prehensile'.

KURLAND [1973] reports that while foraging individuals may walk 'up-right' along a branch, holding to an overhead branch. Angaur macaques do stand bipedally to feed and occasionally to visually scan the distance, but they

were not seen locomoting bipedally. KURLAND [1973] seldom noticed terrestrial behavior, a contrast to the Angaur situation.

### *Home Range, Core Area, Intertroop Antagonism*

#### *Home Range*

KURLAND [1973] provided an estimate of approximately 1,600 by 500 m or 0.8 km<sup>2</sup> as the home range of Indonesian crab-eating macaques. ANGST [in press] reports that on Peutjang Island, where the density was exceedingly high, there are over 400 animals per km<sup>2</sup>. Monkeys were widely scattered and ANGST notes '... I often was not able to delimit a group reliably'. Like KURLAND's, based on a limited sample, our data only provide a rough estimate; however, our range size estimates fit KURLAND's material. Possibly our home range size estimates are skewed by the seasonal fruiting and local abundance of certain preferred food.

Home range sizes of various troops tended to differ, and were likely controlled by food supply and dispersion within the range, the presence of sleeping trees, proximity of adjacent troops, and other factors.

#### *Core Areas*

Definite core areas, e.g. areas of intense use, exist within the home range which were often defined by the presence of some rather tall trees with cleared limbs for travel. They were also located in areas where the forest floor was relatively open, or included large rocky outcroppings. We are uncertain of the function of such features, unless they provide a clearer visual access to possible terrestrial predators. Core areas were also centers of preferred food sources, and the forest floor was often littered with food remains. Unlike core areas associated with Nilgiri langurs and the St. Kitts green monkey, crab-eater core areas are not distinguishable by the odor of urine or feces.

We suggest that home ranges contain a number of seasonally utilized core areas. It is also likely, based on evidence of intertroop antagonism, that core areas are frequented on the basis of intertroop dominance relationships. Troops may visit some areas of the home range only when neighboring troops are absent.

#### *Intertroop Antagonism*

Considerable overlapping of home ranges on Angaur contributed to frequent intertroop relationships. Because of difficult observational conditions,

<sup>13</sup> The animals not only adapt to the environment, they modify it.

much of our evidence of such relationships is primarily based on vocalizations and of animals chasing through the trees. Apparently intertroop relationships are characterized by varying levels of aggression; however, we cannot conclude that Angaur macaques defend a territory.

Native reports indicate that captive animals, or animals from one troop, cannot successfully be introduced into a different troop. Most of our visually recorded instances of intertroop antagonism included branch-shaking demonstrations, exchanges of vocal threats, and chasing through the trees. Episodes were characteristically short, following which there was silence, and we often lost track of the animals.

SHIREK-ELLEFSON's [1967] report of intertroop antagonism suggests that there is considerable home range overlap. FURUYA's [1965] report mentions an intertroop dominance hierarchy and intertroop antagonism. However, our data do not support ANGST [1973, p. 625] who reports 'the relationship of a group to its neighbors is considered as a fading out extension of the social network, rather than a territorial intolerance'. According to ANGST's [1973] reports, the most prominent aspect of intergroup behavior is mutual tolerance. Even with considerable differences in troop dominance rankings, the subordinate troop can feed deep within the home range of the more dominant troop. ANGST partially attributes this mutual tolerance and extensive home range overlap to an adaptation to seasonally changing and often locally-abundant food supplies. A similar food situation occurs on Angaur but the results appear to be the opposite. On Angaur intertroop intolerance seems to be a fact.

ANGST's data agree with ours in some other features, however. For example, he notes considerable overlapping of home ranges. Furthermore, troops rarely incorporate members from other groups. Adjacent troops are familiar to one another, and have established intertroop dominance rankings which apparently reduce friction. Perhaps the intolerance witnessed on Angaur is due to the lack of an intertroop dominance ranking, or the lack of an historical precedence of intertroop relationships. ANGST [in press] feels that one of the features controlling intergroup reactions is '...based ultimately on the relationships of the respective central alpha-males...', and the troop's status vis-à-vis other troops is influenced by the number of males within a troop.

#### *Reactions to Various Weather Patterns*

The Angaur crab-eating macaques showed some general reactions to particular weather patterns. For example, the animals seemed to stay beneath

the leaf cover during the heat of the day with most travel occurring early in the morning and later in the afternoon. During periods of more intense heat, from 1100 to 1400 h, animals feed leisurely and apparently do most of their grooming and resting.<sup>14</sup> Rain does not seem to bother the monkeys [KURLAND, 1973, also notes this]. Whereas animals of some species tend to huddle and slow their activity during periods of heavy rain, this was not necessarily true on Angaur. Movement patterns, however, may be curtailed as there is evidence suggesting that animals moved beneath the leaf cover at the onset of rain storms. Wind tends to curtail movement. Similar observations by POIRIER [1971] for St. Kitts green monkeys have led to the suggestion that swaying branches made distance judgements difficult and the animals seem hesitant to leap through trees. Furthermore, during periods of heavy wind the auditory senses are more likely to be confused, making meetings of adjoining troops more likely.

