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# Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques

Erin P. RILEY[1*], Barbara TOLBERT[1], Wartika R. FARIDA[2]

[1]Department of Anthropology, San Diego State University, San Diego, CA 92182-6040 USA
[2]Research Center for Biology, Indonesian Institute of Sciences, Cibinong – Bogor, Indonesia

**Abstract** Nutritional ecology has been linked to crop raiding behavior in a number of wildlife taxa. Here our goal is to explore the role nutrition plays in cacao crop raiding by Tonkean macaques *Macaca tonkeana* in Sulawesi, Indonesia. From June – Sept 2008 we collected fruit samples from 13 species known to be important Tonkean macaque foods and compared their nutritional value to that of cacao *Theobroma cacao*, an important cash crop in Sulawesi. Cacao pulp was significantly lower in protein, but lower in dietary fiber, and higher in digestible carbohydrates and energy content compared to forest fruits. These findings, combined with the fact that cacao fruits are spatially concentrated and available throughout the year, likely explain why Tonkean macaques are attracted to this cultivated resource. We use these data along with published feeding ecology data to propose strategies to minimize human-macaque conflict. Namely, we recommend the deliberate protection of *Elmerillila tsiampaccca*, *Ficus* spp. and *Arenga pinnata*, fruit species known to be regularly consumed and of considerable nutritional value. We also identify the *A. pinnata* palm as a potential buffer resource to curb cacao crop raiding by macaques. Cacao is a hard-to-process food because the pods have a thick outer skin that encases the seeds and pulp. Aren palm fruit, although lower in digestibility, is easier-to-process, higher in protein, and also available year round. In addition, because the palm has considerable cultural and economic significance for local people, the strategy of planting Aren palm in a buffer corridor is likely to garner local community support [*Current Zoology* : 59 (2): – , 2013].

**Key words** Human-macaque conflict, Foraging efficiency, Buffer crop, *Arenga pinnata*, *Ficus*, Fiber content

Crop raiding is undoubtedly one of the most serious challenges to wildlife conservation. This behavior is particularly pervasive among the nonhuman primates, given the high levels of sociality and intelligence and keen problem-solving skills of the taxa commonly reported as culprits (e.g., capuchins, McKinney, 2011; macaques, Riley and Priston, 2010; baboons, Hill, 2000; chimpanzees, Hockings et al., 2009). Because of the detrimental impact crop raiding can have on human livelihoods and the likelihood of local support for conservation efforts, scholars and conservation managers worldwide are increasingly focusing attention on the development and implementation of effective mitigation programs (Dickman, 2010; Osborn and Hill, 2005; Strum, 1994).

Predicting the patterns of raiding is an important first step in developing mitigation strategies. The ability to develop a successful strategy is largely dependent on behavioral and ecological data from raiding primates. For example, ranging patterns, substrate use, habitat composition, and patterns of forest fruit availability all can shed light on the causes of crop raiding and its frequency and timing (e.g., Naughton-Treves et al., 1998; Siex and Struhsaker, 1999; Riley, 2007b; Hockings et al., 2009). Because crop raiding is a foraging strategy (Strum, 1994), the factors that influence the choice of wild foods are also likely at play when primates raid crops. Foraging theory predicts that animals will forage in a way that maximizes the rate of energy intake (Stephen and Krebs, 1986). Cultivated foods tend to be highly palatable, easier to process, and are typically distributed in a way that minimizes searching costs. Therefore, they often represent the "smarter choice", particularly in areas where anti-raiding strategies by farmers are infrequent or ineffective. Nutritional content, also an important aspect of foraging efficiency, has been shown to play a role in crop raiding behavior (e.g., elephants, Osborn, 2004; Rode et al., 2006a; white-tailed deer, Dostaler et al., 2011). For example, Rode et al. (2006b) suggest that elephants in Kibale National Park, Uganda may raid crops such as maize and bananas to compensate for limited sodium availability in wild foods. Among nonhuman primates, the greater digestibility of human foods, such as maize, has been proposed to explain crop raiding patterns by olive baboons (Forthman Quick and Demment, 1988). Linking crop raiding behavior by nonhuman primates to specific nutritional components of cultivated foods, however, remains largely understudied. In this paper, we explore this relationship in a nonhuman primate endemic to Sulawesi, Indonesia: the Tonkean macaque *Macaca tonkeana*.

The Tonkean macaque is a medium-sized, primarily frugivorous primate that exists in multimale-multifemale social groups (Riley, 2007a). This primate shows considerable ecological flexibility in its ability to use multiple forest strata, including a considerable amount of time on the ground, and to persist in heavily-altered habitats (Riley, 2008). The latter is made possible in part by the ecological strategy of crop raiding. While it is likely that the raiding of subsistence crops has a long history on Sulawesi, the planting of highly palatable cash crops in the post-colonial era has undoubtedly exacerbated human-macaque conflict in the area. For example, in the 1980s the Sulawesi landscape experienced an enormous expansion of cacao acreage, mostly by smallholder production (Akiyama and Nishio, 1996). Cacao *Theobroma cacao*, a perennial tree crop that is frequently planted under forest shade, is one of the primary cash crops raided by macaques and other wildlife (Riley, 2007b; Supriatna et al., 1992). Previous research has found that Tonkean macaques raid cacao crops year-round regardless of levels of forest fruit availability and the frequency of cacao crop guarding by farmers (Riley, 2007b).

