

The Impact of Fallback Foods on Wild Ring-Tailed Lemur Biology: A Comparison of Intact and Anthropogenically Disturbed Habitats

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ABSTRACT Fallback foods are often viewed as central in shaping primate morphology, and influencing adaptive shifts in hominin and other primate evolution. Here we argue that fruit of the tamarind tree (*Tamarindus indica*) qualifies as a fallback food of ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve (BMSR), Madagascar. Contrary to predictions that fallback foods may select for dental and masticatory morphologies adapted to processing these foods, consumption of tamarind fruit by these lemurs leaves a distinct pattern of dental pathology among ring-tailed lemurs at BMSR. Specifically, the physical and mechanical properties of tamarind fruit likely result in a high frequency of severe tooth wear, and subsequent antemortem tooth loss, in this lemur population. This pattern of dental pathology is amplified among lemurs living in dis-

turbed areas at Beza Mahafaly, resulting from a disproportionate emphasis on challenging tamarind fruit, due to few other fruits being available. This is in part caused by a reduction in ground cover and other plants due to livestock grazing. As such, tamarind trees remain one of the few food resources in many areas. Dental pathologies are also associated with the use of a nonendemic leaf resource *Argemone mexicana*, an important food during the latter part of the dry season when overall food availability is reduced. Such dental pathologies at Beza Mahafaly, resulting from the use or over-emphasis of fallback foods for which they are not biologically adapted, indicate that anthropogenic factors must be considered when examining fallback foods. *Am J Phys Anthropol* 140:671–686, 2009. © 2009 Wiley-Liss, Inc.

It has been broadly noted that many primates encounter lean periods during which preferred resources are reduced. It has also been widely documented that alternative foods become essential during these periods (e.g., Brockman and van Schaik, 2005). During such periods, primates often focus on “fallback” resources for survival, and a number of recent workers have suggested that these foods may impact masticatory morphology, and/or drive adaptive shifts in primate and human evolution (e.g., Lambert et al., 2004; Laden and Wrangham, 2005; Vogel et al., 2008; Strait et al., 2009). Despite the presumed impact of these foods, there are numerous challenges in defining the term, and one may read of “fallback foods,” “keystone resources,” and even “keystone fallback foods,” all generally referring to foods that are important when other preferred foods are reduced. Indeed, as pointed out by Marshall et al. (2009), most publications on Malagasy primates have tended to use the term “keystone” rather than fallback foods. Since the majority of these papers were written in the 1990s (see Table 3.1 in Hemingway and Bynam, 2005), they were thus published during the same period when papers indicating the importance of the fallback food concept in great ape feeding ecology were just being published (Constantino and Wright, 2009). It is most likely that this lack of consensus reflects the slow diffusion of the term. We suggest that what have been generally referred to as “keystone” foods in these earlier lemur studies would better fit the more general term of fallback food. Here, we follow the general definition of fallback foods as “foods whose use is significantly negatively correlated

with the abundance of preferred foods” (Marshall et al., 2009). Marshall and Wrangham (2007) also differentiate between “filler” and “staple” fallback foods, with “staple” fallback foods being those that can comprise the entire diet, while “filler” fallback foods never do.

The use of fallback foods in strepsirrhine primates has been noted, but has rarely been directly assessed in terms of the operational definition of fallback foods as noted above. Wright et al. (2005), attempt to link overall fruit availability to weaning and argue that for lemurs, fruits serve as a “keystone resource for reproduction,” but do not test this directly. Hemingway (1998) notes the importance of mistletoe, *Bakerella clavata*, for diademed

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sifaka (*Propithecus diadema*) but does not call it a fallback or keystone resource per se. Irwin (2008), suggests that *Bakerella clavata* buds and flowers may be a fallback resource used by diademed sifaka in relatively intact habitats during the dry season when fruits and flowers are less abundant. Irwin (2008) specifically notes that, given that this species produces food year round, it is a reliable food resource. This species appears to be a staple resource in groups living in fragmented habitats, as it is used every month of the year. However, Irwin (2008) also reports that this species is very important even during times of fruit abundance. As such it would be of interest to see if this resource fits the general definition of fallback food, e.g. if the use of this food is significantly negatively correlated with preferred food abundance. Ralainasolo et al. (2008), document that endangered white collared brown lemurs (*Eulemur cinereiceps*), living within a highly degraded habitat at Manombo special reserve use a relatively high amount (25% of their feeding time across a 9-month-period) of nonendemic, introduced species as food items. Although they do not provide a clear definition of fallback foods, they point out that such nonendemic "fallback food opportunities" may be key to their survival. Soma (2006), has documented the use of an introduced plant species *Leucaena leucocephala*, by ring-tailed lemurs during the dry season when most resources are reduced at the Berenty reserve, and suggests that these may serve as potential fallback foods, although she does not directly test this. Fallback foods have also been linked to morphological traits in subfossil lemurs. For example, Rafferty et al. (2002), point out that *Archaeolemur*'s craniodental adaptations might be related to processing hard or tough fallback foods at critical times of the year.

In this article, we use behavioral, ecological, and phenological data collected over more than a 20-year-period at Beza Mahafaly Special Reserve (BMSR), Madagascar to 1) detail the use of fallback foods by the BMSR ring-tailed lemurs, and 2) assess the impact of specific fallback foods on this population. Given the suggested impact that fallback foods may have on primate and fossil hominin masticatory morphology [i.e., enamel thickness, facial form (e.g., Vogel et al., 2008; Strait et al., 2009; see discussion in Ungar et al., 2009)], we argue that observable patterns of tooth wear, dental pathology, and antemortem tooth loss in the BMSR *Lemur catta* population provide strong evidence that consumption of fallback foods may not necessarily be linked to enhanced processing abilities, especially in the context of habitats impacted by recent human actions, and discuss why this may be the case.

MATERIALS AND METHODS

Study site

Ecological, behavioral, and biological studies of the ring-tailed lemurs at BMSR, Madagascar (23°30'S, 44°40'E), have been carried out since 1987 (see summaries in Sauther et al., 1999; Sussman and Ratsirarson, 2006; Sauther and Cuzzo, 2008). Beginning in 2001, our research expanded outside of the protected reserve to focus on how anthropogenic factors are affecting the behavior and biology of this species. As such, our work provides an extensive and relatively unique dataset for

which to assess the use of fallback foods in a strepsirrhine species.

Data on BMSR phenology, behavior, and overall ecology presented here are based on over 20 years of ecological and behavioral studies (e.g., Sauther, 1992, 1998). BMSR includes a protected, fenced 80 ha parcel of intact gallery forest that has not been significantly affected by human disturbance for more than 20 years (Fig. 1a). This parcel is surrounded by habitat exhibiting various levels of anthropogenic disturbance (e.g., Cuzzo and Sauther, 2004; Sauther et al., 2006). The adjoining forest has been highly impacted by villagers that live in the area, with the adjacent gallery forest now dramatically altered by domestic animal grazing. As such, herbs, seedlings, and young saplings are continuously removed, resulting in very little ground vegetation or bushes remaining (Sauther, 1998; Fig. 1b; see also below). For example, using 25 2 × 2 m² seedling plots, Sussman and Rakotozafy (1994) compared herbs and liana regeneration within the reserve and in areas grazed by domestic animals. Seedling plots located within the gallery forest showed a much greater number of seedlings of herb and liana species used by *Lemur catta* as food resources as compared to the plots adjacent to but outside of the fenced reserve (Sauther, 1998). Mature, old growth (>25 cm DBH), *Tamarindus indica* trees dominate both the intact and disturbed forests (Sussman and Rakotozafy, 1994; Whitelaw et al., 2005). BMSR is a highly seasonal habitat, with both dry (May-September) and wet (October to April) periods (see Sauther, 1998; Yamashita, 2002; Ratsirarson, 2003). This seasonality has a dramatic effect on resource availability, with a reduction of resources during the dry season (see Fig. 2) (Sauther, 1998; Sauther et al., 1999; Yamashita, 2002).