#### *Communication Matrix*

Little comparative data exist for *M. fascicularis* communicative behavior, but for SHIREK-ELLEFSON's [1967] dissertation on visual communication. Our report presents information on some of the more common crab-eating macaque communicative behaviors; however, this brief study hardly provided enough time to compile any representative sample of the total communication repertoire.

#### *Vocal Communication (Table VII)*

Six major classes of vocalizations were recognized: the bark, vocalizations on the screech-scream continuum, guttural calls, growls, a high-pitched chirp warning vocalization continuum, and panting vocalizations. We also recorded four sounds of undetermined significance. Subjectively, e.g. based on our previous studies of rhesus and pigtail macaques, the Angaur macaque's vocal repertoire sounds familiar.

One of the difficulties of dealing with the crab-eating macaque vocal system is the intergradation of the sound system. KURLAND [1973, p. 259]

<sup>14</sup> KURLAND [1973] notes that the smallest number of groups was seen near midday when the sun was most intense. The largest number of groups was seen in the mid-afternoon on an overcast day, or in the evening. KURLAND concludes that climatological conditions may affect the number of groups seen at different times during the day. SHIREK-ELLEFSON [1967] reports a bimodal activity peak which may be associated with daily temperature fluctuations.

Table VII. Production of vocalizations

Vocalization	Specifics of production
Bark vocalizations	Short staccato sounds. The mouth is variously opened (one fourth to one half), the teeth are usually not visible. Sounds are produced with a rapid opening and closing of the mouth. The eyes may be closed and the vocalization accompanied by a slight throwing back of the head. During vocalization there is marked extension and retraction of the stomach muscles as air is forcefully expelled. Sounds classified as barks carry long distances and are difficult to use to localize the vocalizing animals. As tension increases, barks become higher pitched. Bark vocalizations are primarily threat and warning vocals.
Screech/scream vocalizations	High-pitched sounds. Produced with the mouth approximately three fourths open. The teeth may be visible. The mouth rapidly opens and closes during the vocalization. The lips may be retracted over the teeth, especially during extreme tension. Such vocalizations often accompany dominance interactions and moments of high tension.
Guttural calls	Low-pitched vocalizations which seem to be made deep in the throat and produced with a rapid opening and closing of the mouth. The mouth is usually about one fourth open, the lips are slightly retracted. We could not determine the function of such calls.
Growl vocalization	Harsh, gruff, deep sound. Approximating the noise often made when clearing the throat. The significance of the call was not determined; however, it seems to be associated with dominance interactions and tension.
Pant vocalization	We often transcribed this vocal as 'ha-ha'. The sound is produced with a rapid expulsion of air through somewhat rounded lips. The mouth is usually about half open. The vocalization is a series of rapid sounds. The resulting sounds are modulated and staccato. The pant is associated with dominance interactions and threat behavior.
Rolling chirp continuum	This continuum of vocalizations contained a number of inter-related vocalizations distinguishable from one another by the pitch of the sound. The lowest sounds on the continuum were transcribed as 'uhmk', the highest pitched as the rolling chirp. The 'uhmk' sound seems merely to be the first frame of the rolling chirp. However, it seems to have a social meaning of its own. The 'uhmk' sound is made with the mouth open and the tongue protruded. The sound is a staccato expulsion, but not harsh and is rather low-pitched. The rolling chirp is a repeated high-pitched sound produced with the mouth one

Table VII (continued)

Vocalization	Specifics of Production
	fourth open, the tongue slightly protruding and no teeth showing. The sound is high-pitched enough that it might be misinterpreted as a bird call. A slight backward tilt of the head often accompanies the rolling chirp. The 'uhmk' is given on mild excitement, the rolling chirp expresses extreme tension. The one-frame chirp is a variation of the rolling chirp.
<i>Unclassified vocalizations</i>	
Cooing sound	A throaty sound which may function as a greeting call as the animals regroup after the spread during feeding or moving.
Hollow sound	This is a low-pitched, staccato expulsion of air produced deep in the throat. It appears to be given by a subordinate animal.
Purr	A soft, low-pitched sound which might be a mild form of vocal threat, often directed towards us.
'Wak-wak'	This is a short, throaty sound which may be associated with sexual behavior. One of the authors (SMITH) feels the sound is similar to the vocalization which pigtail macaque females emit during copulation.

notes 'Kra macaques seemed to use both highly discrete calls, like the "kra", but also used a graded series of vocalizations'. The intensity (e.g. pitch, volume) of the sound across the continuum seems to determine reactions. Sounds at different ends of the spectrum are distinguishable according to context, as well as by the intrinsic qualities of the vocalizations. The 'rolling chirp continuum' offers an example of three distinguishable vocals on a continuum: the 'uhmk', the threat/warning bark (which KURLAND [1973] apparently labels the 'kra' or alarm contact call), and the rolling chirp, simply represent various states of tension.

