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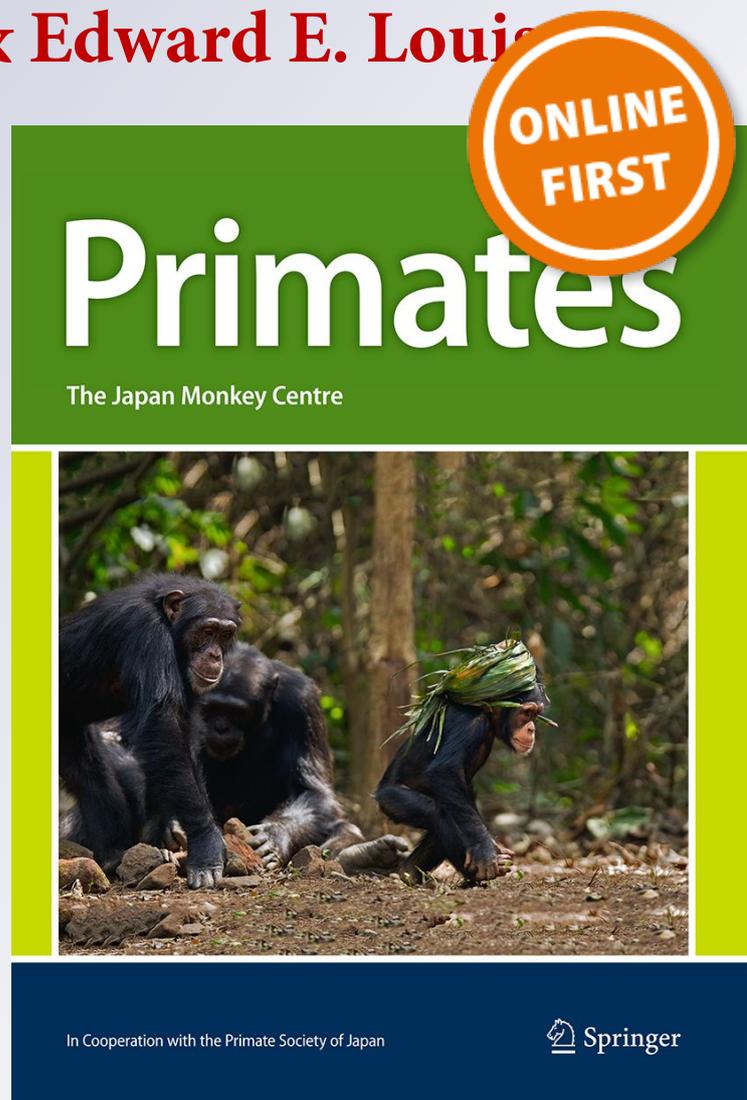
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Primates

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Comparing the use of live trees and deadwood for larval foraging by aye-eyes (*Daubentonia madagascariensis*) at Kianjavato and Torotorofotsy, Madagascar

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Abstract Aye-aye (*Daubentonia madagascariensis*) feeding behavior has become synonymous with deadwood foraging. However, deadwood is not always the most frequently used substrate, as some aye-eyes use live trees more often to access invertebrates. We sought to compare the frequency of aye-aye invertebrate foraging in deadwood and live trees to better understand their feeding behaviors. We followed two male aye-eyes at Kianjavato, a heavily disturbed habitat in southeastern Madagascar, from October 2013 to October 2014, and one male and one female aye-aye at Torotorofotsy, a continuous forest in eastern Madagascar, from July 2014 to December 2015. We collected feeding data by recording the behavior of a focal aye-aye every 5 min for a total of 373 h at Kianjavato and 383 h at Torotorofotsy. Our results showed no difference in the amount of deadwood used between the individuals. However, there was a significant difference in the amount of live tree feeding between the female at Torotorofotsy and one of the males at Kianjavato. We conclude that feeding on invertebrates in live trees is more important to aye-eyes than previously realized and that aye-eyes are

exceedingly flexible in their invertebrate feeding behaviors, adjusting to their habitat by using various substrates.

