JEFFERY W. FROEHLICH, M. A. SCHILLACI, L. JONES-ENGEL, D. J. FROEHLICH, B. PULLEN

A SULAWESI BEACHHEAD BY LONGTAIL MONKEYS (*MACACA FASCICULARIS*) ON KABAENA ISLAND, INDONESIA

ABSTRACT: *The Island of Sulawesi in Indonesia, located east of Borneo on Wallace's Line of faunal separation, is notable for the presence of eight distinct species of macaques. This represents 40% of the species diversity in the genus Macaca in less than 2% of its historical range, roughly half the size of California. These monkeys were derived from two separate, overseas migration events by a pigtail macaque (*M. nemestrina*) ancestor beginning about one million years ago. Almost everywhere else in Indonesia, and also in the Philippines, the longtailed monkey (*M. fascicularis*) now predominates. Despite this recent history of successful dispersion, there is no record of feral populations of longtail monkeys on the Island of Sulawesi.*

An exception to this exclusion is the small volcanic Island of Kabaena, off the southwest coast of Southeast Sulawesi, where there apparently are no recent records of M. brunescens, *the very short-tailed monkey that occupies the adjacent two islands, Muna and Buton. Thirteen of the Kabaena animals were measured in 2002. Because most of these pets were juveniles, growth regression lines were used to compare them with a wild-shot sample of longtailed macaques in Thailand. In comparison with this natural population, the Kabaena females are markedly dwarfed, but the males appear to have an accelerated growth trajectory that predicts an unexpected greater degree of sexual dimorphism on this small island than in continental Thailand. For whatever reason, this remarkable adaptation implies that the longtail monkeys have resided on the island for some time. Data on ranging patterns suggest that the longtailed monkeys only occupy coastal mangrove swamps and gallery forests to an elevation of about 200m. This leaves more than 75% of the island for the anticipated presence of* M. brunescens, *but informants noted that they had not been seen for at least 50 years. There are four hypotheses for this apparent, island-wide competitive exclusion of Sulawesi monkeys from Kabaena. Possibly, they were never present on Kabaena, though the shelf of Sulawesi must have absorbed Kabaena, as it did Muna and Buton, during Pleistocene sea level regressions. Secondly, they may have been extirpated by human habitat degradation, as much of the island has secondary grasslands and tall stands of bamboo, but the longtails would seem to be more susceptible to these anthropogenic factors than animals in the interior forested valleys, surrounded by peaks up to 1500m. Thirdly, they may have lost out to the dwarfing and increased reproductive capacity of the longtails, presumably excluding them from some essential resource, but this seems unlikely in the relatively small area occupied by the longtails.*

Finally, they may have suffered from an epidemic spread by the arrival of the longtail monkeys, or one the longtails were already immune to in the human hosts that introduced them to Kabaena. Much like the colonization of the Americas since Columbus, this disease could spread throughout the island, and may still endanger the rest of Sulawesi. Reciprocally, however, competitive exclusion by diseases endemic in Sulawesi monkeys might be a hypothetical mechanism to explain why Kabaena is the only beachhead for longtail monkeys in Sulawesi, almost surrounded as it is by natural populations of these ubiquitous and highly successful monkeys throughout most of Indonesia.

KEY WORDS: Macaques – Competitive exclusion – Island biogeography – Dwarfing – Disease epidemics

INTRODUCTION

The Sunda Shelf of Indonesia is remarkable because it demarcates the edge of Southeast Asia, a line that bears Alfred Wallace's (1890) name as he first noted the separation of Australian fauna in 1856 on the island of Lombok, just east of Bali. The Island of Sulawesi sits on the equator east of Borneo, across the deep Makassar Strait and Wallace's Line. Sulawesi is all the more remarkable since the fauna is comprised of a high proportion of endemic placental mammals (Musser 1987), including a great species diversity of almost tailless monkeys. Most remarkable of all, these eight purported macaque species *(see Figure1)* amount to about 40% of the diversity in the genus *Macaca* in less than 2% of its modern geographical range, rivaling Darwin's Galapagos finches for the study of speciation mechanisms (Froehlich *et al.* 1998).

Derived from a common ancestor with pig-tailed macaques (*M. nemestrina*) about one million years ago (Cronin *et al.* 1980, Delson 1980, Morales, Melnick 1998), recent evidence suggests that the Sulawesi monkeys may actually have dispersed twice across the Makassar Strait (Takenaka *et al.* 1987, Evans *et al.* 1999). The species (*M. hecki*) at the base of the northern peninsula appears to have arrived intrusively after its neighbouring species (*M. tonkeana, M. nigra*) had already diverged from a previous overseas migrant (Froehlich *et al.* 1996). The Sulawesi monkeys vary in basic colour from gray to brown to black, with contrasting beige or white often decorating the cheeks and backsides, and sometimes with lighter or darker distal limb coloraton. Another feature, especially in the north where *M. nigra* is all black, is a variety of "bad hair days" with central crests, flat tops with lateral crests (*M. ochreata*), and even floppy, middle-parted hair (*M. brunescens*). There is also variation in the shape and position of the ischial callosities and the "bare areas" next to the very short tail (Fooden 1969). Finally, there appears to be systematic variation in the configuration of the estrous swellings of the females (Stallmann, Froehlich 2000). In *Figure 1* seven named species are shown on the island's various peninsulas; the taxon on the Balantak Peninsula has yet to be named.