Habitat structural comparisons presented here are from data collected in 2001 and allow us to directly compare the intact eastern gallery forest with the adjacent anthropogenically disturbed gallery forest just to the south. Because of the variable size of intact versus disturbed habitats large transects would have been possible in some habitats but not others. To make these transects consistent across habitats and reduce bias, 300 m line transect surveys were thus executed in each habitat. A handheld Magellan GPS attached to a Handspring Visor palm device (Handspring, Palm Computing, Sunnyvale, CA), was used to determine the approximate number of kilometers walked. Transects were walked in a predetermined compass direction so as to keep a straight line during the entire 300 m. Every 30 m we located the closest tree to this point (the focal tree) and collected the following: DBH (diameter at breast height) using DBH tape or calipers, tree height using a clinometer (Suunto, Vantaa, Finland), crown diameter, distance from focal tree to the nearest tree, and percent ground cover (0–100%) using a vertical densitometer (Geographic Resource Solutions, Arcata, CA). We recorded a total of 10 data points for each variable and each transect. Finally, to secure an objective measure and description of the number of tamarind trees (*Tamarindus indica*) in these habitats, we conducted 150-m-long line transect surveys specifically for this species. At each 10 m point we constructed a 5 m × 5 m square on each side of the transect line for a total of 15 sample points per habitat. We counted any adult, mature, productive (capable of fruiting) tamarind trees that were in the 5 m × 5 m square.



Fig. 1. Intact gallery forest: (a) compared with adjacent anthropogenically altered gallery forest (b) at Beza Mahafaly Special Reserve.

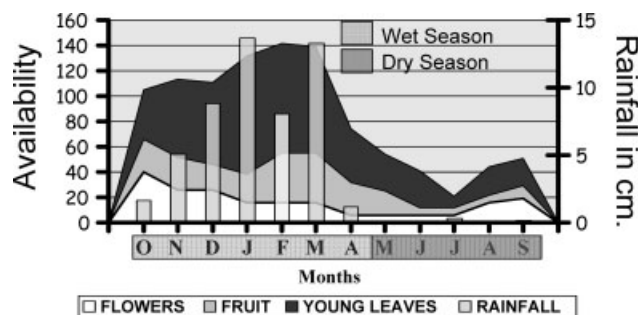


Fig. 2. Phenological availability of fruits used as food by ring-tailed lemurs within the intact gallery forest at Beza Mahafaly Special Reserve during 1987–1988. Phenological scores run from 4 (abundant) to 0 (absent) (see methods). Only two fruit species are available during most of the dry season (May–September). These are *Tamarindus indica* and *Enterospermum pruinatum*. Bars = rainfall; stacked areas = phenological availability.

Study subjects

The reserve and surrounding areas contain nine lemur troops who have been collared and tagged for our long-term studies. Adult ring-tailed lemurs at BMSR average 2,100–2,400 g, depending on habitat (Sauther et al., 2006), live in large social groups of 9–30 individuals (Sauther and Cuzzo, unpublished data), use all layers of the

forest but are also significantly terrestrial, and exploit a wide variety of food resources including fruit, flowers, and leaves (Sauther, 1998; Sauther et al. 1999). As of 2006, population size is ~225 individuals within this study area (Sauther and Cuzzo, 2008) and troops are found within both intact and human-altered habitats. It is important to note that as of 2008, the reserve has been expanded to 4,000 ha, and now includes the disturbed areas described herein.

Dental data (e.g., pathologies, wear, etc.), were collected from 2003 through 2008 at BMSR. Comparative dental data on 24 adult individuals were also collected May–June, 2006, at the spiny forest at Tsimanampesotse National Park (TNP), Madagascar. At TNP, we carried out three 1-km transects to characterize this habitat, and identified 42 plant species used by ring-tailed lemurs, with plants dominated by Euphorbiaceae, Didieraceae, and other xerophytic plant families. Among these 42 species, 22 (52%) are also found either within the BMSR gallery forest or BMSR spiny forest. However, *T. indica* is rare, being found only along a single transect that included a collapsed limestone depression with an ephemeral water source.

Feeding data collection

Feeding ecology data are based on focal animal sampling at 5-min intervals of 16 individuals living in two ring-tailed lemur groups (Sauther, 1992), and over

1,800-h of observations were collected. Both groups (Green and "old" Black) lived within the eastern portion of the gallery forest adjacent to the Sakamena River, which is an ephemeral river that flows only over a roughly 6-week period during the wet season, and is a dry riverbed for the rest of the year (Sauther, 1992). One of these groups (Green) has maintained their home range for more than 20 years; the other group disintegrated in the mid-1990s. These lemur groups also crossed the dry riverbed to exploit the leaves of a local cultigen, the sweet potato known as bageda (*Ipomoea batatas*) during the dry season.

Because ring-tailed lemurs are semi-terrestrial, observation of feeding behavior was excellent. Only a small percentage of feeding bouts during the 5-min samples were missed due to the subject being out of sight to the observers. These occurred during the first two preliminary weeks of observation and are not included in the analyses. Food intake is presented as total number of food items by species and part ingested monthly. Plant parts (e.g., leaves, flowers, fruits) for all ring-tailed lemur food species except *T. indica* fruit were very small and were ingested by the lemurs one item at a time. Each 5-min sample spent feeding on these foods is thus a reflection of the consumption of one food item of that species and part. Data presented here thus represents the minimum actual number of foods actually ingested, rather than simply time spent feeding. Given that the study encompassed over 1,800-h of observational data throughout the year, we are confident that most if not all food species/parts were recorded. A slightly different method was used when comparing use of the fruits of *T. indica*. When feeding on this fruit, the pod would be held in one hand, and the lemur would place the tip into the side of the mouth, and then crack and remove the hard covering (i.e., the exocarp). The individual would then lick the fruit until a single seed with its surrounding flesh could be bitten off. The seed and covering were then swallowed whole. An individual was scored as feeding on *T. indica* only if a seed had been ingested. Otherwise, it was scored as "licking." It should be noted that ring-tailed lemurs primarily focus on ripe fruit of *T. indica* (e.g., Sauther, 1992; Yamashita, 2002; Cuozzo and Sauther, 2006b; Cuozzo et al., 2008) and both feeding and phenology measurements are for ripe, not green *T. indica* fruit.

Plant phenology

Specific phenological and feeding ecology data were collected across a 12-month period from 1987 to 1988 (Sauther, 1992). However, lemur feeding ecology and phenology at BMSR are highly consistent from year to year for nondrought years, with similar patterns reported by Yamashita (2008a), during her work at BMSR in 2000, as well as demonstrated by ongoing yearly phenological data collected by the Water and Forestry Department of the University of Antananarivo (Ratsirarson et al., 2001). The phenology of 119 trees and 31 species were monitored monthly in 1987–1988. Within each troop's home range, all trees directly adjacent to six separate 100-m trails were monitored. These six trails were distributed randomly within each troop's home range. Each phenological sample was made the day just prior to the start of the monthly observations for the troops. Samples included ring-tailed lemur food trees as well as trees not included in their diet during

the 13-month study. Phenological availability was estimated for flowers, fruits, leaf buds, young leaves, and mature leaves for each tree by a scoring system. Tree scores ranged from 0 to 4, with 4 denoting 100% coverage. Thus a tree in full fruit would have a score of 4, a score of 3 if $\sim 3/4$ of the tree's crown had fruit a score of 2 if $1/2$ of the crown was covered, a score of 1 if only $1/4$ was covered, and a score of 0 if none was present. The phenological availability of herbs was not directly assessed (Sauther, 1992). Unless otherwise noted, data come from nondrought years and phenological data are from the intact gallery forest.

Statistical analyses

Simple linear regressions were used to compare phenological availability with food intake. A χ^2 test was used to compare antemortem tooth loss and interstitial tooth wear patterns of troops with home ranges that 1) include the riverbed and thus human crops or nonendemic introduced plant species, and 2) with those whose home ranges do not include these areas. Forest structure characteristics were compared using a student's unpaired *t*-test to determine if there were any significant differences in the means of these variables in each habitat. All tests are two-tailed with significance set at $P < 0.05$.

RESULTS

Ring-tailed Lemur fallback foods at BMSR

Habitat traits for intact riverine gallery forest versus disturbed gallery forest. The comparison of forest characteristics for the intact versus disturbed gallery forest revealed no differences in mean tree height, mean tree DBH, mean nearest neighbor DBH, mean crown diameter, or mean number of mature *Tamarindus indica* trees, which dominate both areas (Table 1). The habitats did differ in ground cover, and thus presence of ground herbs, with the disturbed habitat having relatively little ground cover compared to the intact forest ($t = 6.82$, $df = 18$, $P < 0.0001$). Gemmill and Gould (2008) also compared these same areas during the late dry season (June to September) in 2004, using eight 25 m² plots in both microhabitats. Of the trees used as food resources by ring-tailed lemurs, *T. indica* was the most abundant resource in the intact forest and was the second most abundant resource in the disturbed gallery forest.