Other general characteristics of the vocal repertoire follow. Some vocalizations, especially warning calls, are difficult to pinpoint which may be an adaptation against predation. Since it is difficult to locate the vocalizing animal, it is a rather safe mode of warning others of possible danger. We have no evidence that certain vocalizations are confined to any age/sex class. However, it is very likely that certain calls are restricted to an infant and its mother, and that the adults' vocal repertoire is larger, or different, than that of younger animals. One of the characteristics of the Angaur macaque's behavior during vocalizing is the occurrence of displacement activities such as feeding, self-grooming and scratching.

SHIREK-ELLEFSON [1967] describes a roar vocalization accompanying the open mouth threat. We were unable to confirm this vocalization and accompanying threat pattern. She also describes a staccato-grunt vocalization for which we have no comparative data. The scream threat which SHIREK-ELLEFSON describes as part of the submissive communicative repertoire was witnessed in our study. Finally, SHIREK-ELLEFSON describes a screech vocalization as a component of the submissive grimace facial expression. We can describe a comparable vocalization on Angaur.

#### *The Nonvocal Communication System*

The key elements of the visual, gestural, and postural communication matrix are presented in tables VIII and IX. Admittedly, our study falls short of defining a representative sample of the communication matrix. But then, we do not know what the representative visual communication system would include, for there are little comparative data. As with the vocal system, one of the traits marking the crab-eating macaque's visual communicative system is the intergradation of signals. SHIREK-ELLEFSON [1972, p. 300] notes: 'In crab-eating macaques... all the facial expressions, but one (open-mouth threat) merge into at least one other facial expression. There is a continuum of facial expressions expressing a continuum of motivational states.'

Our study discerned 17 signals in the nonvocal communicative system. Of this number, 9 signals were associated with dominance or threat behavior, 5 were associated with submission or submissive behavior, and 3 were signals of ambivalence. The messages of ambivalence could also function to signal threat or submission. As noted by ANGST [in press] and SHIREK-ELLEFSON [1967, 1972], and is true of most other nonhuman primates, there is a continual combining of vocal and nonvocal cues. This is dependent upon the stimulus and the tension inherent in the situation, as well as the particular animals involved.

SHIREK-ELLEFSON [1967] describes dominance communication among *M. fascicularis* as a multi-threat system. Open-mouth threats maintain the dominance hierarchy and are a conservative force maintaining order. Scream threats permit lower ranking animals to express hostility against higher ranking animals, and the white-pout threat (not seen on Angaur) allows animals of unsettled rank to establish dominance without committing themselves to a dominant position. SHIREK-ELLEFSON [1967, p. 107] notes: 'The three threat system allows aggression to be expressed down, up and across the dominance hierarchy and at the same time reinforces the order of the hierarchy.'

Table VIII. Specifics of nonvocal communication among Angaur crab-eating macaques

Signal	Mode of accomplishment
<i>Dominance and/or threat signals</i>	
Eyelid threat	Rapid eye opening and closing, exposure of lightly colored upper eyelid. Often a close-up threat. A one-to-one signal.
Stare threat	Given facing the object of the threat. The threatening animal fully orients visually on the object. The head may be slightly inclined producing a slight raising of the back. The animal being threatened turns or moves away. A one-to-one signal, which is an intensification of the bark threat.
Open mouth threat	The animal doing the threatening visually orients upon and faces the threatened animal. The mouth is elliptically opened approximately one half, the tips of the teeth may be seen. The head may be tilted slightly back as the mouth opens. A vocal pant may accompany the threat. A one-to-one signal.
Head bob threat	The signaller stares at the threatened animal and opens its mouth slightly. The head is slowly tilted back and forth. The mouth may be opened slightly. The rapid bobbing of the head produces a visual affect. Usually given from static standing position. In more intense situations this signal may be combined with the pant vocalization. The threatened animal moves off or otherwise subordinates itself. A one-to-one signal.
Branch shaking	When given by a young animal (juvenile) it signals intent to play or bravado. Older animals may do so during a dominance interaction and it seems to indicate a high emotional state. May be done by holding a branch or vine and shaking it with the hands, or by jumping up and down with all fours on a branch. ANGST refers to this as a 'dominance display'. One branch-shaking animal may trigger branch shaking from others. It may be a one-to-one or one-to-many signal.
Mounting	Among younger animals this signal is not a consistent dominance message and is often done as play behavior. When the signal is issued in dominance, the dominant animal covers the back of the subordinate and either grasps the ankles with its feet, or keeps the feet on the ground. Pelvic thrusts may not occur. Sometimes the 'mount' is accomplished when the dominant simply sits and touches the buttocks or back of the subordinate animal. This is a one-to-one signal.
Displacement	Approaching another animal who moves away. Crab-eating macaques do recognize dominance distances, the radius of which are dependent upon one's social rank. These distances are obviated during grooming and play. Displacement is a one-to-one signal.