Keywords Aye-aye · Larvae · Feeding behavior · Disturbed forest · Continuous forest

Introduction

Aye-eyes (*Daubentonia madagascariensis*) possess a unique combination of morphological features, including continuously growing incisors, elongated digits, and a ball and socket metacarpophalangeal joint in their third digit (Owen 1863; Cartmill 1979; Martin 1990; Simons 1995; Soligo 2005). It is well documented that aye-eyes use these adaptations to extract and consume larvae from deadwood and other various substrates, a behavior known as percussive foraging (Erickson 1991, 1995; Erickson et al. 1998). In fact, aye-aye percussive foraging has become so synonymous with deadwood that some research, including that aimed at determining presence and examining foraging activities, is focused primarily on deadwood feeding (Albignac 1987; Duckworth 1993; Rahajanirina and Dollar 2004; Farris et al. 2011; Sefczek et al. 2012; Thompson et al. 2016; Miller et al. 2017). Very few studies have considered the behaviors of wild aye-eyes and from what substrates they are extracting invertebrates.

To date, a two-year research project on the island of Nosy Mangabe represents the most complete behavioral study of aye-eyes (Sterling 1993, 1994a). Aye-eyes extracted larvae from a variety of substrates including “fallen deadwood, dead branches on living trees, living trees, dead and living lianas, beneath the bark of living trees and inside parasitized seeds” (Sterling 1993 p. 117; Sterling 1994a p. 146). These results indicated larvae were

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removed from 29 species of trees; less than half (12) of the species were live trees containing larvae within the pith or under the bark (Sterling 1994a, b p. 147). Other observations have supported these findings or added other species to this list: *Afzelia bijuga* (Leguminosaceae) tree galls (Pollock et al. 1985), dendemivavy (*Anthocleista madagascariensis*, Gentianaceae) and dendemilahy (*Anthocleista amplexicaulis*, Gentianaceae) (Erickson 1995), and the fohanasity tree (*Psychotria* sp., Rubiaceae) (Sefczek 2012). Considering Madagascar has high levels of endemic floral species (Myers et al. 2000) and the geographic dispersal of aye-ayes across a variety of habitat types (Ganzhorn and Rabesoa 1986; Simons 1993; Sterling 1994b), it is likely that aye-ayes use even more species of live trees to forage for invertebrates. In fact, because primate feeding behaviors are closely tied to habitat conditions and so habitat composition and resource availability can influence a species' food choice (Clutton-Brock 1977), it is likely that in some locations aye-ayes use live trees more than deadwood to access larvae (Andriamisedra et al. 2015).

As aye-ayes consume invertebrates from both live trees and deadwood (Sterling 1993, 1994a; Andriamisedra et al. 2015), and as habitat conditions can influence food selection, it is important to understand differences in invertebrate assemblages before predicting aye-aye resource use. Previous research on arthropod assemblages indicates four categories of larval plant hosts: (1) healthy host, (2) weakened host, (3) stressed host, and (4) dead host (Hanks 1999). Since various invertebrates require hosts of differing quality, arthropod species diversity within a given habitat is dependent on forest composition (Martikainen et al. 2000) and disturbance history (Bishop et al. 2009). Therefore, habitat conditions could influence which substrates aye-ayes select when foraging for invertebrates. In the case of saproxylic beetles, such as those identified as an important aye-aye resource (Sterling 1993, 1994a), species richness may not depend on diversity of tree species (Lachat et al. 2007), but richness and abundance are strongly related to the presence of large-diameter trees (Grove 2002). Since large-diameter trees are more prevalent in old-growth forests than disturbed or plantation forests (Grove 2002; Lachat et al. 2007), we would expect greater species diversity and abundance of invertebrates—specifically, more of those requiring healthy or weakened hosts—in continuous forest. Interestingly, even though species richness and abundance are greater in shaded or closed-canopy forests, arthropod assemblages in temperate forests tend to concentrate in greater quantities per piece of deadwood in an open-canopy, disturbed forest (Bouget et al. 2013; Jabin et al. 2004). Though it is uncertain how these results translate to tropical forests, this could explain why arthropods are more common and present in greater

numbers around dead hosts in disturbed forests, while a greater diversity and abundance of invertebrates are found in continuous forests.