Our goal in this article is threefold. First, we assess the nutritional value of a portion of the Tonkean macaque fruit diet. Second, we compare the nutritional value of forest fruits and cacao pulp to explore whether nutritional factors play a role in cacao crop raiding by Tonkean macaques. Our third goal is to use the nutritional data to inform conservation and human-macaque conflict management strategies. Namely, we identify specific fruit tree species of high nutritional value that should be protected in macaque habitat as part of in situ conservation efforts. In terms of mitigating human-wildlife conflict, one existing strategy is to plant buffer crops at the forest-farm edge that act as barriers to desirable cash crops (Hockings and Humle, 2009; Dickman, 2010). This strategy has been employed using unpalatable cash crops (e.g., tea and chili) with some success (Parker and Osborn, 2006; Southworth et al., 2010; Hockings and Humle, 2009). An alternative version of this strategy is to establish an exploitable buffer that diverts feeding away from important cash crops. For example, Yuwono et al. (2007) suggest that a buffer zone planted with an abundance of fruit trees could dissuade orangutans *Pongo pygmaeus* from entering oil palm plantations. Here we identify the *Arenga pinnata* palm as a potential species that could be used to test the efficacy of the exploitable buffer strategy.

# 1 Materials and Methods

**1.1 Study area**

   This research was conducted in the Lake Lindu highland plain (1° 19' 07" S, 120° 04' 51" E) in Lore Lindu National Park (LLNP), Central Sulawesi, Indonesia. Comprising approximately 2,200 km$^2$, LLNP is the second largest terrestrial protected area in Wallacea. The park is designated as a UNESCO Man and the Biosphere Reserve due to the critical role it plays in the conservation of endemic fauna and flora, including one of the seven endemic macaques, *Macaca tonkeana*. The Tonkean macaque is currently listed as "Vulnerable" (IUCN 2011) with an estimated remaining population of 150,000 (Riley 2010). As noted earlier, Tonkean macaques are primarily frugivorous with fruit accounting for an average of 81% of feeding records (2 groups; monthly range: 40-93%, but they also consume insects, young leaves, and other vegetative matter (Riley 2007a).

   The Lindu plain is one of two enclaves allowed to exist within the National Park because it is a major rice growing area and has long established human settlements. In its designation as a National Park, the granting of enclave status meant that the Lindu people could maintain their existing agricultural fields and continue to engage in small-scale forest production collection. Although wet-rice agriculture (*sawah*) predominates in Lindu, tree cash crops, such as coffee and cacao, have grown in importance as part of the Lindu economy since the 1980s. Cacao is typically grown as a spatially concentrated monocrop on plantation plots ranging in size from 1–5 ha, with the number of trees in the plantation ranging between 124–1903 (Riley and Fuentes, 2011). Cacao pods are harvested by farmers when the fruit reaches a deep yellow or red color, depending on the varietal. The pods are then cut open, and the wet beans covered in pulp are removed (Fig. 1). It is the sweet pulp that macaques and other raiding wildlife (e.g., forest rats and squirrels) consume (Riley, 2007b). Although the percent contribution of cacao pulp to the diet of macaque groups is unknown, previous research found that macaque crop raiding occurred throughout the course of a six-month period (with raiding peaks coinciding with peaks in cacao fruiting), with one farmer experiencing a loss of 7% of his total cacao harvest due to macaque raiding (Riley, 2007b).

**1.2  Sample collection**

   We opportunistically collected fruit samples from tree species that were fruiting during our study period (June – September 2008). Every attempt was made to collect samples from specific trees where the macaques had previously been observed feeding. If this was not possible, samples were collected from trees within the home range of known macaque groups. Our sample comprised 13 fruit species (Table 1). We focused on fruit because it constitutes the primary component of the Tonkean macaque diet and due to the ease of its collection. We acknowledge that our sample represents a portion of the overall fruit diet; however, our samples did come from species known to be important food resources for Tonkean macaques (Table 1; Riley, 2007b, unpublished data). For each of the species, the ripe fruit pulp was collected as this represented the part consumed by macaques. When trees were deemed impossible to safely climb, samples were collected from the ground. Across the study period, we collected between 2 - 4 samples from multiple trees of each species for most fruits. We also collected the pulp from cacao pods from plantations located at the forest edge. All samples collected were placed on aluminum trays and sun-dried in the field and in a generator-powered drying box until completely dry.

   The fruits collected were cut into small pieces to accelerate the drying process, and ultimately, for chemical analyses. Because the seed fraction of fig fruits is not typically digested by primates, we separated the pulp fraction (including the skin) from the seed fraction and only used the pulp in chemical analyses (Urquiza-Haas et al., 2008). Once dry, samples were stored in labeled paper bags with silica gel. As soon as the required dry weight was obtained (i.e., 50– 80 g per species), we sent samples to the Laboratory of Nutrition Testing Research Center for Biology in Cibinong, Bogor for analysis. We attempted to collect multiple samples from multiple trees of a given species, but sampling was not

conducted simultaneously with behavioral observations and it was limited to a four-month time period. We therefore acknowledge that our data can say little about the nutritional composition of the foods at the time they were consumed or the potential variation in fiber and macronutrient content over a more extended period of time.