Table VIII (continued)

Signal	Mode of accomplishment
Lunging at or slapping branch	The signaller lunges forward and slaps a branch with one or both hands. This may be accomplished while either standing or sitting and may be accompanied by other vocal and/or nonvocal cues. A one-to-one or one-to-many signal.
Anal and/or genital inspection	The dominant animal visually and/or olfactorily inspects the genitalia or anus of the subordinate animal who has presented. A one-to-one signal.
<i>Submissive signals</i>	
Presenting	The signaller presents its buttocks, or side to the dominant animal. The tail may be raised to present the buttocks. The dominant animal may turn or look away, or touch the subordinate animal. The subordinate animal may also be mounted. A one-to-one signal.
Looking or turning away	Usually a response to a stare or look threat. The subordinate animal simply looks or turns away, eventually it gets up and moves off. A one-to-one signal.
Being displaced	The subordinate animal gets up and moves off. Occasionally, the animal being displaced will lip-smack or present before moving. A one-to-one or one-to-many signal.
Being mounted	The mounted animal may lip-smack, face the mounting animal, or reach back and touch the mounting animal. A one-to-one signal.
Grimace	The mouth is slightly open, with corners retracted. The lips are tense and the tips of most of the teeth are exposed. The head is often lifted slightly, the eyes are directed towards and then away from the receiver. The ears are retracted and the body may be crouching. Often accompanied by a scream or screech. The signaller usually moves away. The animal signalling is visibly tense. A one-to-one signal.
<i>Ambivalence</i>	
Yawn	Signals slight threat and uneasiness. The head is thrown back, the mouth is opened slowly and the teeth and tongue are visible. The animal may sit or stand. Often done several times in rapid succession. A one-to-one or one-to-many signal.
Grin	Signals slight tension. Observed once during copulation by a female to a male, and to the observer. The mouth is more opened than during the grimace, about half open, the teeth tips are visible. The signaller faces the recipient. A one-to-one signal.

Table VIII (continued)

Signal	Mode of accomplishment
Lip-smacking	The lips open and close rapidly producing a low sound. The animal usually faces the receiver. Depending upon the intensity of the situation, the ears may be drawn back and the body slightly crouching. The tongue may move in and out of the mouth. Sometimes accompanies other signals, e.g. grimacing. May be accompanied by vocalizations. A one-to-one or one-to-many signal. Also a submissive act.

SHIREK-ELLEFSON [1967] compared her data with those on *M. radiata* [SIMONDS, 1963], *M. mulatta* [HINDE and ROWELL, 1962] and with VAN HOOFF's [1962] summary for several macaque species. All signal emotional states in a similar manner. Two major differences appear to be in the expression of unsettled dominance rank and in signalling social attraction. In the first instance, crab-eaters white-pout threat, bonnet macaques jaw threat, and rhesus show the hindquarters. In the second instance, crab-eaters show the pucker face, bonnets possibly jaw, and rhesus chew and gnash their teeth.

We agree with SHIREK-ELLEFSON's [1967] contention that crab-eaters have a multi-faceted threat system (tables VII, VIII). However, our data and hers record different signals in this system. For example, we observed nothing analogous to the white-pout threat or stalking, which may be analogous to what ANGST [in press] labels strutting. Neither ANGST [in press] nor SHIREK-ELLEFSON [1967], on the other hand, mention eyelid threats (although what SHIREK-ELLEFSON [1967] calls flashing whites may be similar), the stare threat, the head-bob threat or anal and/or genital inspection. Since 'inspection' is a rather unusual pattern, two examples are presented below. Both occurred among young animals.

(August 1, 1625 h) A yearling carries a leaf in its hand and then sits. It strips off the bark with its teeth and hands and commences to chew the stalk. Another yearling approaches, comes over and pulls at the leaf, then it lowers its head into the other's crotch. They then run off and play.

(August 2, 0928 h) A juvenile moves towards another who is displaced. The animal which is displaced stands and presents. The animal doing the displacing seems to smell and visually inspect the anal region for a moment. It then touches the anal region with one or two strokes of cursory grooming. Then they both move off.