In a two-month study of aye-aye feeding traces, Andriamisedra et al. (2015) found that aye-ayes in a protected southeastern rainforest used live trees more often than deadwood for invertebrate foraging. Simultaneously, aye-ayes in an unprotected western dry forest used deadwood more frequently than live trees when foraging for larvae (Andriamisedra et al. 2015). We sought to further evaluate the importance of living trees for aye-aye foraging behavior by analyzing feeding behaviors of aye-ayes in two rainforests over the course of one year. Our goals were to identify species of live tree that aye-ayes use for invertebrate foraging (1), and to compare the frequency of live tree and deadwood foraging in aye-aye invertebrate feeding, monthly and annually (2). Given the greater species richness and abundance of arthropod assemblages in continuous forest (Grove 2002), which likely includes arthropods that use healthy or weakened hosts, we predicted that in continuous forest with minimal human impact, aye-ayes would use live trees more than deadwood to consume invertebrates. Conversely, in a disturbed habitat, where arthropods are more abundant near deadwood and occur as a clumped resource, aye-ayes would use deadwood more frequently than live trees to consume invertebrates.

Methods

Ethical note

All of our research was authorized by Madagascar's Ministry of the Environment, Ecology and Forests. Our research complies with protocols approved by the IACUC of Henry Doorly Zoo and Aquarium in Omaha (97-001, 12-101).

Study sites

We conducted research from October 2013 to October 2014 in the disturbed southeastern rainforest of Kianjavato (21° 17'S and 47° 27'E), and from July 2014 to December 2015 in the continuous eastern rainforest of Torotorofotsy (18° 46' S and 48° 25'E), both in Madagascar (Fig. 1). The Kianjavato Classified Forest consists of a farming area, a coffee plantation, and secondary forest fragments, including Tsitola (954 ha), Ambatovaky (50 ha; connected to Tsitola by a thin forest corridor), and Sangasanga (64 ha) (Holmes et al. 2013, 2016). Torotorofotsy is a Ramsar site (1100 ha) that is connected to Mantadia National Park (Dolch et al. 2004; Peck 2004).

Fig. 1 Locations of the field sites in Kianjavato (*bottom*) and Torotorofotsy (*top*), Madagascar