1.3 Nutritional and statistical analyses

The samples were analyzed for dry matter content, crude protein, lipids, and ash using standard proximate analysis procedures (AOAC, 1990). Given the important role calcium and phosphorus play in fig nutrition (O'Brien et al., 1998), these minerals were also analyzed (AOAC, 1990). Crude protein was determined using the standard formula: N (total nitrogen) × 6.25 (AOAC, 1990). The detergent fiber analysis (van Soest, 1994), which renders the neutral detergent fiber (NDF = the total insoluble fiber in plant cell wall, primarily cellulose, hemicelluloses, and lignin) and the acid detergent fiber (ADF = primarily cellulose and lignin), was also conducted. In the results we report NDF (often considered the best index of total insoluble fiber and of energy available from fiber [e.g., Conklin-Brittain et al. 2006]) as well as ADF (a better index of indigestible fiber if macaques are able to digest hemicellulose). The digestible carbohydrates or the total nonstructural carbohydrates (TNC) were calculated as: %TNC = 100 - % lipid - % crude protein  - % total ash - % NDF. TNC values were calculated using percentages of organic matter because ash, which is included in dry matter (DM), does not contribute energy to food (Conklin-Brittain et al., 2006). We also calculated available or metabolizable energy (ME) of the foods using standard physiological fuel values for carbohydrates, crude protein, and lipids (4, 4, and 9 kcal/g, respectively) and a fiber digestion coefficient of 0.463 that was determined for captive Japanese and rhesus macaques (Sakaguchi et al., 1991). The physiological fuel value of fiber was calculated as 3 x 0.463 = 1.389 kcal/g. Assuming maximal NDF fermentation, we calculated energy per food species as $ME_h$ kcal/g OM = [(4 × %TNC) + (4 × %CP) + (9 × %lipid) + (1.389 × %NDF)]/100 (Conklin-Brittain et al., 2006).

We compared our nutritional data to those published on other frugivorous catarrhines. T-tests were used to compare nutritional composition of fig and non-fig fruits. To test for differences in nutritional composition between the forest fruits and cacao pulp, we used one sample t-tests. We performed arcsine transformations on proportional data to meet assumptions of normality and equal variances required by parametric techniques (Sokal and Rohlf, 1981). Results were considered significant at $P < 0.05$.

# 2 Results

## 2.1 Nutritional composition:  Forest fruits

Among the 13 forest fruit species sampled, differences in the principal macronutrients were evident (Table 2). Crude protein content varied between 3.05% to 9.48% (DM). The mean protein content (5.39%) fell below values reported (plant portion of diet) for African cercopithecines, but was within the range reported for other macaque species (Table 3). Lipid content ranged between 0.16% to 25.72%. The mean lipid content (5.39%) was higher than that reported for African cercopithecines and chimpanzees (plant portion of diet), but was within the range reported for semi-free ranging Japanese macaques (Table 3). NDF values also varied considerably, from 18.63% to 58.31% DM. The mean NDF content (34.42%) was similar to the fruit (or plant) diet of other frugivorous primates (Table 3). ADF values ranged between 14.84% to 43.67% DM. The mean ADF value (27.60%) was similar to those reported for redtail monkeys but higher than those found for blue monkeys, grey-cheeked mangabeys, and chimpanzees (Table 3). Mean calcium (0.48) and phosphorus (0.14) values were lower than those reported for red-tailed guenons in Kibale National Park, Uganda (Table 3).

Figs did not significantly vary in ME, mean protein and lipid content, or mean ADF (indigestible fiber) from non-fig fruit (ME: $t = 1.164$, $df = 10$, $P = 0.272$; Protein: $t = 2.013$, $df = 10$, $P = 0.072$; Lipids: $t = -0.487$, $df = 10$, $P = 0.637$;

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ADF: $t = 0.574$, $df = 10$, $P = 0.579$). Mean fiber content (NDF), however, was significantly lower in figs compared to non-figs (Fig mean: 34.1% OM, Non-fig mean: 52.8% OM; $t = -2.602$, $df = 10$, $P = 0.026$). Likewise, mean TNC was significantly higher in figs than in non-fig fruit (Fig mean: 51% OM, Non-fig mean: 32.3%OM; $t = 2.243$, $df = 10$, $P = 0.049$). In terms of mineral content, figs and non-fig fruit did not significantly vary in their CA: P ratio. However, when *Arenga pinnata*, a clear outlier was excluded from the forest fruit sample, the difference in mean CA: P ratio (Fig: 6.08, Non-fig: 1.42) approached significance ($t = 2.174$, $df = 10$, $P = 0.055$). Among the fig species, there were differences in all components of the fruit pulp (Table 2). Lipid content varied between 2.18%−6.63% OM, with a mean of 3.87% ±1.72%. Fiber content (NDF) varied widely between 24.87-50.48% OM, with a mean of 34.12%±9.81%. Indigestible fiber (ADF) also ranged widely between 22.82% −51.08% OM, with a mean of 39.86% ±11.97%. Protein content also varied widely between 6.38% − 12.26% OM (mean: 8.66% ± 2.28%). Metabolizable Energy showed the least variation across fig species (range: 2.82 − 3.42, mean: 3.42% ± 0.37%).

**2.2 Nutritional composition: Cacao pulp compared to forest fruits**

Mean protein content was significantly higher in forest fruits compared to cacao pulp ($t = 4.899$, $df = 12$, $P < 0.001$; Fig. 2). Lipid content was also significantly higher in forest fruits (6.93%) than in cacao pulp (0.06%) ($t = 5.472$, $df = 12$, $P < 0.001$). Forest fruits were significantly higher in NDF ($t = 10.751$, $df = 12$, $P < .001$) and ADF ($t = 11.6$, $df = 12$, $P < 0.001$) and significantly lower in TNC ($t = -11.030$, $df = 12$, $P < 0.001$). There was no significant difference in phosphorus content ($t = -0.492$, $df = 12$, $P = 0.632$) but on average calcium was significantly higher in forest fruits (0.48% DM) compared to cacao (0.04%; $t = 4.235$, $df = 12$, $P = 0.001$). Mean energy content of forest fruits, as measured by ME, was significantly lower than cacao pulp ME (Table 3; $t = -3.593$, $df = 11$, $P = 0.004$).