Perhaps 'inspection' signals ambivalence and is used between animals of unestablished dominance positions. 'Inspection' may replace mounting in

Table IX. Visual communication in *Macaca fascicularis*

Signal	Situation and meaning
<i>Author: ANGST</i>	
Spreading of the ears and opening of the mouth	threat
Mounting	dominance
'Dominance displays' – strutting with tail up, branch shaking	dominance
Grimace	submission
White-pout face	uncertain meaning
<i>Author: SHIREK-ELLEFSON</i>	
Lunging or slapping at	dominance
Stalking	dominance – perhaps analogous to ANGST's strutting
Open mouth threat	dominance
White-pout threat	dominance
Grimace	submission
Lip-smacking	variable – depending upon the context
Play face	social attraction
Pucker face	social attraction
Flashing whites	social attraction
Embrace	social attraction

The pucker face, flashing whites, and the embrace all seem to function as signals for social attraction, to bring animals together for friendly contact.

some situations, for it occurs in situations in which mounting could occur. Our impression is that the animal 'inspecting' is the most dominant.

Similar 'inspection' behaviors have been reported among colobines [JAY, 1965; POIRIER, 1970]. Female chacma baboons often greet one another by placing a hand beneath the groin or by lowering the head to a subordinate's pelvic region [HALL, 1963]. Observations on a laboratory colony of *M. niger* [POIRIER, 1964] revealed two analogous patterns, penis manipulation and rump fingering. Both were rare and indicated mild dominance. Interestingly, they only occurred among young juveniles. Among Celebes, rump fingering substituted for mounting. Visual genital inspection also occurs among St. Kitts green monkeys [POIRIER, 1971].

The 'inspection' behavior witnessed on Angaur may be part of a greeting

Table IX. (continued)

Signal	Situation and meaning
<i>This study</i>	
Eyelid threat	mild threat
Stare threat	mild threat
Open mouth threat	mild threat
Head bob threat	mild threat
Branch shaking	can be mild threat
Mounting	dominance
Displacing another animal	dominance
Lunging or slapping at	dominance
Anal or genital inspection	submission
Presenting	mild submission
Looking or turning away	mild submission
Being displaced	mild submission
Being mounted	submission
Grimace	intense submission
Yawn	ambivalence, threat
Grin	ambivalence, submission
Lip-smacking	ambivalence, submission

This study did not witness the following mentioned by ANGST [in press]: strutting or the white-pout face, nor the following witnessed by SHIREK-ELLEFSON [1967]: stalking, white-pout threat, play face, pucker face, or flashing whites. This study noted the following two patterns not witnessed by ANGST or SHIREK-ELLEFSON: head bob threat and anal and/or genital inspection. It is quite possible that what we list as the eyelid threat is analogous to SHIREK-ELLEFSON's flashing whites.

behavior, as suggested by HALL [1963] for the chacma baboons. CARPENTER [1940, p. 136] also reports 'that one part of the greeting responses which occur among gibbons almost invariably involves visual, olfactory, and tactile inspection of the genitalia'.

As noted, we did not observe the white-pout face. ANGST [in press] feels the meaning of this signal, which he calls 'hetzen', is unclear. SHIREK-ELLEFSON [1967] contends the white-pout face is a threat gesture given by animals of different age/sex categories. It is most often given by females and juveniles. The white-pout threat is rarely given between troop members who are very distant in dominance status, and occurs when troop members are either rather close in dominance or whose dominance relationship is unstable. These threats occurred during drawn out encounters and served to bring other troop

members to the aid of the threatening animal. The other troop members also emitted the white-pout threat. What SHIREK-ELLEFSON calls a pucker face occurred in similar contexts and morphologically resembled white-pout faces.

ANGST [in press] describes 'dominance displays' consisting of strutting [= stalking of SHIREK-ELLEFSON, 1967] and branch shaking. Both occurred when a dominant animal walked rigidly with its tail flipped over the head. We did not witness stalking or strutting; however, we agree that branch shaking may occur as part of a 'dominance display'. Table IX presents a comparison of the visual communicatory behavior of *M. fascicularis*.

### Social Behavior

#### Grooming Behavior

Because of its duration and the many observational difficulties, this study collected limited analyzable data concerning such common social behavior patterns as play, grooming, and dominance. We concur with KURLAND [1973] that allogrooming (social grooming) is rare and that auto- or self-grooming is more frequent. KURLAND reports no social grooming bouts among riverine groups, and only scant social grooming in other groups. All four cases of social grooming occurred in the afternoon (1200–1600 h). Self-grooming occurred at the rate of one episode per hour of observation. 35% of the self-grooming occurred after the animals spotted the observer, which may represent a displacement activity.

Angaur crab-eating macaques groomed in much the same manner as other primates. The hands and the mouth, separately or in conjunction, pick through the hair. When the hands are used, the thumb and forefinger pick through the hair. Whatever is picked from the hair is visually and/or olfactorily inspected and much of the material is placed in the mouth. Targets for social grooming include the head, neck, the mouth and the back. In addition to social grooming, there is considerable self-grooming and scratching. We agree with KURLAND [1973] that much of the self-grooming and scratching may be forms of displacement activity.