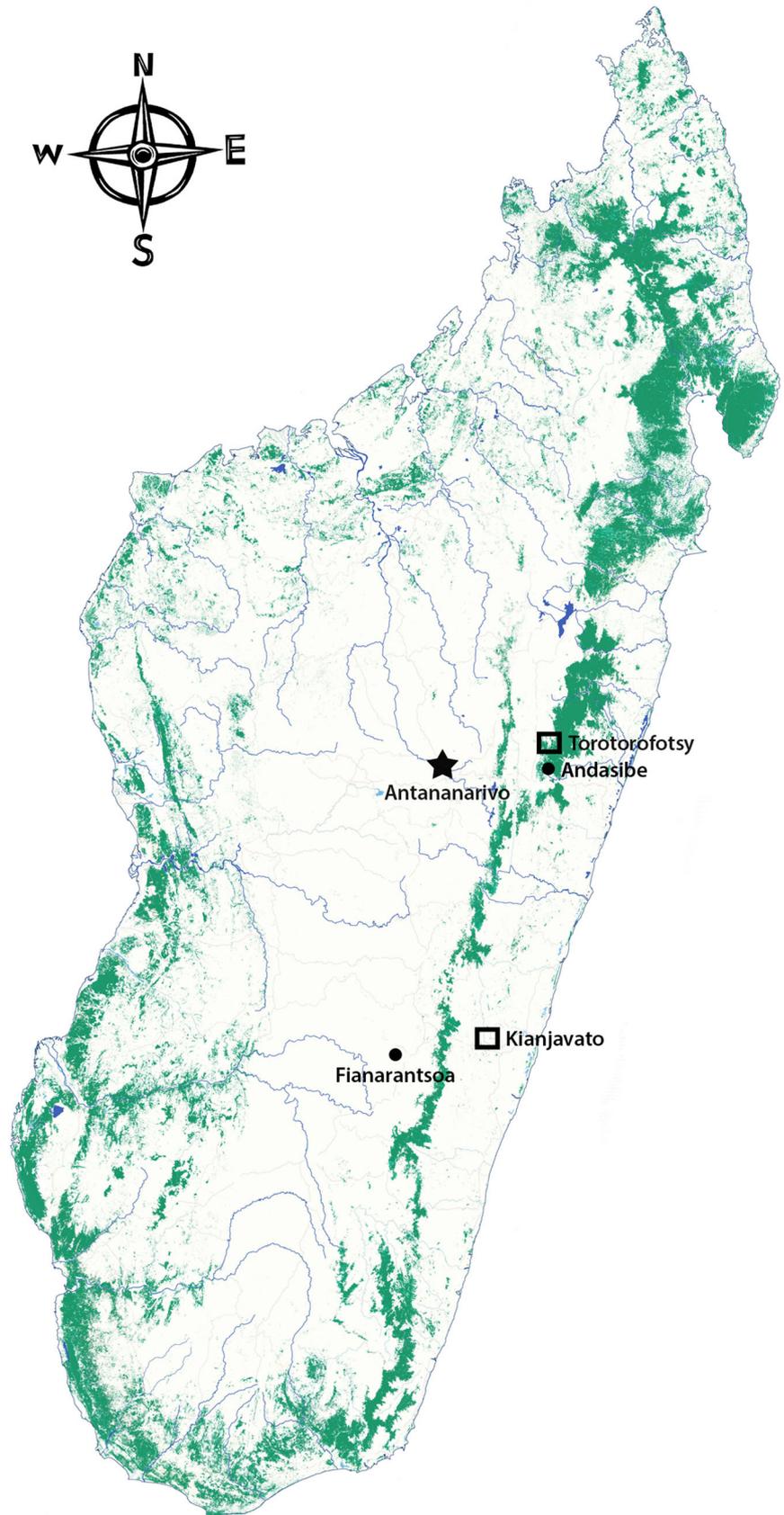




Fig. 2 Feeding traces left in deadwood snag

Behavioral observations

At Kianjavato, we conducted focal follows on two male aye-ayes, Dera and Zeppelin, and at Torotorofotsy we followed one male, Masy, and one female aye-aye, Tsinjo. Aye-ayes at both sites were darted using a CO₂ projection rifle with ~10 mg/kg of Telazol and then fitted with VHF radio collars (Advanced Telemetry Systems®, model number: R410) to allow for easier night follows. Using instantaneous focal sampling (Altmann 1974), we recorded behavior every 5 min over the course of a 6-h follow. We

conducted follows from 6 pm to 12 am or 12 am to 6 am, alternating the start time each day. Whenever feeding events occurred during the interval, we recorded the food item, the quantity of said item whenever possible, and, in the case of invertebrates, the substrate from which they were extracted. For example, invertebrates could be extracted from deadwood (defined here as standing snags, dead branches in live trees, or fallen trees; Fig. 2), living trees (under the bark or within the pith; Fig. 3a, b), or bamboo (Fig. 4).

At Kianjavato, we witnessed aye-ayes feeding on *Canarium* sp. seeds, *Ravenala madagascariensis* nectar, and invertebrates; at Torotorofotsy, we observed aye-ayes feeding on *Canarium* seeds and invertebrates. We focused on invertebrate feeding data for this research. We divided feeding into two categories: feeding from deadwood and feeding from live trees. We compared the frequency of feeding from each substrate within and between each forest.

Data analysis

We performed all statistical tests using SPSS 21. The Shapiro–Wilk test ($\alpha = 0.05$) showed that the data were not normally distributed for live tree feeding events ($W = 0.752$, $df = 49$, $p < 0.001$) and deadwood feeding events ($W = 0.827$, $df = 49$, $p < 0.001$), so a nonparametric test was used. We used the Kruskal–Wallis test with a pairwise comparison ($\alpha = 0.05$) to compare the frequencies of live tree and deadwood feeding between three of the individuals; the male aye-aye at Torotorofotsy (Masy) was excluded from the analysis because of the

Fig. 3 **a** Feeding trace into pith of live tree. **b** Feeding traces left in a live tree