Surrounding Sulawesi on three sides, the longtailed or crab-eating monkey (*M. fascicularis*) similarly dispersed
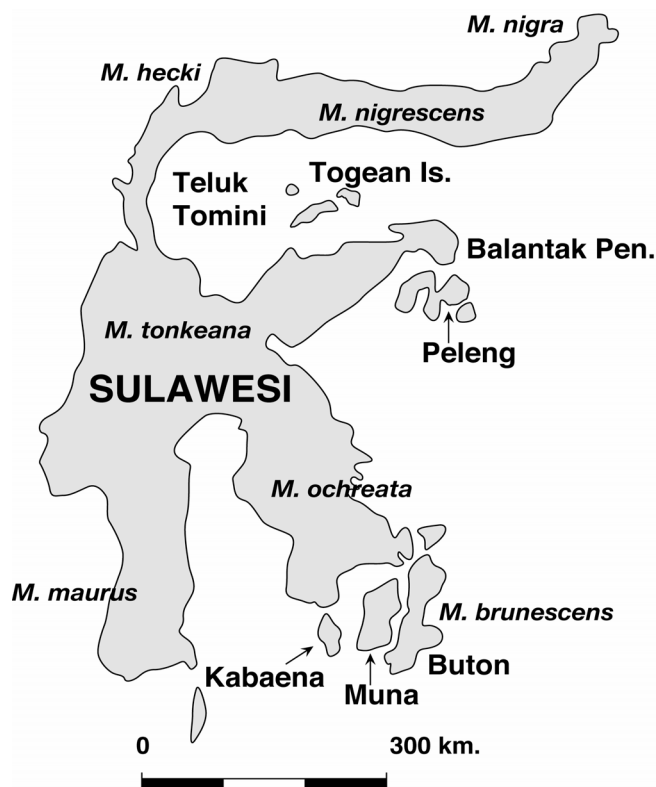

At an early meeting of the American Association of Physical Anthropology, founded by Aleš Hrdlička, a paper on the allometry of dogs was read by Dr. Hrdlička, to which Franz Weidenreich responded that he could not understand how this consideration of jaw size relative to brain size could possibly apply to breeds of domestic "ducks"! Thus was the international flavour of the early years for the Association and a seminal concern with the study of allometry. Correspondingly, we dedicate this paper to P. Y. Sondaar on the occasion of his death in appreciation of his contributions to Indonesian biogeography.

FIGURE 1. Map of Sulawesi showing the islands discussed in the text and the general locations of the various species of the genus Macaca, including a distinctive taxon on the east-central, Balantak Peninsula that is not yet formalized (see Froehlich *et al.* 1998). Similarly, the status of the small Togean Island population is not resolved. The Island of Peleng has no monkey population.
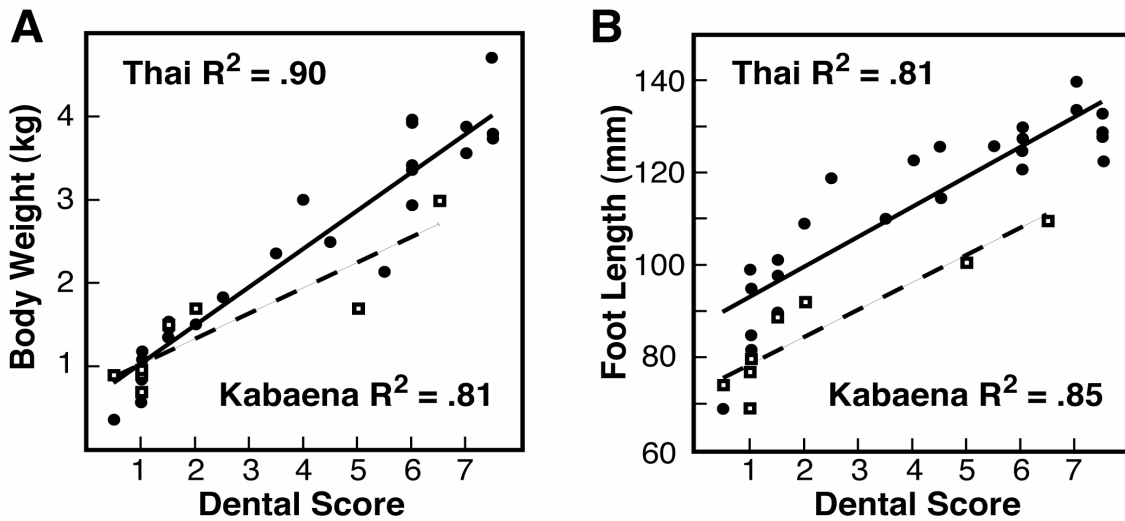
overseas from the Sunda Shelf, and beyond through most of the Lesser Sunda Islands as far as Timor, during the late Pleistocene (Fooden 1995). On Borneo and Sumatra today it is sympatric with the pig-tailed monkeys. Prehistorically, this may also have been the case for Java (Aimi 1981), but elsewhere the crab-eating monkey is exclusive. Living in mangroves and gallery forests was presumably conducive to dispersal on floating rafts of vegetation (Abegg, Thierry 2002).