Fruits. Food availability is very seasonal at BMSR, with ring-tailed lemurs characteristically exploiting resources as they become available, so much so that food species used from one month to the next may change nearly completely (Sauther, 1992, Simmen et al., 2006). Ring-tailed lemurs closely track these resources and use them as they become available, sometimes walking for long distances to monitor these foods (Sauther, 1998). Two species used as foods by ring-tailed lemurs produce fruits asynchronously and thus are available year or nearly year round (Table 2). These are the fruits of "Kily" *T. indica* (Fig. 3a) and "Mantsake" *Enterospermum pruinatum* (= *Coptosperma nigrescens*, Degreef et al., 2001; = *Tarenna pruinatum*, Gemmill and Gould, 2008) (Fig. 3b). All other fruits are available for only short periods, often only several weeks. During the dry season (May to September), there is a dramatic reduction of resources, especially fruit, with only *T. indica* and *E. pruinatum* widely available and utilized by the ring-tailed lemurs during this time (Table 2). At this time ring-tailed

TABLE 1. Summary of forest characteristics by habitat

Habitat	Mean tree height (m)	Mean focal tree DBH (cm)	Mean NN distance (m)	Mean crown diameter (m)	Mean number of mature <i>Tamarindus indica</i> trees	Mean ground cover*
Intact gallery forest	6.77	9.95	1.32	2.82	0.72	75%
Disturbed gallery forest	5.95	10.50	1.86	2.78	0.67	7.5%

DBH = diameter at breast height, NN = tree nearest to sampled focal tree. “*” denotes significant differences.

TABLE 2. Phenological availability fruits and flowers of monitored trees used as food by ring-tailed lemurs within the intact gallery forest at Beza Mahafaly Special Reserve during 1987–1988

Species	November	December	January	February	March	April	May	June	July	August	September	October
<i>Antidesma petiolare</i> FR	0	1	2	1	1	0	0	0	0	0	0	0
<i>Corralocarpus greveii</i> FR	0	0	0	2	2	2	0	0	0	0	0	0
<i>Enterospermum pruinatum</i> FR	0	0	1	2	3	3	2	2	2	1	1	0
<i>Grewia grevei</i>	0	0	2	0	0	0	0	0	0	0	0	0
<i>Grewia humbertii</i> FR	0	0	0	1	3	2	1	0	0	0	0	0
<i>Grewia triflora</i> FR	0	0	1	0	1	0	0	0	0	0	0	0
<i>Gyrocarpus americanus</i> FL	0	0	0	0	0	0	0	0	0	0	2	1
<i>Maerua filiformis</i> FR	0	0	0	0	0	0	0	0	0	2	1	0
<i>Salvadora angustifolia</i> FR	3	0	0	0	0	0	0	0	0	0	0	4
<i>Talinella dolphinensis</i> FR	0	0	2	2	1	1	0	0	0	0	0	0
<i>Tamarindus indica</i> FR	2	2	2	3	1	1	1	1	2	3	3	2

Phenological scores run from 4 (abundant) to 0 (absent) (see methods). Note that only two fruit species are available during most of the dry season (May–September). These are *Tamarindus indica* and *Enterospermum pruinatum*. FR = Fruit, FL = Flower.

lemurs from both microhabitats, intact and disturbed, focus primarily on *T. indica*. For example, Gemmill and Gould (2008) compared two troops at BMSR during this time period in 2004, one troop in the intact forest and the other in the disturbed adjacent forest. They found that for the top 10 foods eaten at BMSR the group living in the intact forest spent the majority of their time feeding on *Argemone mexicana* leaves, and on *T. indica* fruits. Likewise, the group living in the adjacent disturbed gallery forest fed primarily on *T. indica* fruit.

Table 3 illustrates monthly fruit intake. For most months only one or two fruits form the bulk of fruit intake; however given the seasonal environment, the fruit species emphasized change from month to month. During months when other fruits or flowers are available, lemurs focus on those, and limit their use of *T. indica* fruit. For example, in November they fed on little or no *T. indica* fruit, focusing almost entirely on *Salvadora angustifolia* fruits. *T. indica* is not the top fruit used for most months, but it is the top or only fruit eaten across most of the dry season. It is also used in December, but there are few other fruits available at that time (see Table 2). To assess if this resource fits the operational definition of a fallback food (those foods correlated negatively with the abundance of preferred foods), as proposed by Marshall et al. (2009), we conducted a regression analysis comparing *T. indica* fruit intake with the availability of preferred fruits. The result indicates that *T. indica* fruit fits this definition of

a fallback food ($Y = 130.452 - 25.968 \cdot x$, $R^2 = 0.59$, $P = 0.003$, $n = 11$). We also performed a regression analysis between fruit intake and their phenological availability. This analysis illustrates that preferred foods are used both disproportionately, and are also only used when seasonally available. For example, *Salvadora angustifolia* fruit use is markedly tied to its availability ($Y = -0.008 + 0.188 \cdot x$, $R^2 = 0.85$, $P = 0.0001$, $n = 11$) as is *Talinella dolphinensis* fruit ($Y = -0.023 + 0.237 \cdot x$, $R^2 = 0.75$, $P = 0.0003$, $n = 11$); in contrast, *T. indica* use is not tied to its phenological availability for most months ($Y = 0.205 - 0.046 \cdot x$, $R^2 = 0.12$, $P = 0.27$, $n = 11$) (Fig. 4a).

The only other fruit available during the dry season, *E. pruinatum*, is used sparsely, despite it being available for most months (see Table 2). We found no significant relationship between *E. pruinatum* intake and availability of preferred fruits ($Y = 9.199 - 2.855 \cdot x$, $R^2 = 0.36$, $P = 0.89$, $n = 11$). Its use as a food item is also not tied to its phenological availability. Indeed, it is only used during the dry season (Fig. 4b).

Leaves. The ring-tailed lemurs at BMSR use a variety of leaf species (especially young leaves), but these are also highly seasonal (see Fig. 2). Within the intact reserve, terrestrial herbaceous leaves and scrambling shrubs and vines are especially important. For example, the top two leaf resources in terms of both monthly use and yearly total use are both ground plants, one a scrambling shrub, *Metaporana parvifolia obtusa*, and the



Fig. 3. Fallback fruits for ring-tailed lemurs at Beza Mahafaly Special Reserve. Fruits of *Tamarindus indica*, with arrow pointing to the tough fibers that encase the fruit (a) and the small round fruits of *Enterospermum pruinatum* (b).

other an herbaceous plant, *Commicarpus commersonii*, (Table 4). During the late dry season (June–September), when overall food availability is especially low (see Fig. 2), the mature leaves of *Ipomoea batatas* and *Argemone mexicana* become important (Table 4). This is the only time of the year that they are normally used, with these two species alone making up 42% (122 of 290) of the ring-tailed lemur leaf diet during those 4 months (Table 4). Both of these species are introduced, while the majority of other leaves and fruits eaten by ring-tailed lemurs at BMSR are endemic (Ratsirarson et al., 2001; but see discussion on *Tamarindus indica* below). *A. mexicana* (Mexican thistle) is a weed native to the Neotropics, but naturalized world wide (Shaukat et al., 2002), while *Ipomoea batatas* are sweet potatoes cultivated by the local Mahafaly. Unlike the fruit data, we were unable to clearly determine any preferred leaf species, as the top leaf species changed considerably from month to month, and there were few months when lemurs focused on only one leaf species. Also, as we did not assess the availability of herbaceous species directly, we were not able to compare leaf intake of *A. mexicana* and *I. batatas* with availability of preferred leaves.