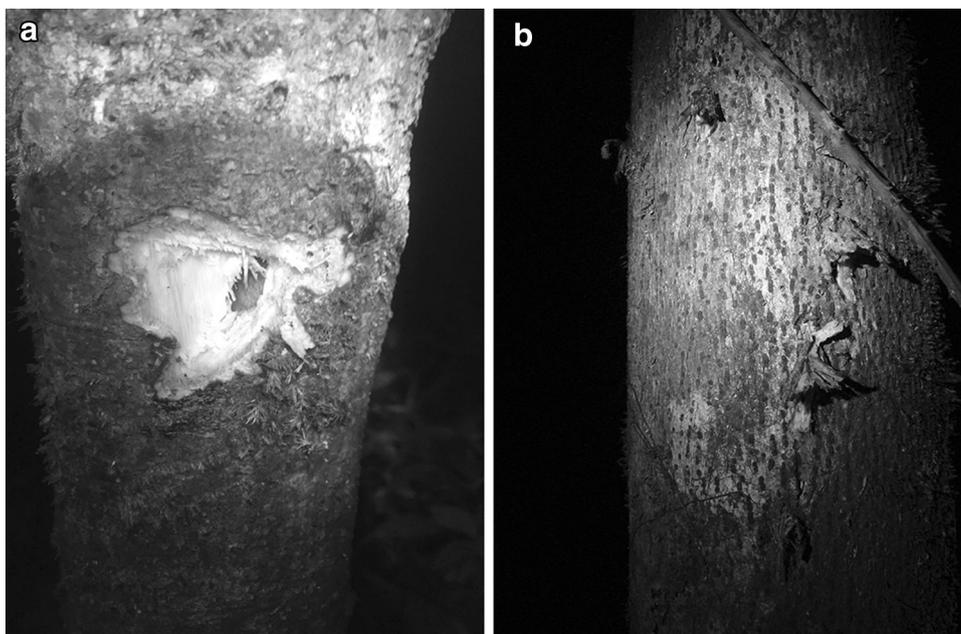




Fig. 4 Feeding trace left in bamboo

small sample size. We looked for significant differences from the Kruskal–Wallis test to determine if there were meaningful disparities in the frequency of deadwood or live tree feeding by aye-ayes, and a pairwise comparison to identify significant differences between individual feeding frequencies. Instantaneous focal sampling never results in truly independent data points and the resulting significance values should be treated with caution. In addition, given the small sample sizes, the results should only be considered a preliminary account of the behaviors present in both forests.

Results

We collected a total of 346 h of behavioral data over 69 nights at Kianjavato, and an additional 399 h at Torotorofotsy during 167 nights. With regards to the two males in Kianjavato, we followed Dera for 38 nights (Table 1),

averaging 4 h 45 min per follow ($\sigma = 1\text{ h }21\text{ min}$), and we followed Zeppelin for 31 nights (Table 1), averaging 5 h per follow ($\sigma = 1\text{ h }28\text{ min}$). In Torotorofotsy, we followed the male Masy for eight nights (Table 2), averaging 2 h 3 min per follow ($\sigma = 56\text{ min}$), and the female Tsinjo for 159 nights (Table 2), averaging 2 h 24 min per follow ($\sigma = 57\text{ min}$). Follows on the aye-ayes in Torotorofotsy were shorter due to those aye-ayes often traveling out of sight and poor observation conditions during adverse weather conditions.

The aye-ayes at Kianjavato foraged from two species of live trees, Tavia (*Rhopalocarpus crassinervius*, Rhopalocarpaceae) and Hovana (*Dypsis linea*, Arecaceae) (Table 4 in the “Appendix”), as well as bamboo (*Bambusa vulgaris*, Poaceae). The aye-ayes at Torotorofotsy, in contrast, consumed invertebrates from 56 species of live tree, including from Rotra (*Eugenia* sp., Myrtaceae), the live tree most frequently used for invertebrate consumption (Table 4 in the “Appendix”), as well as from unidentified species of bamboo.

We witnessed 890 feeding events by Dera and Zeppelin at Kianjavato. Of these, 44.9% occurred at deadwood, and 55.1% occurred at living trees (Table 3; Fig. 5). Both Dera and Zeppelin used deadwood (44.8 and 45.2%, respectively) less than live trees (55.2 and 54.8%, respectively; Table 3; Fig. 5). Dera used live trees 279 times and deadwood 226 times when consuming invertebrates, and Zeppelin used live trees 211 times and deadwood 174 times (Table 1). On average, the aye-ayes in Kianjavato used deadwood 16.67 times per month ($\sigma = 14.89$) and used live trees 20.42 per month ($\sigma = 27.60$). Despite the total number of feeding events at live trees outnumbering those