**2.3 Nutritional composition: *Arenga pinnata* fruit compared to other forest fruits and cacao pulp**

In comparison to other forest fruits, Aren palm fruit was lower in protein and lipid content, ME, and indigestible fiber (ADF) and higher in fiber content (NDF) and digestible carbohydrates (TNC) (Table 2). Calcium bioavailability was substantially higher in Aren palm fruit (CA: P ratio = 35.4) compared to the other forest fruit (range: 0.21−15.44). Compared to cacao pulp, Aren palm fruit was higher in protein and fiber content (NDF) and lower in ME and digestible carbohydrates (TNC). The indigestible fiber (ADF) of Aren palm fruit, although higher than that of cacao pulp, was the lowest among the forest fruits (14.84% DM; Table 2) and lower than values reported for other frugivorous catarrhines (Table 3).

# 3 Discussion

As part of our assessment of the nutritional value of Tonkean macaque foods, we found that the sampled portion of the Tonkean macaque fruit diet was similar in overall nutritional composition to that reported for other macaque taxa (Table 3). Although fiber is often considered to be a marker of a low quality diet, there is evidence that it serves a beneficial role in the diets of a number of herbivores, including nonhuman primates. For example, Sakaguchi et al. (1991) demonstrated that captive rhesus and Japanese macaques are able to digest 46.3% of a high-fiber diet, indicating that as hindgut fermenters they show considerable capacity to gain energy from fiber (cf. Conklin-Brittain et al. 1998). The fact that the mean fiber content (NDF) was similar to the fruit (or plant) diet of Japanese macaques, as well as other frugivorous primates, suggests that Tonkean macaques may also be able to benefit from a high-fiber diet. At the same

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time, primates undoubtedly benefit from the inclusion of easily digested foods in their diets. Fig fruits, which are a consistent and staple food for Tonkean macaques (Riley 2007a), were lower in fiber content and higher in digestible carbohydrates compared to other forest fruit species. These factors combined with the greater availability of calcium in figs may explain why Tonkean macaques are attracted to them (cf. Conklin and Wrangham 1994; O'Brien et al. 1998).

A key goal of this study was to determine whether nutritional factors play a role in cacao crop raiding. Because cacao pulp had significantly lower levels of protein and lipids compared to forest fruits, Tonkean macaques do not appear to be attracted to cacao fruit for these nutritional components. In other wildlife taxa, studies show that fiber concentrations of crops are linked to food choice and crop raiding behavior. For example, Rode et al. (2006b) found that crops raided by elephants in Kibale National Park, Uganda have lower fiber concentrations than do wild foods. The findings in our study show that cacao pulp has significantly lower fiber levels and significantly higher levels of digestible carbohydrates, indicating greater digestibility compared to forest fruits. Cacao pulp also had, on average, significantly greater energy content than did the forest fruits sampled. The fact that cacao fruits are spatially concentrated and available throughout the year, along with the findings on its digestibility and energy content, may explain why Tonkean macaques are attracted to this cultivated resource.

Since fruit is typically a poor source of mineral nutrition (NRC 2003), the mineral concentrations of cultivated resources may also explain crop raiding by wildlife. For example, in addition to having lower fiber concentrations, crops raided by Kibale elephants had higher sodium concentrations than wild foods (Rode et al., 2006a). In our study, we measured the levels of two minerals: Calcium and Phosphorus. Mineral nutrition, specifically of Ca and P, is an unlikely contributing factor to macaque crop raiding for three reasons. First, forest fruits do not appear to be deficient in calcium; in fact, the mean value was comparable to that recommended by the NRC (2003) for the overall diet. Second, cacao pulp has very low concentrations of calcium compared to forest fruits (CA: $P = 0.28$). Third, cacao pulp and forest fruits show comparable phosphorus levels.

*In-situ* conservation efforts for nonhuman primates may be aided by integrating information on feeding ecology with data on nutritional composition of known food resources. Although nonhuman primates often raid crops regardless of pattern of forest fruit availability (Naughton-Treves et al. 1998; Riley 2007b; but see Siex and Struhsaker 1999), the *initial* development of crop raiding is linked to a decrease in natural forage available as a result of agricultural expansion (Strum 1994). In any given primate species, not all groups whose ranges include matrix (agriculture-forest) habitat will raid crops (e.g., Riley 2007b). Therefore, the deliberate protection of key tree species known to be regularly consumed and of considerable nutritional value to primates may prevent against the *future* development of crop raiding and contribute to broader in-situ conservation efforts. A number of forest fruit species stand out from our sample. For example, figs have considerable nutritional value and show high densities in many areas of Sulawesi [e.g., 23.3 trees/ha, Karaenta Nature Reserve, South Sulawesi (Zahrah 1988 as cited in Supriatna et al., 1992); 34.8 trees/ha, Lore Lindu National Park (Riley, 2010a)], making them an important staple food for the Sulawesi macaques, and hence worthy of deliberate protection. *Elmerillia tsiampacca*, a preferred Tonkean macaque food, also stands out in our dataset for its high nutritional quality (i.e., high protein, lipid, and energy content with medium levels of fiber; Table 2). Villagers in Lindu frequently seek out this species for the construction of dug-out canoes (Riley, 2007b), and thus it may be overselected in forest areas close to villages. Given their generally positive perceptions toward macaques (Riley and Priston, 2010), villagers could be willing to switch to other sources of timber if they knew how important *E. tsiampacca* is to the diet of Tonkean macaques. The third forest fruit species that should be actively protected in Sulawesi is *Arenga pinnata*, the sugar palm. Previous research has found that aren palm fruit is an important food for Tonkean macaques; the fruit is available year round and 52% of the feeding records of one study group was devoted to this fruit (Fig. 3;

Riley 2007a). The importance of this species for the Tonkean macaque diet and aspects of its nutritional composition led us to consider how the Aren palm might be incorporated into a crop raiding mitigation strategy.