The impact of fallback foods on BMSR ring-tailed lemur biology

T. indica is a physically and mechanically challenging food resource. All fruits used by ring-tailed lemurs at BMSR except *T. indica* are small and easy to swallow with little to no processing required (e.g., Fig. 3b) (Sauther et al., 1999). *T. indica* fruits are very large, and possess both hard and tough outer casings as well as tough fibers encasing the fruit (Fig. 3a) (Sauther, 1992, 1998; Yamashita, 2000, 2002, 2003, 2008b; Cuozzo and Sauther, 2004, 2006a, 2006b; Cuozzo et al., 2008). However, *L. catta* possess among the thinnest enamel of all extant primates for which data are available (e.g., Shellis et al., 1998; Godfrey et al., 2005). At BMSR, this species shows a remarkably high frequency of tooth wear and pre-mortem loss (defined here as complete absence of the tooth crown with only worn roots remaining, or no trace of the tooth remaining with healed gingiva), with over 20% of the study population displaying tooth loss (Sauther et al., 2002; Cuozzo and Sauther, 2004, 2006a, 2006b; Cuozzo et al., 2008; Millette et al., 2009). Figure 5 illustrates the range of extensive tooth wear and pre-mortem tooth loss, from individuals with intact dentition to nearly edentulous lemurs. This range of severe wear and tooth loss is seen across all troops, i.e., both those living within the intact gallery forest as well as those living in the adjacent, anthropogenically altered gallery forest (see Fig. 2) (Cuozzo and Sauther, 2004, 2006b). As we have argued elsewhere (e.g., Cuozzo and Sauther, 2004, 2006a, 2006b; Cuozzo et al., 2008), this high frequency of excessive wear, and the resulting tooth loss, is primarily related to the challenging physical, mechanical, and chemical properties of *T. indica*. Specifically, consuming this fruit requires processing the hard, tough outer casing as well as the continual scraping of tough internal fibers across ring-tailed lemur's thin tooth enamel (Cuozzo and Sauther, 2004, 2006a, 2006b; Cuozzo et al., 2008).

It is important to note that this dramatic pattern of wear and tooth loss is not the result of the population maintaining an excessively high number of old individuals due to the “protection” of individuals in a reserve. Indeed, there is intense predation pressure on these lemurs by both feral and endemic animals (see review in Goodman, 2003; Brockman et al., 2008; Sauther and Cuozzo, unpublished data). Among the ring-tailed lemur skeletal sample housed at BMSR, there is a concave mortality curve, with near equal numbers of young and old specimens recovered within the reserve (Cuozzo and Sauther, 2006b), which is similar to the mortality curve of sympatric sifaka (*Propithecus verreauxi*) (Richard et al., 2002). There are also high rates of dental wear in preadult ring-tailed lemurs (Cuozzo and Sauther 2006b). Figure 6a illustrates a typical preweaned (~4-months old) individual from the intact gallery forest with no visible wear. However, Figure 6b shows a postweaned individual, also from the intact gallery forest, whom, at only ~10-months old (based on the pattern of dental eruption), exhibits severe wear on the deciduous teeth. As ring-tailed lemurs are weaned in the months before the difficult dry season, these young individuals are shifting to an adult diet that emphasizes *T. indica* fruit (Sauther et al., 1999), with dramatic effects on their deciduous teeth. We have observed postweaned juveniles frequently processing tamarind fruit (Cuozzo and Sauther, 2006b).

TABLE 3. Total number of fruits and flowers eaten by plant species and month within the intact gallery forest at Beza Mahafaly Special Reserve during 1987–1988

Fruit species	November	December	January	February	March	April	May	June	July	August	September	October	Yearly total
<i>Antidesma petiolare</i> FR	0	6	71	13	3	0	0	0	0	0	0	0	93
<i>Azima tetracantha</i> FR	0	0	0	0	0	0	0	0	0	0	0	3	3
<i>Catanaregum spinosa</i> FR	0	0	0	0	0	0	0	0	0	5	1	20	26
<i>Cissus microdonta</i> FR	0	0	0	0	0	12	8	1	0	0	0	0	21
<i>Corralocarpus greveii</i> FR	0	0	0	6	14	0	0	0	0	0	0	0	20
<i>Cynachum nodosum</i> FR	0	2	0	0	0	0	0	0	0	0	0	0	2
<i>Enterospermum pruinatum</i> FR	0	0	0	0	0	0	37	19	3	0	0	0	59
<i>Flacourtia ramontchi</i> FR	0	0	0	0	0	5	0	0	0	0	0	0	5
<i>Grewia clavata</i> FR	0	0	32	174	3	0	0	0	0	0	0	0	176
<i>Grewia greveii</i> FR	0	0	0	0	0	3	0	0	0	0	0	0	3
<i>Grewia humbertii</i> FR	0	0	0	0	11	2	2	0	0	0	0	0	15
<i>Grewia leucophylla</i> FR	0	0	0	0	123	75	2	0	0	0	0	0	200
<i>Grewia triflora</i> FR	0	0	5	20	7	0	0	0	0	0	0	0	32
<i>Gyrocarpus americanus</i> FL	0	0	0	0	0	0	0	0	0	0	22	5	27
<i>Lablab boivinii</i> FR	0	0	0	0	0	0	4	1	0	0	0	0	4
<i>Maeurua filiformis</i> FR	0	0	0	0	0	0	0	6	2	0	0	0	8
<i>Marsdenia</i> sp. FL	0	0	11	2	0	0	0	0	0	0	0	0	13
<i>Salvadora angustifolia</i> FR	231	0	1	0	0	0	0	0	0	0	0	245	477
<i>Scutia myrtina</i> FR	0	0	3	24	2	0	0	0	0	0	0	0	29
<i>Seyrigia gracilis</i> FR	0	0	2	2	22	2	5	12	1	20	0	1	67
<i>Talinella dauphinensis</i> FR	0	9	208	200	0	0	0	0	0	0	0	0	408
<i>Tamarindus indica</i> FL	26	0	0	0	10	5	11	3	1	0	112	120	288
<i>Tamarindus indica</i> FR	10	106	42	57	102	113	88	170	186	147	25	52	998
<i>Quivisianthe papinae</i> FL	0	0	0	0	0	0	0	0	0	26	365	0	391
<i>Vitex</i> sp. FR	0	0	15	0	0	0	0	0	0	0	0	0	15

FR = fruit, FL = flower.

As it is possible that this pattern of tooth wear and loss is simply the normal pattern of wear for this species, we expanded our work in 2006 to include the spiny forest at TNP, where *T. indica* is rare (Sauther and Cuozzo, 2008). In striking contrast to our observations at BMSR, no individuals in this population displayed significant tooth loss (Table 5), with the lone individual noted in Table 5 showing functional loss (through excessive wear) of only the left and right first maxillary molars (Cuozzo and Sauther, in preparation). In the BMSR gallery forest, over 20% of the population displays the same (or often an even greater) degree of tooth loss, primarily the result of excessive wear (Cuozzo and Sauther, 2006b). Although the two samples differ in size, the trend seen at TNP indicates a dramatically different pattern. This has been supported by our analysis of 16 *L. catta* museum specimens housed across three collections from other locations in southern Madagascar, none of which come from riverine gallery forest habitats dominated by tamarind, (Cuozzo and Sauther, 2008, in prepa-

ration). Of these, only one shows antemortem tooth loss, and in this case only a single tooth (Cuozzo and Sauther, 2008, in preparation). Severe tooth wear and antemortem tooth loss have also been qualitatively described at the Berenty reserve (see Cuozzo and Sauther, 2006b), a habitat where tamarind dominates the *L. catta* diet (e.g., Simmen et al., 2006), but is rare in other habitats where *T. indica* is not frequent, such as Tsimanampetse and the museum samples we have examined. It is thus clear that the use of tamarind fruit, and its challenging properties, as an important resource, corresponds to the pattern of severe tooth wear and tooth loss seen in the BMSR ring-tailed lemur population (e.g., Cuozzo and Sauther, 2006b, 2008; Cuozzo et al., 2008).