Table 1 Number of nights followed and traces in substrates each month for Dera and Zeppelin at Kianjavato, Madagascar, Oct 2013–Oct 2014

Date	Dera			Zeppelin		
	# of night follows	Substrate		# of night follows	Substrate	
		Deadwood	Live tree		Deadwood	Live tree
Oct 13	8	40	17	0	–	–
Nov 13	4	28	23	3	4	1
Dec 13	1	4	0	1	3	5
Jan 14	2	8	2	1	1	0
Feb 14	3	22	0	1	5	0
Mar 14	2	4	12	5	29	12
Apr 14	2	9	2	0	–	–
May 14	2	2	5	1	2	1
Jun 14	4	28	29	4	8	33
Jul 14	1	8	4	3	19	32
Aug 14	4	29	71	5	43	54
Sep 14	4	34	112	5	50	47
Oct 14	1	10	2	2	10	26

Table 2 Number of nights followed and frequency in substrates each month for Tsinjo and Masy at Torotorofotsy, Madagascar, Jul 2014–Dec 2015

Date	Masy			Tsinjo		
	# of night follows	Substrate		# of night follows	Substrate	
		Deadwood	Live tree		Deadwood	Live tree
Jul 14	0	–	–	10	7	41
Aug 14	0	–	–	6	0	13
Sep 14	0	–	–	12	15	33
Oct 14	0	–	–	14	7	44
Nov 14	1	0	0	10	6	38
Dec 14	0	–	–	6	1	20
Jan 15	2	2	6	4	3	10
Feb 15	1	0	3	7	4	20
Mar 15	1	1	1	12	7	30
Apr 15	1	0	2	6	4	16
May 15	1	1	2	10	6	29
Jun 15	0	–	–	10	11	37
Jul 15	0	–	–	13	7	56
Aug 15	0	–	–	12	5	25
Sep 15	0	–	–	8	5	27
Oct 15	0	–	–	12	6	43
Nov 15	1	1	2	8	4	18
Dec 15	0	–	–	2	0	6

Table 3 Occurrences of invertebrate feeding by Dera and Zeppelin at Kianjavato, Madagascar, Oct 2013–Oct 2014, and by Tsinjo and Masy at Torotorofotsy, Madagascar, July 2014–Dec 2015

Kianjavato			Torotorofotsy		
Individual	Occurrences of feeding in deadwood	Occurrences of feeding in live trees	Individual	Occurrences of feeding in deadwood	Occurrences of feeding in live trees
Dera	226	279	Tsinjo	98	506
Zeppelin	174	211	Masy	5	16
Subtotal	400	490		103	522
Total	890			625	

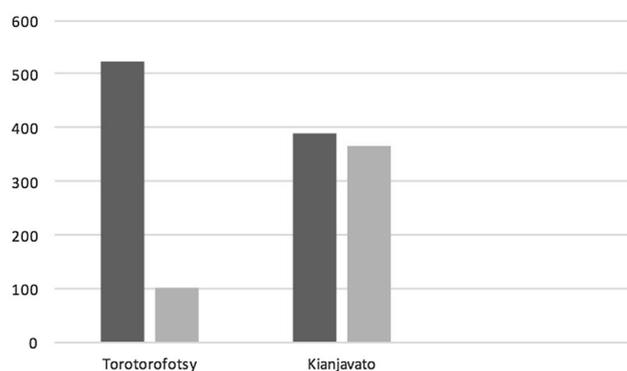


Fig. 5 Number of traces in live trees (dark gray bars) and deadwood (light gray bars) at Torotorofotsy and Kianjavato

at deadwood, there were fewer months when live tree feeding was witnessed more often than deadwood feeding. Dera had 5 months out of the 13 with more live tree feeding events and Zeppelin had 5 months out of 11 with more live tree feeding events (Table 1). Also, despite the greater frequency of live tree feeding, the longest single feeding event for either aye-aye was at a dead tree (~85 min).