There is some debate, however, as to whether this dispersal was totally natural. The more traditional view was one of human introduction to the isolated, deepwater oceanic islands (Medway 1970, Hill 1966, Fooden 1975). The time-span for these introductions could be on the order of 40,000 years, in accord with early human occupation in Australia, New Guinea and some major offshore islands such as New Ireland (e.g., Allen *et al.* 1988, Roberts *et al.* 1990). Genetic data seem to support this view with similarities between the Lombok and Bali longtailed macaques, but with the macaques from the adjacent island of Sumbawa (and Timor further to the east) showing more affinity to Javan and Sumatran longtail monkeys (Kawamoto Suryobroto 1995, Tanaka, Terao 1995). Others
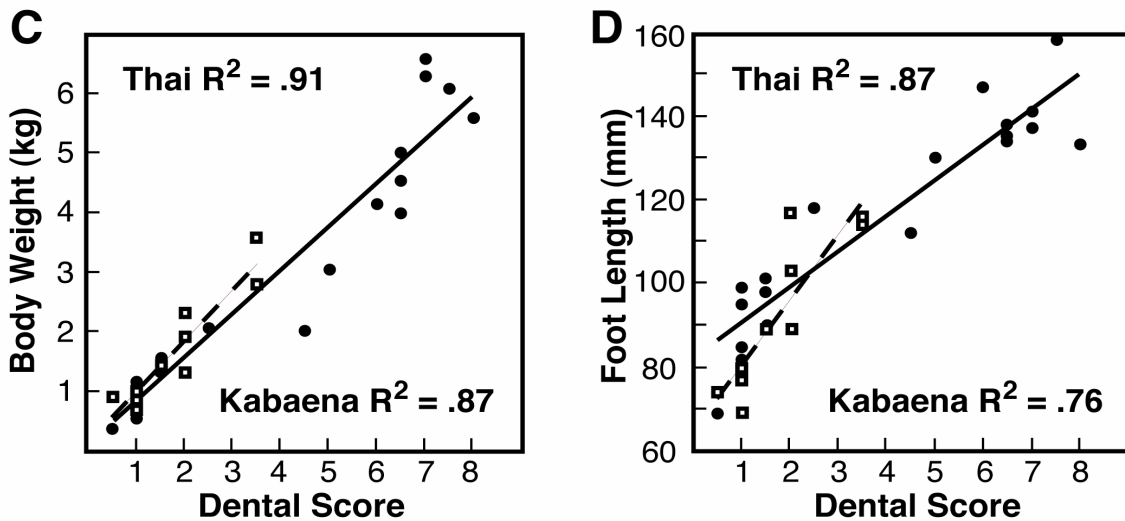
FEMALE

MALE

FIGURE 2. Regression growth lines and scatter plots for female and male weight and foot length in two sampling areas of *Macaca fascicularis* as follows: Kabaena Island (with open, square symbols and a dashed line) and Thailand (solid circles and regression lines).

have argued that this same pattern of continuity and discontinuity in morphological traits among deepwater island macaque populations supports the natural dispersal and stochastic evolution of longtailed monkeys (Abegg, Thierry 2002, Aimi *et al.* 1982, Fooden 1995).

Given this parapatetic pattern of near ubiquity for longtailed monkeys in the Indonesian Archipelago, it is noteworthy that they are absent on Sulawesi and in the Mentawai Islands west of Sumatra (Abegg, Thiery 2002). Some have argued that older populations of macaques were already established on these islands by land bridges (Groves, 1976) and/or earlier overseas dispersals (Abegg, Thierry 2002), thereby competitively excluding later intrusions by longtailed macaques. An exception to this apparent exclusion from Sulawesi is the exclusive presence

of longtailed macaques on the small offshore Island of Kabaena *(Figure 1)*, first noted by Elbert (1912).