Given the potential effect of habitat alteration on these patterns, we also compared the percentage of tooth loss among adult females (greater than three years of age) living within the intact gallery forest with females living in the anthropogenically-altered forests (Table 6). We included only adult females, as female ring-tailed

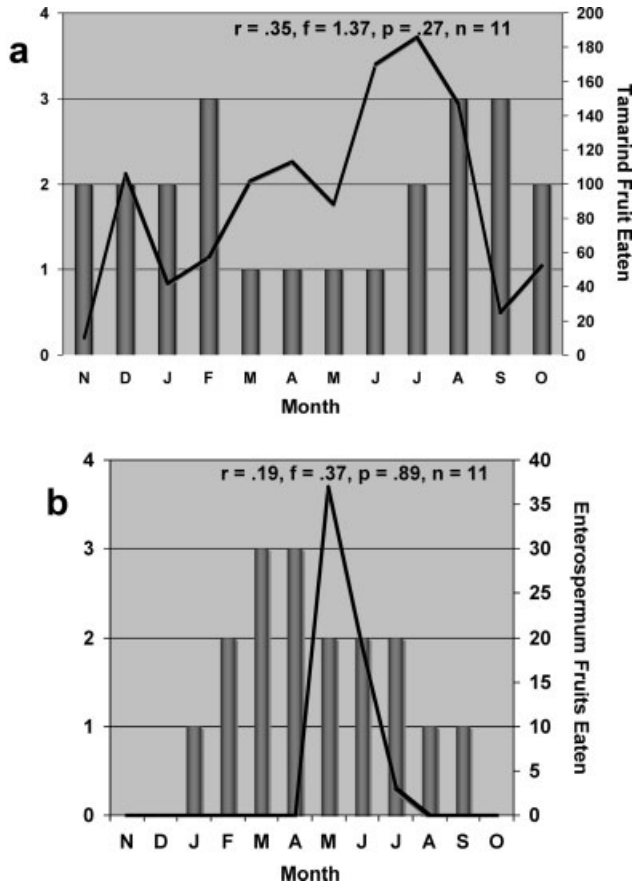


Fig. 4. (a) Relationship between phenological availability (bars), and lemur intake (lines), within the intact gallery forest at Beza Mahafaly Special Reserve: *Tamarindus indica* fruit, (b) Relationship between phenological availability (bars), and lemur intake (lines), within the intact gallery forest at Beza Mahafaly Special Reserve: *Enterospermum pruinatum* fruit.

lemurs usually remain in their natal groups, thus their patterns of tooth wear and loss should directly reflect their habitat (e.g., Sauther et al., 1999). Females living in altered habitat show both more frequent, and a greater percentage, of tooth loss ($P < 0.05$), indicating that the impact of tamarind fruit as a fallback on the biology of this population is being enhanced by human actions.

As noted previously, leaf use varies by species throughout the year, with two introduced species, *A. mexicana* and *I. batatas* being important foods during the dry season. These species are likely additional fallback food resources. For example, Gemmill and Gould (2008) documented that during the dry season of 2004, *A. mexicana* and *I. batatas* were respectively the top, and third most, important food resources for intact gallery forest lemurs at BMSR. *A. mexicana* leaves are extremely fibrous and requires lemurs to gnaw through the fibers to ingest the leaves (Figs. 7a,b). This plant only grows in the disturbed areas along the sandy river bottom. Those groups whose home range includes the riverbed, and who thus have access to these resources, exhibit a number of dental pathologies not seen in other groups. These pathologies appear related to the processing of *A. mexicana*. This includes a peculiar pattern of interstitial wear that primarily occurs between the

molars, and/or the between the anterior molar and the most distal premolar (see Fig. 8). Such interstitial wear appears related to repeatedly pulling the fibers of *A. mexicana* across and between these teeth (Fig. 7b) as lemurs chew off sections of the plant. We compared 43 female ring-tailed lemurs for interstitial wear relative to whether their home range included the riverbed and hence access to *A. mexicana*. Interstitial wear is markedly tied to riverbed access with 41.2% (7 of 17) of individuals living in this area of the reserve exhibiting such wear. In contrast, only 3.8% (1 of 26) living away from the river exhibit this dental pathology ($\chi^2 = 11.98$, $df = 1$, $P < 0.0005$). Such wear allows leaf stems and other leaf materials to subsequently become wedged between the teeth, which can create damage to gum tissue (Fig. 9a,b). A consequence of this interstitial wear is that these impacted materials may decay and lead to dental decay and/or gingival infection, as seen in Figure 9b.

DISCUSSION

Fallback fruits at BMSR

Numerous other researchers have noted the importance of *T. indica* for the BMSR ring-tailed lemurs (e.g. Yamashita, 2002, 2008b; Gemmill and Gould, 2008), and *T. indica* has been called a keystone resource for ring-tailed lemurs at both BMSR and the Berenty reserve by a variety of researchers (Jolly, 1966; Sussman and Rakotozafy, 1994; Sauther, 1998; Blumenfeld-Jones, 2006; Mertl-Millhollen et al., 2006; Gemmill and Gould, 2008). We agree with Marshall et al. (2009), that given the different meanings of this term to biologists and ecologists, it would be better to call this plant species a fallback resource when referring to its use by a single primate species (see below). As noted at this site, the strong seasonality of resource availability, especially fruits, creates a bottleneck during the dry season when most resources become less available for ring-tailed lemurs. Our results indicate that *T. indica* fits the operational definition of a fallback food for wild ring-tailed lemurs at BMSR, in that it is an important resource during the dry season of reduced food availability, and its use is negatively correlated with the availability of preferred foods (see overview by Marshall and Leighton, 2006; Marshall et al., 2009), with preferred fruits defined here as those fruits used disproportionately, relative to other fruits. In addition, it is the only food resource that is used every month of the year (Table 3). While *E. pruinatum* does not fit the operational definition of a fallback food, it is an additional fruit resource during the dry season and is the only other fruit emphasized during normal, non-drought year, dry seasons. Other researchers have noted its use as a dry season resource at BMSR (Gemmill and Gould, 2008). A key characteristic for both plants is that as they fruit asynchronously they are available year or nearly year round.

How *T. indica* fits into current classifications of staple versus filler fallback foods is more difficult (Marshall et al., 2009). Our analysis shows that there are no resources used by ring-tailed lemurs that provide the only food during low preferred food availability, thus fitting the definition of a staple fallback food (Marshall and Wrangham, 2007). However, when we distinguish between fruits and leaves, *T. indica* fruit does appear to fit the description of a "staple" fallback fruit (Marshall and Wrangham, 2007), in that it can serve as the only

TABLE 4. Monthly total number of leaves used as foods (based on 5-min focal samples) within the intact gallery forest at Beza Mahafaly Special Reserve during 1987-1988

Leaf species	November	December	January	February	March	April	May	June	July	August	September	October	Yearly total
<i>Acacia roovumae</i> (tree).	0	0	0	0	0	0	0	0	0	4	20	0	24
<i>Acalypha</i> sp. (climbing vine)	0	0	0	0	3	0	0	0	0	0	0	0	3
<i>Antidesma</i>	4	1	1	0	0	0	0	0	0	0	0	0	6
<i>madagascanariense</i> (shrub)													
<i>Argemone mexicana</i>	0	0	0	0	0	0	0	5	23	2	0	0	30
(ground herb)													
<i>Aristolochia aurita</i>	0	2	1	2	1	2	0	0	0	0	0	0	8
(climbing vine)													
<i>Bytneria voluily</i> (shrub)	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Capparis chrysomeia</i>	0	0	0	2	0	0	0	0	0	1	3	0	4
(climbing vine)													
<i>Cedrelopsis grevei</i> (tree)	0	7	1	0	2	0	0	0	2	2	0	32	44
<i>Commicarpus</i>	1	1	10	4	3	16	6	24	7	9	0	2	83
<i>commersonii</i> (ground herb)													
<i>Crotalaria</i> sp. (ground herb)	0	0	6	1	1	0	0	0	0	0	0	0	8
<i>Flueggea obovata</i> (shrub)	0	0	0	0	3	0	0	0	0	0	0	0	3
<i>Gloriosa superba</i>	0	14	1	0	0	0	0	0	0	0	0	0	15
(ground herb)													
<i>Ipomoea batatas</i> (climbing vine)	0	0	0	0	0	0	1	28	22	42	7	0	93
<i>Justicia glabra</i> (ground herb)	0	0	4	3	3	2	3	2	1	7	3	0	28
<i>Maerua filiformis</i> (tree)	0	0	0	0	0	0	0	0	0	13	0	0	13
<i>Marsdenia</i> sp. (climbing vine).	0	12	13	28	6	0	1	0	0	0	0	2	62
<i>Metaporana parvifolia</i>	17	59	54	39	24	14	15	6	24	0	3	15	270
<i>obtusa</i> (scrambling shrub)													
<i>Paederia grandidieri</i>	0	0	2	3	2	26	40	7	2	0	0	0	82
(climbing vine)													
<i>Lalab purpureus</i> (climbing vine)	0	0	0	2	25	9	6	0	1	5	0	0	48
<i>Secomone</i> sp. (ground herb).	0	0	1	0	13	2	5	12	7	0	0	1	20
<i>Talinella dauphinensis</i> (shrub)	11	9	3	1	3	28	34	0	0	0	0	3	92
<i>Tamarindus indica</i> (tree)	2	1	4	0	5	4	0	0	0	1	6	2	13

The dry season of reduced food availability is May through September. Plant type (ground herb, shrub, tree, climbing vine) is noted in parentheses.