The mitigation strategy of buffer cropping has focused almost exclusively on crops that are *not* attractive to wildlife (Parker and Osborn, 2006; Southworth et al., 2010; Hockings and Humle, 2009). This focus is understandable; it is assumed that buffer crops that are highly palatable will attract wildlife to the edge and increase the likelihood of crop raiding once the buffer crop has been depleted (e.g., Goldsmith, 2005). Indeed, if crops have not already been planted in an area, recommended crop raiding prevention strategies include planting less palatable crops near the forest edge (Naughton-Treves et al., 1998) and setting up an appropriately wide enough buffer zone to discourage crossing into croplands (e.g., more than 20m from the edge for Buton macaques; Priston et al., 2012). However, in situations where raiding is *already* occurring, we argue that another strategy may prove effective: establishing exploitable buffer zones. There is some evidence that this strategy can be successful: in Costa Rica, fruiting live fence trees and plots planted with plantains were successful in drawing white faced capuchins *Cebus capucinus* away from important cash crops (Baker and Shutt, 2005). The decision regarding what diversionary crop to plant may be aided by foraging theory. As a foraging strategy, crop raiding comes with costs and benefits (Strum, 1994). The consumption of cacao pulp makes sense from a foraging efficiency perspective; it has a high caloric content, is easily digested, and exists in a dense spatial distribution. However, because cacao pods have a thick outer skin that encases the seeds and pulp, it is a hard-to-process food. Therefore, in Sulawesi a mitigation strategy could involve planting palatable resources that mimic the caloric density and spatial distribution of cacao but that are easier to process.

Re-enter, *Arenga pinnata* palm fruit. The sugar palm grows naturally throughout the Asian humid tropics, but it can also be easily cultivated (Mogea et al., 1991). In areas where macaques are already attracted to cacao gardens, the goal of planting either a corridor or plot of Aren palms would be to satiate the macaques so that their foraging impact on cacao is reduced. As noted earlier Aren fruit is an important food for Tonkean macaques and because the fruit is available throughout the year, it could mimic the perennial nature of cacao fruiting. Although Aren palm had a lower percentage of digestible carbohydrates compared to cacao pulp (Table 2), it had the lowest level of indigestible fiber (ADF %DM) of all the forest fruits sampled. In fact, its ADF level (14.84% DM) is more similar to cacao (4.68%) than to the forest fruit mean (28.67%), making it an attractive choice among forest fruit species for a buffer crop. The overall difference in digestibility between Aren fruit and cacao pulp may be offset by Aren fruit's higher protein content and the fact that it is substantially easier to process than cacao. Aren fruit is also an important source of calcium as illustrated by its very high Ca: P ratio, a measure of calcium availability (Table 2). A high Ca: P ratio (that is, due to low P intake) has been linked with positive health benefits. For example, it has been shown to be favorable for bone mineralization in adult rats (Koshihara et al., 2005). This attribute might also contribute to the attractiveness of Aren palm fruit as a buffer crop.

We also consider the Aren palm a good candidate for buffer cropping because it has considerable cultural and economic significance for villagers throughout much of Sulawesi. The Aren palm is considered such an important resource because of the many benefits and products it provides (Mogea et al., 1991). For example, hair fibers from the stalks are used to construct household items and the sap from the tree is tapped to produce palm sugar or various forms of alcoholic beverages. Many of these products are easily obtained from the tree without its felling, thus human use does not necessarily inhibit macaque use. If people were afforded access to the Aren palm as a buffer crop, it is highly likely that this planting strategy would garner local support; an important factor to consider when designing efforts to mitigate human-wildlife conflict (Dickman, 2010). Because the Aren palm is easily propagated, it has already attracted attention for use in agroforestry systems and in efforts to rehabilitate unproductive and erosion-prone sites (Mogea et al.,

1991). The main limitations to using the Aren palm as a buffer resource are the number of years before flowering (10–12 years) and its relatively short life span (12 –20 years) (Mogea et al., 1991).

In this study we examined the nutritional value of the fruit portion of the Tonkean macaque diet and demonstrated the significance of nutritional and feeding ecology for understanding and mitigating crop raiding behavior. There is still much to learn regarding the nutritional ecology of Tonkean macaques. Future research could 1) expand the nutritional analysis to include other important food items such as insects, leaves, and other vegetative matter; 2) measure potential variation in nutritional composition of the diet across space and time (Chapman et al., 2003); and, 3) examine concentrations of other important minerals such as sodium, potassium, and magnesium to fully understand the role mineral nutrition plays in the feeding ecology of macaques, including the consumption of cultivated resources. The effectiveness of crop raiding mitigation strategies, such as buffer cropping, also needs to be tested in the field. For example, because the establishment of an exploitable buffer could potentially result in negative effects (e.g., attracting more macaques) , we recommend that the use of the Aren palm as a buffer resource first be tested for effectiveness in a limited area before being implemented more broadly.