Situated on the same shelf as the adjacent Islands of Muna and Buton, the relatively small Island of Kabaena (ca. 4000 km²) has a considerable variety of habitats rising to elevations of 1500 meters above sea level (asl). Although there are large areas of open grassland and high stands of bamboo up to the tops of low ridges, presumably the result of anthropogenic fires, extensive valleys of rain forest still exist in the interior. The presence of longtailed monkeys and the absence of the Sulawesi macaque taxon found on Muna and Buton (*M. brunescens*), therefore, is an exception to these hypotheses regarding the dispersal of longtailed macaques and their competitive exclusion from a few islands that demands explanation.

19

SUBJECTS AND METHODS

After first observing a middle-aged pet monkey from Kabaena Island in 2001 in Kendari, the capital of Southeast Sulawesi, one of us (JWF) arranged with Operation Wallacea to visit the island for five days in 2002. During this time, twelve pet monkeys were sampled on Kabaena, plus one more later in the town of Bau Bau on the Island of Buton. A series of body measurements and photographs were taken of these longtailed monkeys that had been captured on Kabaena. Their mouths were also examined to ascertain the dental formula and wear. With the help of an interpreter informal ethnographic interviews were conducted to determine the provenance of each pet and to gather information on the distribution of longtailed monkeys on the island. In addition, informants were asked about the local stories regarding the origin of these monkeys and if they recalled ever seeing or hearing of short-tailed, Sulawesi monkeys on Kabaena Island, like those on the adjacent Islands of Muna or Buron.

Since the animal observed in Kendari in 2001 appeared to be remarkably dwarfed for her age, with very compact cheek teeth, a major hypothesis of this research was that dwarfing is a predictable outcome of an extended period of occupation and evolution on a small island (e.g., Sondaar 1977). Only one of the 13 animals sampled in 2002, however, was nearly adult, with crowded and incompletely erupted third molars, but already showing monthly sexual swellings. Under natural circumstances she could have already been pregnant. (The 2001 pet in Kendari could not be relocated; presumably, it had died.) The only comparisons that could be made with these mostly subadult data, therefore, were growth allometric, by way of least squares regressions of the raw data.

For comparison, an extensive, wild collected sample of *M. fascicularis* from Thailand was used to show the pattern of normal growth in the two comparable measurements, weight and foot length. Although this sample comprised two subspecies and their possible hybrids, the growth scatter plots appeared to be largely homogeneous and suitable for the purpose of growth allometry. The youngest animals (i.e., no adult teeth) of both sexes in the available small samples were pooled as a baseline for the separate growth regressions of each sex and sample. The least square regression lines for the samples were compared for differences in slope and intercept with a t-test approximation utilizing the pooled variance. The usual formula is compared to a t distribution with the degrees of freedom equal to the sum of the error degrees of freedom from an ANOVA model.

Dental age based on a linear sequence of dental eruption stages was scaled from zero, a neonate with no teeth, to eight, an old adult with severe third molar wear, based on the presence of exposed dentin. Although our dental ages cannot at this time be approximated for chronological age, they provide a developmental basis for comparing the two samples. The robustness of the regression lines is indicated by the R-squared values. Finally, as an approximation of the degree of dwarfing in the young adult Kabaena female, a single specimen t-test was compared to the available Thai sample of equivalent or older females for foot length.

RESULTS

The previous observation of dwarfing in a Kabaena adult female appears to be supported by the regression lines for weight and foot length *(Figures 2A, B)*. Starting from approximately the same intercept (cf. birth weight) the Kabaena females grow in weight at a slower rate than Thai females to Age-class 6.5, when the canines and/or third molars are incompletely erupted. At this age the Kabaena female appears to be at the lower end of the weight range in the Thai sample. As noted in *Table 1*, the slope of this regression line is significantly lower and growth is slower than in the Thai sample.

Similarly, the foot length of the Kabaena females is smaller than the Thai animals at each Age-class from a full deciduous dentition onward. The intercepts for the regression lines (with similar slopes) in *Figure 2B* are significantly different *(Table 1)*. Evaluated a different way, the foot of the female from Kabaena is almost 2 cm shorter than the 12 comparable females (Age-classes 6 to 7.5) in Thailand, a highly significant difference (P<0.002). A further way of looking at this difference is that the adult female foot length on Kabaena is comparable to juveniles with their deciduous incisors being replaced in Thailand.

Unexpectedly, the Kabaena male sample does not show the same dwarfing as the females on the small island. For body weight, neither the slope nor the intercept are significantly different from Thai males in the small sample from Kabaena *(Table 1)*, though the slope appears greater for these males than it is in Thailand, and it is significantly greater *(Table 2)* than the Kabaena female sample (P<0.0 01). For foot length, however, both the intercept and the slope are significantly different for males on Kabaena from those in Thailand *(Table 1)*. As with the female Kabaena sample, the birth size (cf. intercept) of the foot is significantly smaller than it is in Thailand *(cf. Figures 2B, D, Table 1)*. From this starting point a linear model of foot growth is significantly accelerated on Kabaena compared to Thailand, surpassing the latter at Age-class 2.5 when the central incisors are being replaced. The Kabaena males also grow significantly faster than the females (P<0.006), a five-fold difference *(Table 2)* from that found between the sexes in Thailand (P<0.05).