We witnessed 625 feeding events at Torotorofotsy by Tsinjo and Masy. Of these, 83.5% occurred at live trees, with only 16.5% occurring at deadwood (Table 3; Fig. 5). Both Tsinjo and Masy used live trees (83.8 and 76.2%, respectively) more often than deadwood (16.2 and 23.8%, respectively). On average, the aye-ayes in Torotorofotsy

used deadwood 4.12 times per month ($\sigma = 3.77$) and live trees 20.88 times per month ($\sigma = 16.38$). At no point was deadwood feeding more frequent than live tree feeding for either Tsinjo or Masy (Table 2). Despite the greater frequency of live tree feeding, the longest single feeding event for each aye-aye occurred at a fallen lavaka (*Dypsis* sp.) tree (~ 75 min).

The Kruskal–Wallis test with a pairwise comparison indicated a significant difference in the frequency of live tree feeding between individuals ($H = 6.909$, $df = 2$, $p = 0.032$). The pairwise comparison resulted in no significant difference in monthly live tree feeding between Tsinjo and Zeppelin ($\chi^2 = -1.465$, $p = 0.429$) or between Zeppelin and Dera ($\chi^2 = 0.928$, $p = 1.000$). However, there was a significant difference in monthly live tree feeding between Tsinjo and Dera ($\chi^2 = 2.586$, $p = 0.029$), with Tsinjo consuming more invertebrates from live trees more frequently. There was no significant difference in deadwood feeding among these three individuals ($H = 5.511$, $df = 2$, $p = 0.064$).

Discussion

Recent literature has focused on the relationship between aye-ayes and deadwood (Farris et al. 2011; Sefczek et al. 2012; Thompson et al. 2016). However, our findings and those of Andriamisedra et al. (2015) suggest that this deadwood focus may be too strongly emphasized and that live trees should be given greater consideration. The perceived importance of deadwood is largely based on earlier reports of aye-aye feeding behaviors in habitats with limiting factors. For example, early reports indicated that aye-aye foraging for larvae in deadwood was a major component of their behavior (Petter 1977 p. 46). However, the same report also mentioned that aye-ayes used coconuts heavily as well, indicating that this population was likely in a degraded or small forest patch near plantations (Petter 1977). Another study, on Nosy Mangabe, also determined that aye-ayes consistently used deadwood for larvae foraging (Sterling 1993, 1994a). However, despite the intact nature of this forest, it is possible that this variation in feeding behavior was due to the limited size of the island (~ 520 ha), with aye-ayes becoming overpopulated and adapting their feeding behaviors accordingly. Going forward, our results necessitate a rethinking of aye-aye feeding behaviors and habitat requirements, and therefore have important consequences for future aye-aye research and conservation. As previously mentioned, these data sets are small and results are preliminary; further research is being conducted to elaborate the suggestions herein.

Our first objective was to identify live trees that aye-ayes use when foraging for invertebrates. Excluding

foraging efforts in bamboo at both locations, aye-ayes used two species of live tree in Kianjavato and 56 species at Torotorofotsy (Table 4 in the “Appendix”). Of these 58 species of trees, two (*Macaranga cuspidata* and *Ocotea* sp.) were previously identified by Sterling (1993, 1994a) as live trees used by aye-ayes to forage for larvae. This increases the number of live trees aye-ayes use for invertebrate foraging from 16 to 72. Although we witnessed aye-ayes removing larvae from a wide array of substrates, we use the term invertebrates because (1) we could not witness all of the types of invertebrates removed, so we cannot eliminate the possibility that aye-ayes were consuming adult insects, and (2) we were unable to observe what aye-ayes were extracting from two trees at Torotorofotsy: vakona (*Pandanus utilis*) and *Ravenala madagascariensis*. When foraging at *Ravenala*, aye-ayes gnawed into the base of the leaves; when foraging on vakona, aye-ayes sat atop the leaves and gnawed into them (Fig. 6). Recent samples from these trees revealed that vakona contained adult insects, larvae, and seeds, while *Ravenala* contained some adult insects but mostly water. It is possible that vakona is used for either invertebrate or seed consumption. Additionally, *Ravenala* may be used by aye-ayes as a source of water, as Sterling (1993) found at Nosy Mangabe, rather than as a source of invertebrates. However, the flowers of *Ravenala* may be used to consume nectar and/or invertebrates (Sterling 1993, 1994a; Ancrenaz et al. 1994). Considering the array of habitat types in which aye-ayes persist, from rainforests in the east to drier forests in the west and north, and the floral diversity present in these locations, this list may represent only a small portion of the live trees aye-ayes use for invertebrate foraging.