On Angaur, grooming was performed by all age classes, from yearlings to adults. Social grooming is often reciprocal, with the roles of groomer and groomee rotating. Where we determined dominance, i.e. in bouts involving juveniles and adults, dominant animals (the older animal) were groomed longest. Cursory grooming is often a means whereby one animal elicits grooming from another. Cursory grooming also may be a means of dissolving dominance differences. Grooming was also elicited by presenting to another

animal and by stare-threatening, in which grooming obviated a possible threat or attack.

The groomed animal was relaxed, the grooming animal intent. The groomee either sat or lay on its stomach and often shifted positions during the bout, presenting various parts of its body for inspection and grooming. Not enough grooming events were witnessed to establish their place in the daily activity cycle. However, it is our impression that much of the grooming occurred later in the morning and early in the afternoon during the rest periods, after the animals had completed the morning feeding and much of the daily travel. Grooming frequently occurred under the leaf cover, creating an observational difficulty.

In sharp contrast to what we observed among other macaques, i.e. rhesus, bonnet, and pig-tail macaques, the crab-eaters on Angaur partook in minimal social grooming behavior. Whether this is a valid observation or due to poor observational conditions, we cannot ascertain. However, the long grooming bouts and grooming clusters characteristic of other macaques were not witnessed, even on days when we were in close and prolonged contact. As ROSENBLUM *et al.* [1964, 1966] have noted, there are differences in amount of tactile contact among various macaques. Crab-eating macaques may be one of the species in which prolonged physical contact is not characteristic of social behavior.

#### Dominance Behavior

We observed few complete dominance sequences. Most of our recordings are truncated sequences of vocal exchanges. A dominance hierarchy does exist, however, we can say nothing of its stability nor its ontogeny. Older animals dominate younger ones, adult males dominate adult females, and the dominance order among juveniles seems to be based upon relative size. Unlike the situation among bonnet and rhesus macaques, coalitions in dominance are infrequent. Furthermore, the sequences we witnessed to completion involved only two interacting animals and were relatively short. When chasing occurred, other animals were not necessarily drawn into the altercation, as occurs among rhesus and bonnet macaques. Most dominance interactions involved an exchange of visual cues. The following example is somewhat atypical, as it involves a coalition of an adult male with two juveniles against a third juvenile.

(August 17, 0827 h) 'One Eye' (an adult male of the Lighthouse group) and two juveniles sitting nearby threaten a third juvenile. The threatened juvenile screeches very loudly. A grimace accompanies the vocalization. The threat involves eyelid flashing and staring. One of the threatening juveniles then begins to groom 'One Eye'. 'One Eye' sits and is groomed

on his back and neck. Then he lays down and is groomed on his stomach. Before moving away, he presents to the juvenile groomer.

It is our opinion that many, and perhaps most, dominance interactions are accomplished using subtle visual, postural, and gestural cues. Vocalizations are emitted during more intense dominance sequences or when the dominance distance between animals is great.

SHIREK-ELLEFSON [1967] notes that among the Singapore Botanic Garden animals, males were arranged in a rigid dominance hierarchy, and no reversals in dominance occurred during her 6-month study. SHIREK-ELLEFSON [1967, p.38] feels that a youngster's ultimate dominance position is related to its mother's rank in the hierarchy. 'Individual personality and strength also contribute to dominance position, but the original attitudes and behaviors are developed within the limits of the mother's dominance abilities.'

ANGST [in press] notes that dominance hierarchies of Indonesian crab-eating macaques are linear, and age-influenced. 'Probably when approaching 20 years the males start to get senile and thus drop in the dominance hierarchy.' ANGST also reports a relationship between dominance position and kinship affiliation: '...high ranking kinship is correlated with a rise in rank over older males...' Apparently the influence of kinship on status is stronger for females than males. 'All adult females of one genealogy tend to have the same status in relation to other genealogies.' The members of a genealogy are equals, and dominance among them is functionally less important than among members of different genealogies. Dominance rankings among male juveniles and infants are generally linear and age-correlated. Although a young male tends to reach its mother's rank, when males approach adulthood they tend to overtake all the females. The alpha male mounts females more frequently than other lower-ranking males. In time subordinate animals tend to become peripheral.

ANGST notes some interesting relationships among females in the dominance hierarchy. Data from his Basel Zoo observations suggest that very old, sterile females become somewhat peripheral. On the other hand, low-ranking females with black babies (natal coat infants) become more central than females without infants. Apparently females are attracted to mothers with small infants; a black infant affords access to the central part of the troop. Furthermore, carrying a black infant inhibits aggression, and to some extent allows subordinate females access to the central part of the troop.