For perspective, the foot size of Kabaena males, from the dental stage of first molar eruption through the replacement of the incisors, can be comparable to Thai males with fully erupted second molars. Alternatively, these very young Kabaena males are already similar to the young adult female in body size. Although there are no older males in the Kabaena sample, it would seem likely that they are on a developmental path to be larger than Thai adults, with

TABLE 1. Comparisons of regression slopes and intercepts for *Macaca fascicularis* between two geographical areas: Kabaena Island, Indonesia and Thailand.

Parameter: Slope

Sex	Variable	Thailand	Kabaena	t-Value	Degrees of Freedom	Significance
F	weight	0.46	0.31	2.23	32	P<0.02
F	foot	6.56	5.90	0.55	32	P<0.29
M	weight	0.73	0.87	1.08	26	P<0.15
M	foot	8.49	15.53	2.22	26	P<0.02

Parameter: Intercept

Sex	Variable	Thailand	Kabaena	t-Value	Degrees of Freedom	Significance
F	weight	0.59	0.71	0.52	32	P<0.30
F	foot	86.57	72.87	3.15	32	P<0.002
M	weight	0.15	0.12	0.06	26	P<0.48
M	foot	82.10	64.84	2.37	26	P<0.02

TABLE 2. Regression slope comparisons for the sexes of *Macaca fascicularis* in two geographical areas: Kabaena Island, Indonesia and Thailand.

Area	Variable	Difference	t-Value	Degrees of Freedom	Significance
Kabaena	weight	0.56	4.25	12	P<0.001
Thailand	weight	0.27	4.47	44	P<0.0001
Kabaena	foot	9.64	2.98	12	P<0.006
Thailand	foot	1.94	1.72	44	P<0.05

a much greater degree of sexual dimorphism than in Thailand.

This is a remarkable finding given the small size of the island. In fact, the survey data indicate that the island is effectively much smaller for longtailed monkeys than its 3,966 km^2 would suggest. All sightings and the provenances of the sample were at elevations below 200 m asl in the vicinity of streams. Moreover, two field seasons of the Operation Wallacea team at about 300 m asl and above never revealed any evidence of monkeys. A simple planimeter tracing at the 200 m contour shows that over 75% of the island exceeds this elevation. With several areas of steep coastline or open grassland and bamboo, the discontinuous mangrove swamps and gallery forests provide considerably less than 1,000 km^2 of adequate habitat for the longtailed macaque population.

DISCUSSION

The faster growth trajectory of Kabaena males implies greater adult size and sexual dimorphism than in Thailand. An alternative projection, however, would predict an early offset of physical growth with retarded, but then presumably relatively accelerated tooth eruption. This could result, however, in physically large males, that had not yet developed their full cheek teeth or canine weaponry; this might be ecologically maladaptive and a great social disadvantage for these subadult males.

A subjective assessment of the Thai scatter plots *(Figures 2C, D)*, however, might also suggest that there would be a better fit of a sigmoid growth curve with an adolescent spurt around Age-class 5, or following second molar eruption when the premolars are being replaced. At this time it has been shown that males can be under considerable nutritional stress (Froehlich *et al*. 1981). From this perspective the Kabaena data appear even more distinctive, with the projection of either a later growth spurt or a different, decelerating female-like trajectory that could arrive at a final size comparable to Thai adult males.

In either case, the distinctive combination of dwarfed females with unchanged or even larger males would imply an unexpected evolutionary process and a relatively long time frame on Kabaena Island for this to occur. The alternative hypothesis of a recent, bottlenecked introduction of genetically small pets would not account for different

growth trajectories in the two sexes. That is not to say that the introduction could not have been ten thousand years ago or earlier, and still accompanying human movement. Regardless of exactly when or how this immigration occurred, and because Kabaena is a fringing island, like Buton and Muna, on a shelf no deeper than 200 m (Fooden 1969), it is likely that the island was inhabited by Sulawesi monkeys when the longtails first arrived.

Without further study – indeed, without a confirmation of the predicted, large adult male size – one can only speculate on the processes of adaptation that produced this differential pattern of growth in Kabaena longtailed macaques. While smaller, faster reproducing females, with smaller birth weights in their babies, might be predicted on small islands, given the paucity of taxa on these islands (MacArthur, Wilson 1967, Sondaar 1977), larger males would imply either greater sexual selection for these highly competitive females in the limited area or considerable niche partitioning between the sexes in a marginal habitat, or both. Given that Harcourt and Schwartz (2001) have found that body size is a strong predictor of extinction in primates on small, Sunda Shelf islands, this must be a risky reproductive strategy for these males.