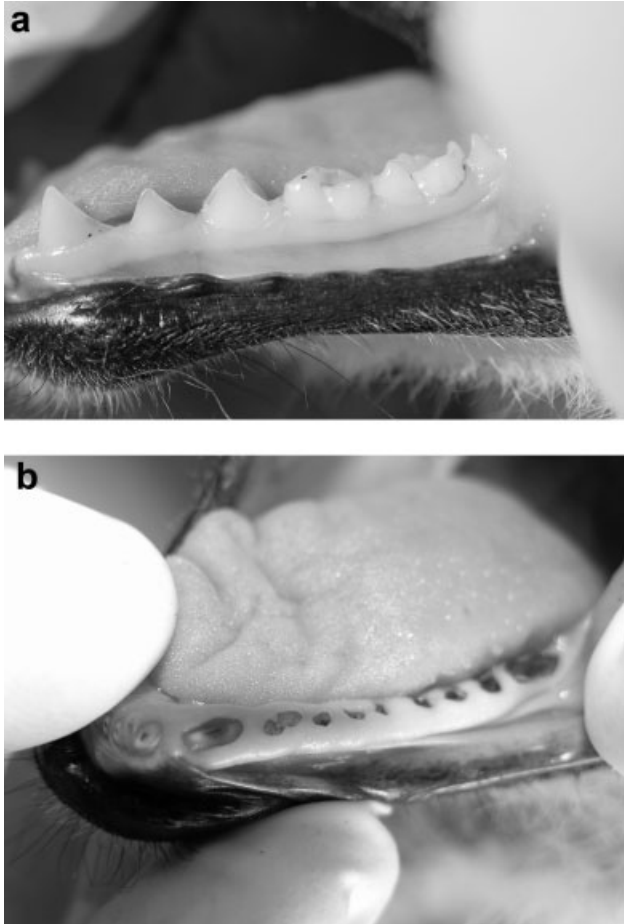


Fig. 5. Tooth loss in ring-tailed lemurs at Beza Mahafaly Special Reserve. (a) Limited wear for mandibular teeth in *Lemur catta* (Green 303). (b) Absence of *Lemur catta* mandibular teeth, with only worn roots remaining (Blue 138).

fruit source when other, preferred foods are not available.

Marshall et al. (2009) expect that staple fallback foods are usually low quality, and filler fallback foods are high quality, based on rate of nutrient yield. Lambert (2007) ties quality to energy yield and posits a continuum of fallback strategies, from low quality fallback foods (e.g., bark and leaves) that are abundant, but that require anatomical adaptations at one end, to high quality fallback foods (e.g., fruits and seeds) that are less abundant but may be mechanically protected (hard shells for example). *T. indica* exhibits a “staple” fallback fruit pattern, but is not necessarily a low quality resource. It does appear to fit most closely to Lambert’s (2007) description of a high quality fallback food. As noted by Yamashita (2008a), ripe *T. indica* at BMSR has a high sugar content that makes this fruit an important energy resource for ring-tailed lemurs. In this sense, it is not a low-quality resource. However, *T. indica* is also the toughest of foods used by ring-tailed lemurs at BMSR, with overall toughness of their *T. indica* diet greater than the sympatric sifaka (Yamashita, 2008b), *Propithecus verreauxi*. At BMSR *T. indica* fruit is the top fruit consumed by both ring-tailed lemurs and sifaka (Loudon and Sauther, unpublished data). However, while ring-tailed lemurs focus on ripe fruits, sifaka feed almost exclusively on

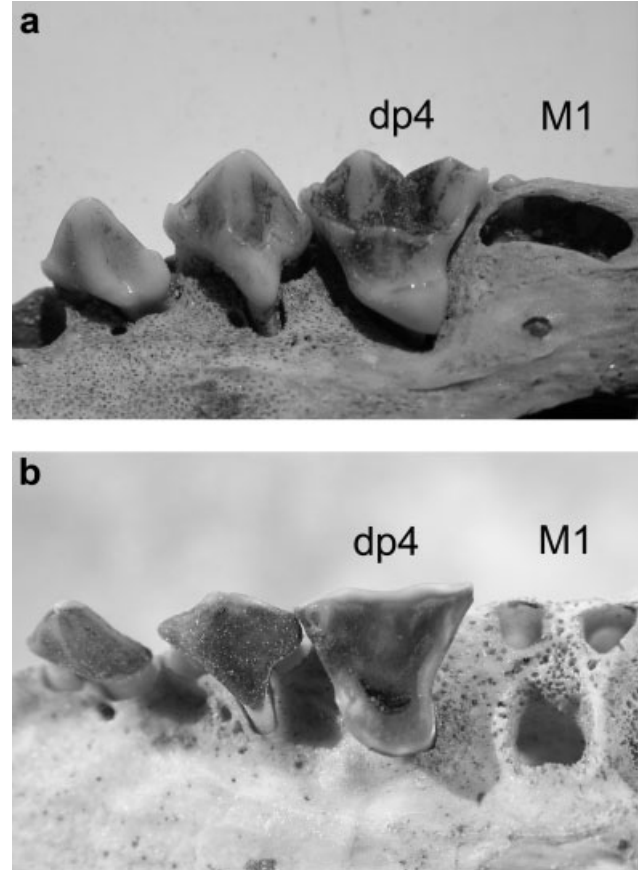


Fig. 6. Deciduous tooth wear in subadult ring-tailed lemurs at Beza Mahafaly Special Reserve. (a) Pre-weaned individual ~4-months old (b) Post-weaned individual ~10-months old.

TABLE 5. Number and percentage of antemortem tooth loss in individual adult ring-tailed lemurs from the gallery forest and surrounding habitat at Beza Mahafaly Special Reserve compared with samples from Tsimanampetse National Park

% Antemortem tooth loss ^a	Beza Mahafaly	Tsimanampetse
0	116 (78.9%)	23 (95.8%)
1–10	9 (6.1%)	1 (4.2%)
11–20	10 (6.8%)	0
21–30	5 (3.4%)	0
31–40	2 (1.4%)	0
41–50	1 (0.7%)	0
51–60	2 (1.4%)	0
61–70	1 (0.7%)	0
71–80	0	0
81–90	1 (0.7%)	0
91–100	0	0
Total % with loss	21.1%	4.2%
	<i>n</i> = 147	<i>n</i> = 24

^a % tooth loss represents the number of teeth missing in an individual ÷ by the total of number of tooth positions (36) × 100.

unripe fruits, which are not as tough (Yamashita, 2008b). Sifaka at BMSR neither show the pattern nor the extent of wear seen in BMSR ring-tailed lemurs (Cuozzo and Sauther, 2006b). In this sense, for ring-tailed lemurs, it is a resource that is relatively more

TABLE 6. Number and percentage of antemortem tooth loss in individual female adult ring-tailed lemurs from the intact and anthropogenically altered gallery forest at Beza Mahafaly Special Reserve, 2003–2008

% Antemortem tooth loss ^a	Intact gallery forest	Anthropogenically altered gallery forest
0	35 (89.2%)	24 (68.6%)
1–10	1 (2.6%)	5 (14.3%)
11–20	2 (5.1%)	1 (2.9%)
21–30	0	0
31–40	1 (2.6%)	2 (5.7%)
41–50	0	1 (2.9%)
51–60	0	1 (2.9%)
61–70	0	1 (2.9%)
71–100	0	0
Total % with loss	10.3%	31.4%
	<i>n</i> = 39	<i>n</i> = 35

Females are greater than three years of age in this sample.

^a % tooth loss represents the number of teeth missing in an individual ÷ by the total of number of tooth positions (36) × 100. $\chi^2 = 5.11$, $df = 1$, $P < 0.02$.