#### *Play Behavior*

Play behavior was infrequently recorded. Crab-eating macaques involve themselves in social and self-play. Although most play behavior occurs be-

tween infants and juveniles, we recorded some brief play wrestling bouts between juveniles and adults. Invitations for social play involved general animation of behavior, i.e. gamboling, hanging from a branch and kicking the feet, patting at leaves, running past another with a leaf or twig in one's mouth, and jumping up and down on a branch. Juveniles would branch-shake, apparently signalling a playful mood, and other juveniles would run to the branch-shaking animal and play would begin. We never witnessed a play face as recorded by KURLAND [1973] and SHIREK-ELLEFSON [1967].

Social play commonly involved wrestling, chasing, and jumping through the trees, slapping at one another, and competing for a leaf or stick. Social play occurred either in pairs or in groups of 4-6 animals. Most play occurred in the later morning and early afternoon, that is, after the rather intense feeding and moving period. Older animals were tolerant of playful animals in their midst. Indeed, as we mentioned, older animals sometimes engaged in brief play sequences. Most forms of self-play or solitary play involve patting at leaves, rolling about a branch on one's back and stomach and jumping back and forth between branches. Not infrequently, self-play incited social play. In fact, one function of self-play may be an invitation for social play to any animals in the vicinity.

KURLAND [1973] reports that periods of play among immatures and infants were observed in the morning and late afternoon. Play bouts lasted from a few minutes to 20 min or more. Playing animals exhibited relaxed open-mouth faces, loping and gamboling locomotor patterns, rough-and-tumble activity, and chasing. SHIREK-ELLEFSON [1967, p. 38] notes that adult males often play with juveniles, especially older juveniles. 'One juvenile I male, Sidney, was particularly attractive to the adult males, and was sought out, carried around, and sometimes stolen from a larger play group to be played with alone.'

Adult play in crab-eating males agrees with SIMONDS [1965] data for adult bonnet macaque males. It would be most interesting to study the socializing role of play behavior in these two species. Youngsters who play with adult males might rise faster and farther in the dominance hierarchy than 'non-attractive youngsters'. In fact, SHIREK-ELLEFSON [1967, p. 38] notes that adult males backed up the attractive Sidney in agonistic interaction. Thus, Sidney was establishing a highly dominant position among his peers. 'Sidney's mother ranked 21 out of 22 females, and yet her son was apparently on his way to becoming a highly dominant member of the troop.'

Table X. Comparative overview of major points discussed

*Physical appearance*

The reports suggest some morphological variation in the crab-eating macaque gene pool. The Angaur animals compare most favorably with animals in Indonesia.

*Adaptability*

All the studies agree that these are very adaptable animals who seem to fare well when in contact with humans. They appear to adjust well under the pressure of human destruction of the econiche. Crab-eating macaques appear to favor secondary forest growth.

*Daily cycle*

When this is mentioned, there is agreement that there are daily activity cycles which may be tied to temperature fluctuations.

*Observability*

All observers agree that crab-eating macaques are difficult to observe and that they generally require a long habituation period. Their forest-dwelling habits make them difficult subjects.

*Vigilance behavior*

Most studies agree that this is a male function. However, our study and that by FURUYA suggest the possibility of adult females playing a control role. We also suggest a control role for juveniles within the juvenile subgroup.

*Group size*

Group sizes seem to vary widely. The minimum size is reported by KURT and SINGA to be six animals. Within the ranges for group size, most studies report a figure of 30. The mean and modal sizes vary. Multi-male groups are reported by all the observers. Only this study and KURLAND's report juvenile subgroups. ANGST, FURUYA, and this study mention peripheral and/or solitary animals. FURUYA discusses the process of peripheralization on Kijima Island.

*Sexual Behavior*<sup>15</sup>

We recorded only a few instances of sexual behavior, and these were unclear. On 30 July we witnessed a juvenile briefly stroking its penis, but this may not be evidence of sexual behavior *per se*. On 8 August we witnessed a brief mounting with intromission and 8–10 pelvic thrusts between a male and female in the lighthouse group. The male faced the observer and showed a grin face throughout the sequence. (The grin face is signalled in a somewhat ambivalent situation.) This male and female were considered to be in a consort relationship. On 9 August we recorded a vocalization which SMITH [1973] feels may be analogous to the vocalization emitted by pig-tail macaque females during copulatory behavior. On 13 August this same female picked a whitish substance, possibly ejaculate, from her thigh and genital region.

<sup>15</sup> One of the problems of recognizing sexual behavior is the lack of physical evidence of estrous.

Table X. (continued)

*Birth peaks*

The only studies mentioning the existence of birth peaks are those by ANGST, SHIREK-ELLEFSON and the present authors. The months vary and the times seem to be at odds. There appears to be a bimodal peak. Sexual behavior is not a common component of social behavior, or at least is infrequently witnessed.

*Feeding habits*

Crab-eating macaques are vegetarians or they may best be described as opportunistic omnivores.