Nevertheless, the apparent length of time that longtailed monkeys have been evolving on Kabaena, by whatever mechanisms, reflects on the likelihood of alternative explanations for the presumed absence of Sulawesi monkeys on the island, the primary objective of this study. Surveys have found only vague oral traditions and recollections of short-tailed Sulawesi monkeys on the island. (Indeed, a reference to a short-tailed monkey pet from at least two informants turned out to be a *M. fascicularis* amputee.) A couple of interviewed older residents vaguely recalled Sulawesi monkeys, but they had not been seen in about 50 years. Another stated that the frequency of these sightings was much less than one in a thousand.

This is surprising given the likelihood of Sulawesi macaque presence and the amount of the island that they could still inhabit. Of the 3,000 km² above 200 m asl, there are about 2,000 km² in a contiguous area of high mountain peaks and forested interior valleys with no human inhabitants. The area below 200 m asl, that the parapatric longtails could inhabit, must also be much less than 1,000 km². Rijksen (1978) in Sumatra and personal (JWF) observations in Borneo indicate that longtails rarely forage more than 300 m away from their nocturnal "refuging" in the trees above water. In both places, pigtailed monkeys (*M. nemestrina*) were more nomadic in the inland forests (Crocket, Wilson,1980). Indeed, Fooden (1975) argued that the robust body-build and terrestrial tendencies of these pigtails may have been adapted to savanna-like, Pleistocene ecosystems. This assessment could also easily apply to *M. brunescens*, especially on the nearby, relatively flat, dry island of Muna.

Thus, it seems likely that the larger, more terrestrial Sulawesi monkeys were present when the smaller, gallery forest adapted longtailed macaques were introduced, or

stray migrants floated on flotsam to Kabaena Island perhaps as long as ten thousand years ago, or more. The logical hypothesis that the island was uninhabited by monkeys seems unlikely. Kabaena occupies the same Sulawesi shelf as the adjacent and similarly arid Muna Island. In addition to similarly extensive woodland savannas and a relatively low human population, there is also much unoccupied forested habitat on Kabaena. Finally, oral tradition seems to recall their presence.

Given the above discussion of Kabaena habitat and the ecology of the two monkeys, it also seems very unlikely that forest destruction by fire or other anthropogenic influences, such as hunting, could account for the absence of Sulawesi monkeys on Kabaena. Indeed, it seems more likely that the longtails would have been vulnerable to these factors. Therefore, competitive exclusion of Sulawesi monkeys by the newly arrived longtails must be considered.

Exclusion through competition for resources does not seem a likely hypothesis for the apparent absence of *M. brunescens* on Kabaena Island. Since the longtailed macaques occupy such a small part of the island, it does not seem likely that they could exclude the endemic animals from the whole. A study by Harcourt and Schwartz (2001) indicates that longtails survive on Sunda Shelf islands as small as 23 km², while pigtails exist on no island smaller than 839 km², and then in sympatry with longtailed macaques. In this context the endemic Sulawesi monkeys are such generalists, in contrast to the more specialized "crab-eaters", that it seems very unlikely that an essential nutrient or other resource would be unavailable on the rest of the island.

An alternative hypothesis of competition, first proposed by Wheatley (1980) for malaria in longtailed monkeys, could be differential resistance to disease when in sympatry with other macaques. Fooden (1994) has also reported that several species of macaques have natural, benign malarial infections (that are experimentally virulent in other macaque species), presumably with some evolved resistance to these pathogens. *M. fascicularis* exhibits up to five malaria species (three on Java), while *M. nigra* (in North Sulawesi) exhibits only one. If *M. fascicularis* evolved these differences while speciating at a later time than macaques like the Sulawesi species (Abegg, Thierry 2002), it is also possible that they could have coevolved relationships with other diseases.

Recent work strongly supports the bidirectional exchange of diseases between humans and macaques in Sulawesi (Jones-Engel, 2002, Jones-Engel *et al.* 2001). The same mechanism of bidirectional pathogen transmission should also be present among other macaque species, especially on continental areas with larger faunas and longer human contacts. Like a "Typhoid Mary", longtailed macaques could have acted as resistant carriers for viruses or other pathogens that could easily spread throughout and decimate a naïve Sulawesi species when contacted during dispersal, especially if carried by a local vector such as mosquitoes. Another potential and interesting scenario, with

human introduction of the longtailed macaques on Kabaena, is resistance to some disease in these human hosts that was virulent for the Sulawesi monkeys on Kabaena. These hypotheses of a competitive edge by disease resistance, however, do not account for the geographical confinement of the longtails solely to Kabaena Island.

Since any proposed dispersal mechanism, other than unlikely land bridges, involves an extreme bottlenecking of the founders, it is predictable that these disease or resistance carrying mechanisms could be subject to the same contingent sampling effects as genetic traits. If carriers arrived, this could give the stray immigrants a great competitive edge, in contrast to the alternative model of an overwhelming advantage for the resident species that might otherwise exclude the immigrants (Abegg, Thierry 2002). For example, a derived disease and the two monkey species (*M. nemestrina* and *M. fascicularis*) might have coevolved in the continental center of Sundaland and then dispersed during a subsequent sea level regression (Abegg, Thierry 2002), while pigtails more isolated in Java (Aimi 1981), and quite possibly also on Bali, might have been naïve to this new disease, thus accounting for their absence today, in contrast to the coevolved sympatry of the two species in Borneo and Sumatra.