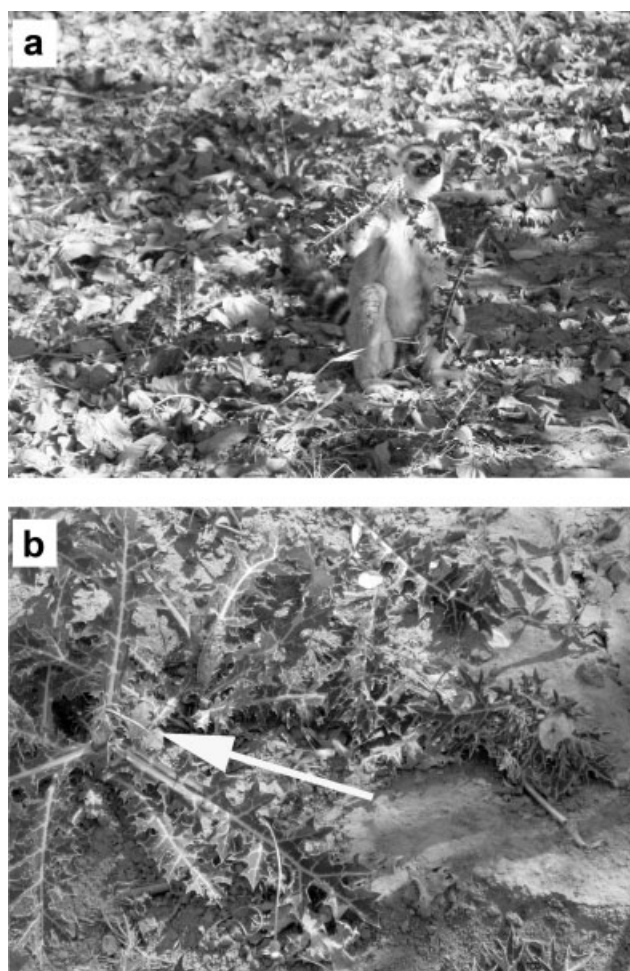


Fig. 7. Ring-tailed lemur feeding on *Argemone mexicana* at Beza Mahafaly Special Reserve: (a) shows a lemur in the process of biting off a portion of the leaf; (b) shows the fibrous “strings” from a plant that has been processed by the lemur. The leaf has been chewed at the base to remove the leaf stem. Photos by Marni La Fleur.



Fig. 8. Interstitial wear in a ring-tailed lemur with access to the BMSR riverbed. Note resorption of mandibular bone between m1 and m2.

abundant during the dry season (indeed it is one of the few fruits available), but it is also more mechanically challenging than other fruits, all of which are small and much less tough (Yamashita, 2008b). The ability to mechanically process specific foods, especially those fallback foods that allow survival during periods of nutritional stress, may provide a selective advantage that likely plays a key role in the evolution of primate and hominin dental and/or masticatory morphology (e.g., Vogel et al., 2008; Strait et al., 2009), for example enamel thickness. A number of studies support this view (e.g., Lambert et al., 2004; Ungar, 2004; Teaford and Ungar, 2007; Vogel et al., 2008; Strait et al., 2009; but see Porter et al. 2008, for a discussion of the role of preferred and year-round foods in explaining morphological adaptations in several New World primates). Dental morphology often reflects a strong correspondence to dominant foods (see reviews in Lucas, 2004 and Cuozzo and Yamashita, 2006). We should thus expect ring-tailed lemurs to develop behavioral, anatomical and/or physiological adjustments to the challenging mechanical properties of *T. indica* (Lambert, 2007).

Ring-tailed lemur dental morphology, although possessing some adaptations for processing leaves [e.g., elongated shearing crests (Seligsohn, 1977; Yamashita, 1998)], does not demonstrate specialized folivorous adaptations, for example as seen in *Propithecus* sp. (Yamashita, 1998; see review in Cuozzo and Yamashita, 2006). Yamashita (2008b) recently suggested that the mechanical properties of *T. indica* may be selecting for a more folivorous, i.e. more sifaka-like dental morphology, in ring-tailed lemurs. However, this remains to be directly tested, as this lemur species is found within a wide variety of habitats in southern Madagascar, including high altitude as well as spiny forest habitats (Goodman et al., 2006), where *T. indica* is likely to be rare or absent. To date, the dental morphology of *Lemur catta* living in tamarind-dominated forests, where most behavioral and ecological studies have taken place, has not been evaluated in terms of the presence of folivorous features (e.g., elongated shearing crests).

We recently documented a rapid increase in tooth size in the BMSR *L. catta* population, likely attributed to the excessive use of *T. indica* fruit. We collected data on

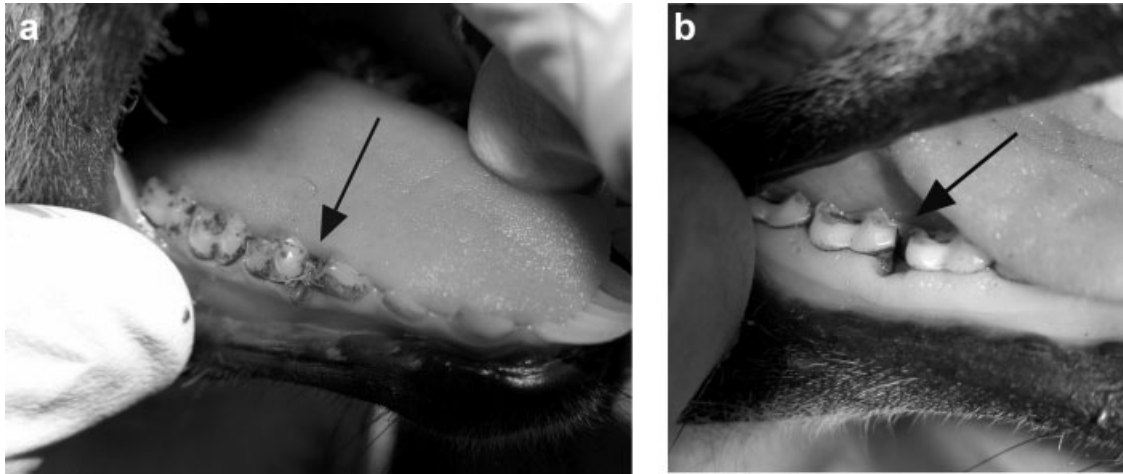


Fig. 9. Leaf stems and other leaf material wedged between the molar teeth in a ring-tailed lemur with access to human crops and introduced plants: 9a shows both a leaf stem and other leaf material wedged between p4 and m1; 9b shows the hole in the gum after removal of the stem and leaves as well as decayed root and gingival resorption in a wild ring-tailed lemur at BMSR. Arrow denotes the area of interstitial wear and pathology (i.e. dark area on mesial border of m2).

dental dimensions (see Sauther et al., 2001) of several teeth frequently used when processing tamarind fruit, collected from dental casts prepared in 1987/1988, prior to a severe drought in the early 1990s, during which mortality rates increased dramatically (Gould et al., 1999, 2003). We collected the same dental measurements from a ring-tailed lemur sample, all born after the early 1990s drought, in 2003/2004. Data from the 2003/2004 set indicate a significant increase in several measurements in the population, when compared to dental dimensions from the sample prior to the drought (Cuozzo and Sauther, 2006a), thus suggesting a microevolutionary shift, similar to that documented in other vertebrates, resulting from an emphasis on a single food, during a period of extreme ecological stress (Cuozzo and Sauther, 2006a). In a high attrition environment, such as that seen at BMSR resulting from frequent consumption of tamarind, increased tooth size would have been beneficial for processing a large, challenging food like tamarind fruit. During this drought, tamarind was one of the few foods available for the BMSR ring-tailed lemurs, thus its use apparently resulted in a rapid, biological shift in this population with individuals with larger tooth dimensions better able to survive the drought, and thus produce surviving offspring. In this example the importance of this fallback food was likely enhanced during periods of reduced food availability, such as during the drought in 1991–1992 (see detailed discussion in Cuozzo and Sauther, 2006a).

Lambert (2007), has pointed out that primates using fallback strategies that focus on high quality foods may develop behavioral adjustments and tool use. It is also possible that ring-tailed lemurs may buffer themselves from morphological change via behavioral changes. At BMSR, dentally impaired lemurs (i.e., those with greater than 10% tooth loss) show a variety of behavioral adjustments to such tooth loss. This includes spending time foraging when others are resting, retrieving partially processed tamarind pods that have been discarded by others, and novel processing of tamarind pods including removing ripe tamarind fruit's hard exocarp by hand (Cuozzo and Sauther, 2006b; Millette et al., 2009).