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**Table 1 Forest fruit species sampled ($n = 13$) and known contribution to Tonkean macaque diet**

| Species | Family | Vernacular name | Contribution to diet[a] (% feeding records) | |
| --- | --- | --- | --- | --- |
| | | | Anca group | CH group |
| *Areca vestiaria* | Palmae | Pinang merah[c] | 0.26 | — |
| *Arenga pinnata* | Palmae | Enau[d] | 52 | 1.3 |
| *Artocarpus teysmanii* | Moraceae | Teah[d] | 4.5 | — |
| *Artocarpus vriescana* | Moraceae | Baloli[d] | 3.1 | — |
| *Elmerillia tsiampacca* | Magnoliaceae | Takasa[d] | 2.8 | 20.7 |
| *Ficus elmeri* | Moraceae | | 0.52 | 1.6 |
| *Ficus virgata* | Moraceae | Ara[c] | — | 6.3 |
| *Ficus sagittata* | Moraceae | | 1.1 | 1.3 |
| *Ficus sp.* 1[b] | Moraceae | | n | n |
| *Ficus sp.* 2 | Moraceae | | n | n |
| *Pandanus sp.* | Pandanaceae | Pandan[c] | 0.77 | 12.5 |
| *Pinanga sp.* | Palmae | Pinang hitam[c] | 1.9 | 4.1 |
| *Timonius teysmanii* | Rubiaceae | Kalambio[d] | 0.77 | 0.33 |

[a] These data come from previous research conducted on two groups of Tonkean macaques (Riley 2007b; unpublished data); percent feeding records derive from scan sampling data (total number of feeding records: Anca = 479; CH = 359; Riley 2007a). [b] Many species of figs in Lore Lindu National Park are unidentifiable. Overall, consumption of fig fruits accounted for 22% and 51% of the feeding records for Anca and CH groups, respectively (Riley 2007b). [c] Bahasa Indonesia. [d] Bahasa Lindu/Tado. n: Observations of macaques consuming this species come only from *ad libitum* data (Riley, unpublished data).  —: not observed

**Table 2 Results of nutritional analyses: Crude protein, lipids, NDF, ADF, calcium, phosphorus (% DM and % OM) and metabolizable energy (ME)**

| | % Dry Matter (DM) | | | | | | | | % Organic Matter (OM) | | | | | ME[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DM | Protein | Lipid | NDF | ADF | Ca | P | Ca: P ratio | OM | Protein | NDF | ADF | TNC | Kcal/g (incl. NDF) |
| *Areca vestiaria* | 90.03 | 4.76 | 9.47 | 48.66 | 24.57 | 0.17 | 0.10 | 1.7 | 85.33 | 6.20 | 63.34 | 32.18 | 18.13 | 2.96 |
| *Arenga pinnata* | 86.26 | 4.31 | 0.16 | 32.19 | 14.84 | 1.77 | 0.05 | 35.4 | 78.34 | 6.38 | 47.64 | 22.32 | 45.75 | 2.77 |
| *Artocarpus teysmanii* | 90.3 | 9.48 | 5.95 | 22.16 | 20.18 | 0.42 | 0.15 | 2.8 | 85.61 | 6.47 | 58.58 | 26.26 | 31.56 | 2.64 |
| *Artocarpus vriescana* | 91.10 | 5.28 | 4.51 | 24.07 | 17.56 | 0.05 | 0.23 | 0.21 | 87.30 | 6.64 | 30.26 | 22.18 | 57.42 | 3.49 |
| *Elmerillia tsiampacca* | 92.19 | 7.98 | 25.72 | 39.34 | 31.63 | 0.10 | 0.15 | 0.66 | 90.33 | 9.59 | 47.24 | 38.05 | 12.29 | 4.31 |
| *Ficus elmeri* | 90.31 | 5.41 | 6.63 | 18.63 | 16.93 | 0.38 | 0.06 | 6.33 | 82.96 | 7.22 | 24.87 | 22.82 | 59.07 | 3.79 |
| *Ficus rirgata* | 82.65 | 5.83 | 3.55 | 20.62 | 26.24 | 1.39 | 0.09 | 15.44 | 76.19 | 9.25 | 32.75 | 42.43 | 52.35 | 3.43 |
| *Ficus sagittata* | 85.43 | 4.40 | 4.22 | 23.36 | 22.51 | 0.60 | 0.11 | 5.45 | 80.75 | 6.38 | 33.86 | 32.96 | 53.65 | 3.42 |
| *Ficus sp.1* | 92.27 | 6.34 | 2.18 | 38.87 | 38.17 | 0.43 | 0.29 | 1.48 | 83.46 | 8.23 | 50.48 | 50.01 | 38.46 | 2.82 |
| *Ficus sp.2* | 93.44 | 5.30 | 2.78 | 47.94 | 41.61 | 0.50 | 0.29 | 1.72 | 87.59 | 12.26 | 28.66 | 51.08 | 51.37 | 3.64 |
| *Pandanus sp.* | 90.94 | 3.86 | 3.84 | 58.31 | 43.67 | 0.27 | 0.11 | 2.45 | 87.98 | 4.82 | 72.88 | 54.76 | 17.50 | 2.34 |
| *Pinanga sp.* | 84.90 | 4.03 | 0.59 | 34.49 | 28.30 | 0.04 | 0.07 | 0.57 | 81.41 | 5.83 | 49.89 | 41.25 | 43.42 | 2.74 |
| *Timonius teysmanii* | 86.76 | 3.05 | 0.54 | 38.76 | 32.60 | 0.11 | 0.07 | 1.57 | 83.28 | 4.21 | 53.64 | 45.41 | 41.40 | 2.64 |
| *\* Theobroma cacao* | 85.15 | 3.20 | 0.04 | 5.75 | 4.68 | 0.04 | 0.14 | 0.28 | 83.38 | 4.51 | 8.10 | 6.62 | 87.34 | 3.79 |
| *Forest Fruit Mean (SD)* | *88.97 (3.36)* | *5.39 (1.75)* | *5.39 (6.65)* | *34.42 (12.4)* | *27.60 (9.48)* | *0.48 (0.53)* | *0.14 (0.08)* | *5.83 (9.77)* | *83.89 (4.04)* | *7.19 (2.17)* | *45.70 (14.71)* | *37.50 (11.52)* | *40.18 (15.83)* | *3.15 (0.57)* |

*cultivated resource

[a] Metabolizable energy (ME$_h$ kcal/g OM) was calculated as = [(4 x %TNC) + (4 x %CP) + (9 x %lipid) + (1.389 x %NDF)]/100 (Conklin-Brittain et al. 2006).