The absence of longtailed monkeys on the rest of Sulawesi, however, might not be due solely to a resident advantage over stray colonists (Abegg, Thierry 2002) in the absence of any advantage for the immigrants. For example, it appears that *M. hecki* did, in fact, invade Sulawesi after *M. tonkeana* and *M. nigra* were already established (Froehlich *et al.* 1998). With respect to the more ecologically specialized, less physically competitive longtails, however, their failure to colonize Sulawesi may only have been a sampling bias leaving the colonists without their coevolved disease advantage,

Alternatively, given the long isolation of the Sulawesi monkeys, their incredible species radiation, and their facility of disease exchange, it is also suggested that they also might carry diseases that were incompatible with immigrant longtails. In this case, the Kabaena success of the longtailed macaques could be a sampling exception to this hypothetical disease defense, or one of isolation by distance that deleted the relevant disease in the Southeast Sulawesi macaques. Without this totally hypothetical presence of a competitive edge by an endemic disease resistance in Sulawesi monkeys, the rest of Sulawesi could be vulnerable to the same mechanism that excluded *M. brunescens* from Kabaena. Thus, the presence of longtailed macaques on Kabaena Island, and often as pets throughout the rest of Sulawesi, could be like a ticking time bomb of ecological disaster for the rest of the Sulawesi monkeys.

All of this is entirely hypothetical in the absence of a thorough study of disease antibodies and pathogens. What is a clear conclusion, however, is that no conventional ecological mechanism seems adequate to explain the success of the longtailed macaque beachhead on Kabaena Island, their unique life history adaptation to the island, and their total competitive exclusion of the Sulawesi monkeys that must have been present on Kabaena when they arrived, perhaps thousands of years ago. Secondly, it seems imperative that answers to these questions be found in order to prevent the same thing from happening throughout the rest of Sulawesi.

REFERENCES

ABEGG C., THIERRY B., 2002: Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society* 75: 555–576.

AIMI M., 1981: Fossil *Macaca nemestrina* (Linnaeus, 1766) from Java, Indonesia. *Primates* 22: 409–413.

AIMI M., BAKAR A., SUPRIATNA J., 1982: Morphological variation of the crab-eating macaque, *Macaca fascicularis* (Raffles, 1821), in Indonesia. *Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates* (2): 51–55.

ALLEN J., GOSDEN C., JONES R., WHITE J. P., 1988: Pleistocene dates for human occupation of New Ireland, northern Melanesia. *Nature* 331: 707–709.

CROCKET C. M., WILSON W. L., 1980: The Ecological separation of *Macaca nemestrina* and *M. fascicularis* in Sumatra. In: D. G. Lindburg (Ed.): *The Macaques: Studies in Ecology, Behavior and Evolution.* Pp. 148–181. Van Nostrand Rheinhold, New York.

CRONIN J. E., CANN R., SARICH V. M., 1980: Molecular evolution and systematics of the genus *Macaca.* In: D. G. Lindburg (Ed.): *The Macaques: Studies in Ecology, Behavior and Evolution.* Pp. 31–51. Van Nostrand Pheinhold, New York.

DELSON E., 1980: Fossil macaques, phyletic relationships and a scenario of deployment. In: D. G. Lindburg (Ed.): *The Macaques: Studies in Ecology, Behavior and Evolution.* Pp. 10–30. Van Nostrand Pheinhold, New York.

ELBERT J., 1912: *Die Sunda-Expedition des Vereins für Geographie und Statistik zu Frankfurt am Main*, Vol. 1. Minjon, Frankfurt.

EVANS B.J., MORALES J.C., SUPRIATNA J., MELNICK D. J., 1999: Origin of Sulawesi macaques (Cercopihecidae: *Macaca*) as suggested by mitochondrial DNA phylogeny. *Biological Journal of the Linnean Society* 66: 539–560.

FOODEN J., 1969: *Taxonomy and Evolution of the Monkeys of Celebes (Primates: Cercopithecidae).* Karger, Basel. 148 pp.

FOODEN J., 1975: Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana Zoology* 67: 1–168.

FOODEN J., 1994: Malaria in macaques. *Internat. J. of Primatology* 15: 573–596.

FOODEN J., 1995: Systematic review of Southeast Asian longtailed macaques, *Macaca fascicularis* (Raffles [1821]). *Fieldiana Zoology* 81: 1–206.

FROEHLICH J. W., SUPRIATNA J., HART V., AKBAR S., BABO R., 1998: The Balan of Balantak: a possible new species of macaques in Central Sulawesi. *Tropical Biodiversity* 5: 167–184.