Excessive tooth wear, although not quantified, has also been noted (see earlier discussion) at the gallery forest habitat at the Berenty reserve (Soma and Crawford, personal communications; see Cuozzo and Sauther, 2006b), located in Southwestern Madagascar, where *T. indica* is also the dominant tree resource (Simmen et al., 2006). We do not see such a pattern at the spiny forest of Tsimanampesotse, where *T. indica* is very rare, and where there are no known plants with the same challenging mechanical traits. Of the 14 *L. catta* foods recently examined at Tsimanampesotse, none exhibited the toughness values of unripe *T. indica* fruit at BMSR (Yamashita et al., unpublished data). Such regional differences indicate that not all ring-tailed lemurs have as dentally challenging a diet as those at BMSR.

Ring-tailed lemurs at BMSR both begin to exhibit severe tooth wear, and lose their teeth, starting at an early age (Cuozzo and Sauther, 2006b), and exhibit such a high level of tooth wear, that we suggest that this population represents a mismatch between a fallback food, and dental morphology for the BMSR ring-tailed lemurs. There are at least several reasons why this may be the case. One possibility is that ring-tailed lemurs are capable of using *T. indica* in moderation, but that they are disproportionately emphasizing it at BMSR. For example, anthropogenic forces may have altered either the habitat, or the ecological community, in such a way to result in an over-dependence on this fruit. We have shown that outside of the protected gallery forest, ground herbs and other resources have been removed such that during a normal, nondrought, dry season *T. indica* is one of the few food items available (Whitelaw et al., 2005). Our results reported here (Table 3), indicate that percentage of antemortem tooth loss is indeed higher in these areas. However, this type of tooth loss has been observed since the inception of our long-term, 20-year research at BMSR, and has historically occurred among all troops both within and outside of the protected gallery forest parcel (Sauther et al. 2002). As habitat alteration and destruction have increased over this time in areas outside of the protected parcel, it is highly possible that this pattern reflects more recent anthropo-

genic change that exacerbates the already existing pattern of severe wear and tooth loss.

As noted, it is also possible that a change in the ecological community has occurred. For over 2,000 years, human activity, either direct (e.g., hunting, clearing of forests), or indirect (e.g., increased cattle grazing), has dramatically altered Madagascar's fauna, including the extinction of all of the island's "giant" lemurs (e.g., Godfrey and Jungers, 2002, 2003; Burney et al., 2003, 2004; Perez et al., 2005). Thus, the surviving lemurs live within communities, and in habitats, that are very different from those in which these species evolved. At BMSR, living ring-tailed lemurs are part of a remnant community that once included at least six large (>10 kg) lemur species (Godfrey et al., 2001), all of which became extinct during the past 2,000 years, some only within the past millennium (e.g., Godfrey and Jungers, 2002; Burney et al., 2004). While *T. indica* dominates the gallery forests at BMSR, the surrounding dry spiny forests are dominated by other species, such as *Alluaudia procera* (Ratsirarson et al., 2001). Today ring-tailed lemurs live within both areas, but it is possible that the large now extinct, sympatric lemurs primarily used gallery forest habitats, and may have been able to more effectively process large tamarind fruit, without the negative impact on their dentition, as seen in *L. catta*. For example, several of the large extinct lemurs from this area (e.g., *Archaeolemur*) possessed extremely thick dental enamel (Godfrey et al., 2005), which would likely have provided some resistance to the challenging mechanical properties of tamarind fruit. With the extinction of these large forms, ring-tailed lemurs are now able to exploit, or even disproportionately consume, a resource that in the past may have been more limited to them. Critical to this is determining how long *T. indica* has been a dominant tree species in gallery forests such as Berenty and BMSR. While recent molecular data indicate that *T. indica* in Madagascar is most closely related to those of continental Africa, where it is known as a long-domesticated plant (e.g., Diallo et al., 2007), the origin of tamarind trees in Madagascar is debated, and is known to correlate to areas of human settlement (e.g., Schatz, 2001; Du Puy et al., 2002), though DuPuy et al. (2002) suggest that the reliance on tamarind by lemurs in southern Madagascar indicates it being endemic to the island. Also critical is to determine the plant community before human occupation in the area. If, for example, human impact has reduced the dry spiny forest community, then this may have also led to ring-tailed lemurs searching out and exploiting these gallery forest environments. These questions are the focus of our ongoing work in southern Madagascar. This work will also determine the tooth wear patterns of nearby *L. catta* populations who live within the spiny forests.

Fallback leaves at BMSR

It is more difficult to operationally define fallback leaf resources at BMSR. The lemurs exploit a wide variety of leaves and for most months switch to newly available leaf species much like they do with fruits. However, there are no leaves that can be operationally defined as fallback resources. The dry season does appear to be a challenge in terms of both fruit and leaf resources. We found that two introduced species, *I. batatas* and *A. mexicana*, are important at this time, especially during the late dry season months of July and August during which

they comprised nearly 50% of the *L. catta* leaf diet (Table 4). Naturalized *I. batatas* is commonly found in the dry riverbed, but the BMSR lemurs will also move considerable distances from the reserve, and across the riverbed, to exploit planted crops of *I. batatas*. From a conservation perspective, *I. batatas* leaves are an important source of protein during the dry season (Gould and LaFleur, in preparation). However, using such resources makes these lemurs extremely vulnerable to both aerial predators such as the harrier hawk (*Polyboroides radiatus*, Sauter, 2002), as well as dogs, as there are few or no trees to escape to when exploiting these resources (Sauter, personal observations).

A. mexicana is also an important dry season leaf resource at BMSR, and is exploited during both normal and drought years (Gould et al., 1999; Gemmill and Gould, 2008). However, it is not used in the gallery forest of Berenty (Simmen et al., 2006). This plant has a number of mechanical challenges that include thin fibrous leaf parts that appear to lead to marked interstitial wear in those individuals living near the riverbed. This type of wear leads to additional dental pathologies such as decayed roots and gingival resorption (see Fig. 9b). There is at least one other documented case in Madagascar where the addition of a nonendemic plant resource produces negative results. As previously noted, Soma (2006) documented that during the dry season of low food availability at Berenty, ring-tailed lemurs focus on *Leucaena leucocephala*, an introduced species. Since its introduction 15 years ago, this species has become one of the most important fallback foods at Berenty, as it has a very high protein content [36.1 g of protein per 100 g dry weight (Soma, 2006)], with leaves, flowers, and unripe seeds all consumed. Soma (2006) describes introduced species at Berenty as important fallback resources and notes that *L. leucocephala* is heavily used during the dry season when preferred fruits are not available. However, *L. catta* is not physiologically adapted to using this plant, which has led to "bald lemur syndrome" in individuals focusing on this plant (e.g., Jolly, 2008). This condition involves the massive loss of hair across the body and is related to a nonprotein amino acid, mimosine, which reduces cell division (e.g., Jolly, 2008).

Both of these examples indicate that, as primates include new fallback resources in response to anthropogenic effects, these foods are also challenging, as they may have neither dental nor physiological adaptations for these new foods. The data we present above (e.g., Table 3) illustrate that short-term human actions linked to forest degradation and the removal of the forest under-story over the past 20 years enhance the impact of a specific fallback food (tamarind) on BMSR ring-tailed lemur tooth wear and loss. In addition, the role of tamarind and its negative impact on the biology of these lemurs transcends recent human actions and may also be linked to human-influenced extinctions over the past 2,000 years that resulted in the elimination of the larger lemur species that were once a part of the original community.

CONCLUSIONS

We would argue that understanding the role of fallback foods for primate species can be quite complicated. For example, at a gross level, animals require a variety of nutrients, and determining the relative importance of

different types of fallback foods is important. For the BMSR ring-tailed lemurs that live within a complex habitat which includes both intact gallery forest and anthropogenically altered landscapes, they have the behavioral plasticity to include new and novel resources such as *A. mexicana* and *I. batatas*. However, there may be costs to such behavior, both in terms of predation and dental pathology. *T. indica* fruit is an important fallback resource, but appears to be over-emphasized in this population, resulting in a dramatic, but clearly identifiable anatomical marker, seen in patterns of dental pathology (i.e., severe tooth wear and frequent antemortem tooth loss). We tie this to a lack of alternative fruits during the dry season, as well as the timing of weaning, which result in young lemurs having to deal with the mechanical challenges of *T. indica* fruits right from the start. These effects are exacerbated in areas affected by anthropogenic change. Since many primate habitats have been dramatically altered by human actions, we propose that anthropogenic change is an important additional factor that must be taken into account when determining the role of fallback foods in shaping primate traits.

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