**Table 3 Nutritional composition of Tonkean macaque fruit diet compared to other frugivorous catarrhines**

| | Protein (%) | Lipids (%) | NDF (%) | ADF (%) | Ca (%) | P (%) |
|---|---|---|---|---|---|---|
| *Results from this study* | | | | | | |
| *Forest fruit mean* | 5.39 | 5.39 | 34.42 | 27.60 | 0.48 | 0.14 |
| *(SD)* | (1.75) | (6.65) | (12.4) | (9.48) | (0.53) | (0.08) |
| | | | | | | |
| *Other studies* | | | | | | |
| *Cercopithecus ascanius[a]* | 19 – 19.8 | 7.9 – 9.2 | — | 16.3 – 27.5 | 0.58 – 0.86 | 0.25 – 0.31 |
| *Cercopithecus ascanius[b]* | 16.6 – 17.6 | 3.4 – 3.6 | 31.3 – 31.7 | 19.0 – 19.7 | — | — |
| *Cercopithecus mitis[b]* | 16.2 – 17.6 | 2.6 – 3.5 | 32.3 – 33.2 | 19.9 – 20.2 | — | — |
| *Lophocebus albigena[b]* | 15.7 – 16.3 | 3.4 – 3.9 | 32 – 33.9 | 19.8 – 21.0 | — | — |
| *Macaca fuscata[c]* | 3.21 – 15.74 | — | 5.7 – 95.28 | — | — | — |
| *Macaca fuscata[d]* | 3.89 – 15.55 | 1.46 - 9.56 | 39.35 - 64.78 | — | — | — |
| *Macaca silenus[e]* | 4.9 - 6.9 | — | 44.8 - 54.4 | — | 0.31 | 0.20 |
| *Pan troglydytes[f]* | 9.5 | 2.5 | 33.6 | 19.6 | — | — |
| | | | | | | |
| *NRC suggested requirements[g]* | | | | | | |
| *Macaca sp.* | 8 | — | 10 | 5 | 0.55 | 0.33 |

**All values are percent dry matter.**

[a]Rode et al. (2006b)—Range for three study groups at Kibale National Park, Uganda; Values represent plant and insect portion of the diet; Ripe fruit comprised 44.6% – 59.7% of the diet (Chapman and Chapman, 2000).

[b]Conklin et al. (1998) –Kibale National Park, Uganda; Range of means for two study groups per primate species; Values represent the plant portion of the diet; Fruit comprised 20 – 25% of their diets.

[c]Iwamoto (1982)—Koshima Islet, Japan; Values represent fruit and seed portion of the diet (between 19.7 – 63.2% of the diet); NDF estimated by multiplying crude fiber by 2 (cf. NRC 2003).

[d]Jaman et al. (2010)—Semi-naturally forested enclosure, Primate Research Institute, Inuyama, Japan; Values represent fruit portion of the diet; Fruit/nuts comprised 39.5% of feeding records.

[e] Dierenfeld and McCann (1999)—Semi-free ranging on St. Catherine's Island, Georgia, USA; Range represents temporal variation; Values represent fruit portion of the diet; Fruit comprised 40.2% of feeding time; Median values reported for mineral content.

[f]Conklin et al. (1998)—Kibale National Park, Uganda; Mean of one group; Values represent the plant portion of the diet; Fruit comprised approximately 75% of the diet.

[g]Recommended values for overall diet (NRC 2003).