*Home range, core areas, intertroop antagonism*

Our data on the size of troop home ranges compare favorably with those of KURLAND. Intertroop antagonism is suggested by our report, SHIREK-ELLEFSON, and FURUYA. Both ANGST and FURUYA reject the notion of territoriality, our data are unclear on this point. There appears to be considerable overlapping of home ranges.

*Social behavior*

Because of the lack of data, there is a difficulty in trying to compare communicative behavior from troops in different locales. There is agreement, however, that these animals possess a specific alarm call, which KURLAND labels the 'kra'. The communication matrix appears to possess a considerable amount of intergradation.

Grooming does not appear to be as frequent a pattern as is common to rhesus macaques. KURLAND and this report witnessed minimal amounts of grooming behavior, but this may be due to observational difficulties. Sexual behavior is infrequent; however, ANGST, FURUYA, SHIREK-ELLEFSON, and this study report consort relationships.

Near the end of our study (early August) the animals seemed considerably more alarmed by our presence, and frequently fled. A rise in intergroup dominance was also noted, evidenced particularly by a sharp increase in submissive vocalizations. Furthermore, the animals began to extend their home range. Though merely suggestive, these data buttress our impression that we were witnessing the beginning of the breeding season. This would fit with ANGST's [in press] suggestion that crab-eating macaques mate during the summer months. Furthermore, as he notes, mating is inconspicuous and infrequently witnessed.

*Consort Behavior*

There is good evidence that crab-eating macaques establish consort relationships. As early as July 2 we noted the possibility that the most conspicuous male and female of the lighthouse group were in a consort relation-

ship. The male followed the female; they were very often in close proximity. This particular relationship continued throughout the study. And, as we noted, we witnessed the male mounting the female once during the study. The only other mention of consort relationships is found in ANGST's [in press] study. He notes 'I also exclude data on males having consorts. After all the data are scant and thus conclusions must be made cautiously.' But, he continues that consort relationships can be observed throughout the year, both in the wild and in the zoo. Consort relationships do not seem to affect the female's status.

### Control Role

The importance of the control role among nonhuman primates has been noted by a number of authors [BERNSTEIN, 1964, 1966, 1969, 1970; DEVORE and HALL, 1965; GARTLAN, 1968; SCHALLER, 1965; SMITH, 1973]. In at least one troop (lighthouse) on Angaur, the control role was played by an adult female. Throughout the entire course of our study she demonstrated many behaviors traditionally assigned to the control role. This bears out BERNSTEIN's [1970] contention that this role can be performed by a female.

KURLAND [1973, p. 257] notes the expression of the vigilance role or 'control role' among Bornean crab-eaters. He suggests, however, that this was a male role, '... 10 cases could be seen and all were calls of the adult male. However, in only four of these was I sure that it was the same adult male.' ANGST [in press] notes: 'In crab-eaters... we find the highest concentration of roles in the central alpha-male, as e.g. the social control role, leader role and group protection role.' Among the Basel Zoo group the alpha male utters the alarming calls more frequently than any other animal. Only FURUYA [1965, p. 312] reports the possibility of a female playing the control role. 'In other words, in this troop an active female in the peripheral part Ten played the role of the young adult male of the peripheral part in the natural troop.' FURUYA refers to the fact that this female would watch and threaten the observer.

### Summary

This article discusses the results of 75.30 h of observation of an exotic crab-eating macaque population living on Angaur, Palau, Micronesia. The present population may be descendent from a single pair of monkeys introduced in the early 1900's. These animals have survived a number of natural calamities and have increased in number. We estimate a total population of approximately 600 animals. Angaur macaques would make interesting subjects in a genetic study of microevolutionary change.

A major goal of the present study was to confirm the existence of animals on Angaur and to ascertain population density and the feasibility of longer behavioral studies. The Angaur monkeys could and should be the focal point of a longer study. Preliminary data suggest some differences between animals on Angaur and crab-eating macaques living in Malaysia and Indonesia (table IX). Overall, however, our brief study indicates that the Angaur macaques behave similarly to crab-eating macaques in other areas of the world.

### Acknowledgements

We would like to thank the following for their help and encouragement. A colleague, Dr. D. HUGHES, first brought the island and its monkeys to our attention. We should like to thank Fr. T. McGRATH, S.J., then of the University of Guam, for all his help in making the requisite contacts and in obtaining permission to enter the Trust Territories. For help on Koror and Angaur we thank Mr. R. OWENS, Head of the Biology Laboratory, Koror, and Fr. F. YOACH, S.J., of the Catholic Mission, Koror. Fr. J. BIZKARRA, S.J., helped us on Angaur as did Mr. S. TELEI who helped locate the monkeys. We also thank Mr. D. MOORE and Mr. W. REYNOLDS, then of the US Coast Guard. Ms F. SABURO's encouragement and friendship were valued. The principal investigator's wife and two children were instrumental in handling daily matters and for maintaining the all-important contacts with the Angaurese.

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