FROEHLICH J. W., SUPRIANA J., MUSKITA Y., 1996: Biodiversity and the conservation biology of *Macaca nigra*: an anthropological view. *Tropical Biodiversity* 3: 83–102.

FROEHLICH J. W., THORINGTON R. W., Jr., OTIS J. S., 1981: The Demography of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. *Internat. J. of Primatology* 2: 207–236.

GROVES C. P., 1976: The Origin of the fauna of Sulawesi (Celebes). *Zeitschrift für Sauertierkunde* 41: 201–216.

HARCOURT A. H., SCHWARTZ M. W., 2001: Primate evolution: a biology of Holocene extinction and survival on the Southeast Asian Sunda Shelf islands. *Amer. J. of Phys. Anthrop.* 114: 4–17.

HILL W. C. O., 1966: *Primates, Comparative Anatomy and Taxonomy. VII. Catarhini, Cercopithecoidea, Cercopithecidae. Interscience.* New York. 934 pp.

JONES-ENGEL L., ENGEL G. A., SCHILLACI M. A., BABO R., FROEHLICH J. W., 2001: Detection of antibodies to selected human pathogens among wild and pet macaques in Sulawesi, Indonesia. *Amer. J. of Primatology* 54: 171–178.

JONES-ENGEL L., 2002: *Bidirectional Pathogen Transmission among Humans and Nonhuman Primates on the Indonesian Island of Sulawesi.* Ph.D. Thesis, University of New Mexico, Albuquerque. 115 pp.

KAWAMOTO Y., SURYOBROTO B., 1995: Gene constitution of crab-eating macaques (*Macaca fascicularis*) on Timor. *Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates* 4: 41–61.

MACARTHUR R. H., WILSON E. O., 1967: *The Theory of Island Biogeography.* Princeton University Press, Princeton. 203 pp.

MEDWAY L., 1970: The Monkeys of Sundaland: Ecology and systematics of the cercopithecids of a humid equatorial environment. In: J. R. Napier, P. H. Napier (Eds.): *Old World Evolutionary systematics and Behavior.* Pp. 513–553. Academic Press, New York.

MORALES J. C., MELNICK D. J., 1998: Phylogenetic relationships of the macaques (Cercopithecidae:*Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *J. of Hum. Evol.* 34: 1–23.

MUSSER G. G., 1987: The Mammals of Sulawesi. In: T. C. Whitmore (Ed.): *Biogeographical Evolution of the Malay Archipelago.* Pp. 73–93. Clarendon Press, Oxford.

RIJKSEN H. D., 1978: *A Field Study of Sumatran Orang Utans (*Pongo pygmaeus abelli Lesson 1827). Veenman and Zonen, Wageningen.

ROBERTS R. G., JONES R., SMITH M. A., 1990: Thermoluminescence dating of 50,000-year-old human occupation site in northern Australia. *Nature* 345: 153–156.

SONDAAR P. Y., 1977: Insularity and its effects on mammal evolution. In: M. Hecht, P. Goody, B. Hecht (Eds.): *Major Patterns in Vertebrate Evolution.* Pp. 671–707. Plenum Press, New York.

STALLMANN R. R., FROEHLICH J. W., 2000: Primate sexual swellings as coevolved signal systems. *Primates* 41: 1–16.

TAKENAKA O., HOTIA M., TAKENAKA A., KAWAMOTO Y., SURYOBROTO, B., BROTOISWORO E., 1987: Origin and evolution of Sulawesi macaques: 1, Electrophoretic analysis of hemoglobins. *Primates* 25: 87–98.

TANAKA H., TERAO K., 1995: Geographic distribution of the α_1-antitrypsin (α_1-AT) variants in crab-eating macaques (*Macaca fascicularis*). *Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates* 9: 63–71.

WALLACE A. R., 1890: *The Malay Archipelago: Land of the Orang-utan and the Bird of Paradise; A Narrative of Travel with Studies of Man and Nature.* 10th Ed. (Rev.). Macmillan and Co., London. (Reprinted 1962, Dover, New York.) 515 pp.

WHEATLEY B. P., 1980: Malaria as a possible selective factor in the speciation of macaques. *J. of Mammalogy* 61: 304–307.

Jeffery W. Froehlich
Department of Anthropology
Las Lomas at Redondo
University of New Mexico
Albuquerque, 87131 New Mexico
USA
E-mail: jfroehl@unm.edu

M. A. Schillaci
Department of Social Sciences
University of Toronto at Scarborough
Scarborough, Ontario
Canada

L. Jones-Engel
Department of Psychology and National
Primate Research Center
University of Washington
Seattle, WA
USA

D. J. Froehlich
Department of Biology
Austin Community College
Austin, TX
USA

B. Pullen
Royal Veterinary College
University of London
London, UK