**Fig. 1 Cacao tree (top) and a farmer removing the beans and pulp (white part) from a cacao pod (bottom).**
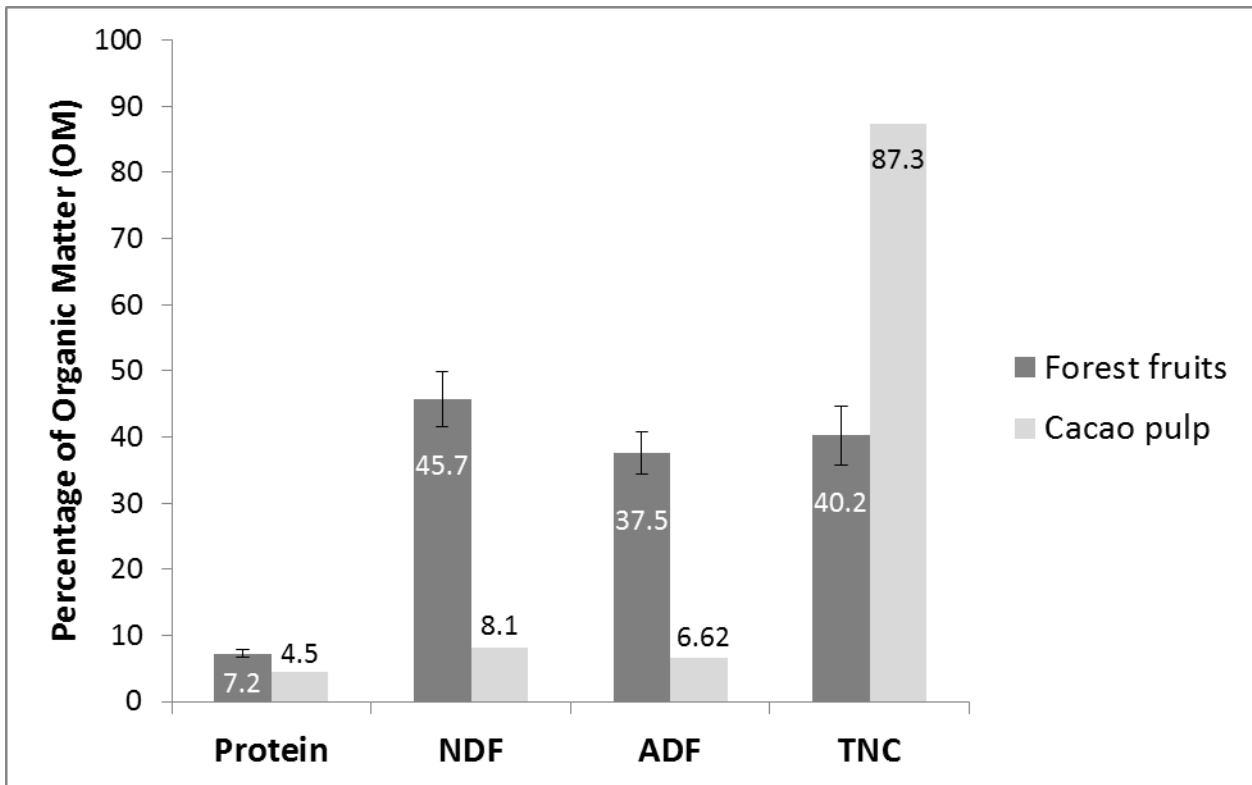
**Fig. 2 Comparison of mean values of protein, NDF, ADF and TNC for forest fruits with cacao pulp values. Error bars represent standard error of the mean.**
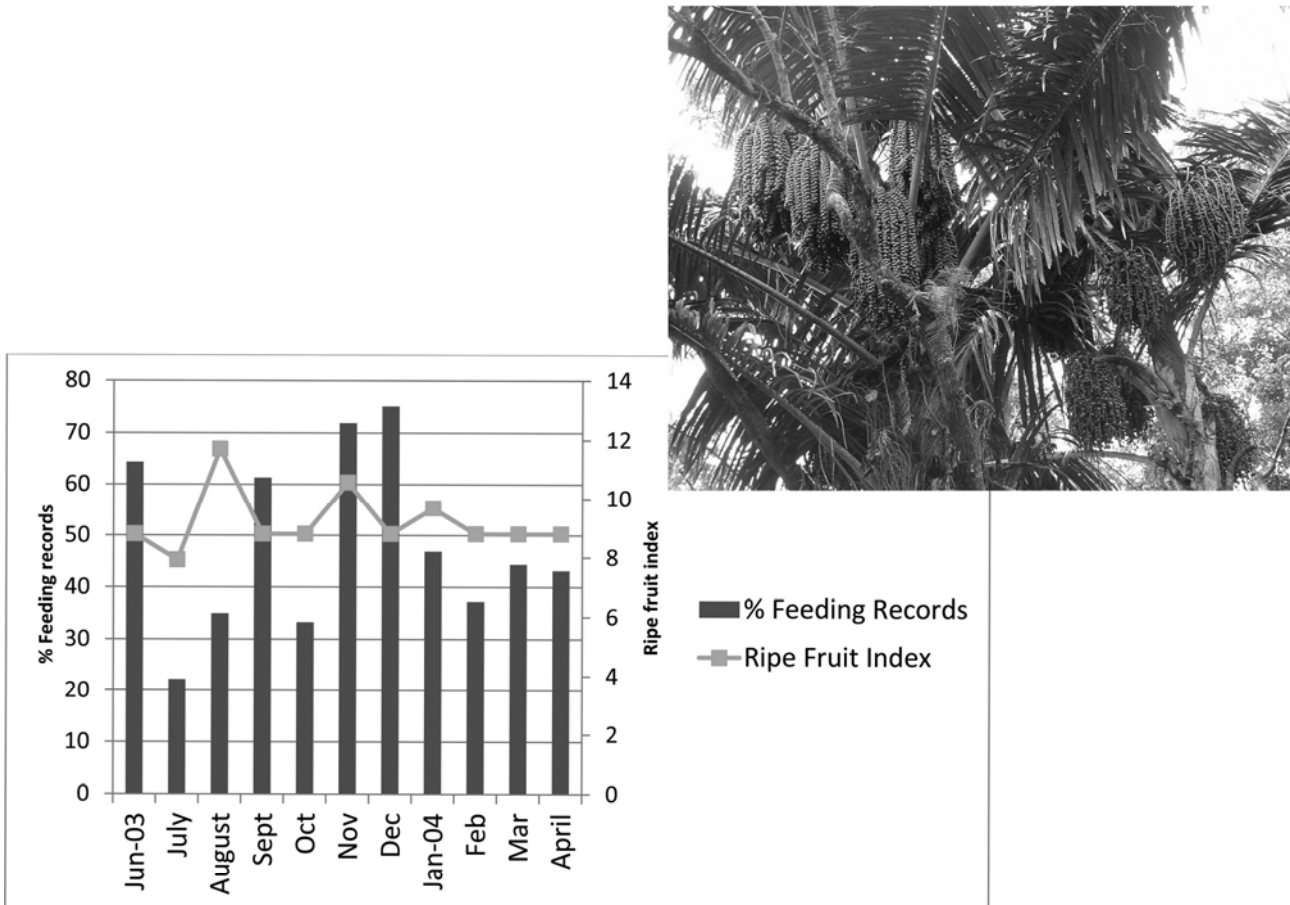
** $P \leq .001$

**Fig. 3** *Arenga pinnata* **palms (right) and Availability of ripe Aren palm fruit and percent feeding records devoted to Aren fruit over an 11-month period (Riley, unpublished data)**

Percent feeding records derive from scan sampling data. The ripe fruit index was calculated by multiplying the mean abundance score by the density of Aren palms in the habitat (Riley, 2007a).