Our second objective was to determine the frequency of live tree foraging compared to deadwood foraging. Our findings are similar to those of Andriamisedra et al. (2015), but emphasize an even stronger reliance of aye-ayes on live tree feeding. We observed more live tree than deadwood use by all four aye-ayes. Andriamisedra et al. (2015) examined feeding traces, whereas our observational



Fig. 6 Tsinjo feeding on top of a vakona tree

follows allowed us to tease apart more details. As might be expected, there was no difference between the two males at Kianjavato for either live tree or deadwood feeding. Surprisingly, unlike the results from Andriamisedra et al. (2015), there was also no significant difference in the monthly live tree feeding between Tsinjo, the female at Torotorofotsy, and Zeppelin, a male at Kianjavato. Also unexpectedly, there was no significant difference in deadwood feeding among all compared individuals (Zeppelin and Dera from Kianjavato and Tsinjo from Torotorofotsy). However, there was a significant difference in the monthly live tree feeding between Tsinjo and Dera, with Tsinjo using live trees more often. The lack of significant difference in live tree feeding between Tsinjo and Zeppelin but significant difference in live tree feeding between Tsinjo and Dera may be due to forest sizes. Tsinjo lives in the continuous forest of Torotorofotsy and was therefore expected to have more live tree feeding (Andriamisedra et al. 2015). Within Kianjavato, Zeppelin occupies the larger forest of Tsitola (954 ha) and the connected forest of Ambatovaky (50 ha), while Dera occupies multiple smaller forest fragments such as Sangasanga (64 ha), Ambatovaky, and a portion of Tsitola (Holmes et al. 2013, 2016; Randimbiharirinirina et al. 2016). It is possible that Tsinjo and Zeppelin showed no significant difference in live tree feeding because they both occupy larger forest parcels. However, because Dera is in smaller forest parcels, there was a significant difference in live tree feeding between him and Tsinjo, as predicted. Based on our findings and those of Andriamisedra et al. (2015), it seems that in more continuous forest parcels, aye-ayes are more likely to consume invertebrates from live trees. Curiously, as there was no significant difference in deadwood feeding between individuals, it does not appear that aye-ayes in more discontinuous forests are compensating by consuming more invertebrates in deadwood. Instead, it is possible that they compensate by consuming a different resource.

Despite the limited scope of our data set, it is important to consider these results in the broader picture of aye-aye feeding behaviors. The aye-ayes in Kianjavato showed an increase in live tree feeding from July to October (Table 1). This is between the end of the cold/rainy season (mid-May to mid-September) and the beginning of the hot/dry season (mid-September to December) (Sterling 1993; Wright 1999; Vasey 2005), a period when many lemurs experience resource scarcity (Hemingway and Bynum 2005; Schmid and Kappeler 2005; Vasey 2005). Sterling (1993, 1994a) showed that the cold/wet season is when aye-ayes consume the fewest *Canarium* seeds (considered a critical resource for aye-ayes: Iwano and Iwakawa 1988; Iwano 1991; Sterling 1993, 1994a) and the greatest amount of larvae. Therefore, it is possible that during the cold/wet season, Dera and Zeppelin were switching their feeding

efforts from *Canarium* seeds, which became unavailable, to invertebrates in live trees. Conversely, the aye-ayes in the continuous forest of Torotorofotsy always used live trees more frequently than deadwood for invertebrate feeding (Table 2). If species richness and abundance is greater in continuous forest than in disturbed forests, as found in temperate climates (Grove 2002; Lachat et al. 2007), then it is possible aye-ayes would not need to alter their invertebrate feeding habits when other resources, such as *Canarium*, become scarce.

One possible explanation for the differences in substrate use between sites is habitat quality. It should be noted that most information on saproxylic invertebrate assemblages comes from studies in temperate forests; tropical forest studies are severely lacking (Grove and Stork 1999). Until the necessary studies are conducted, we can only postulate that invertebrate assemblages in continuous and disturbed tropical forests follow similar trends to those in temperate forests. As mentioned earlier, there are four hosts for saproxylic invertebrates: healthy, weakened, stressed, and dead (Hanks 1999). Since saproxylic invertebrate species richness and abundance are both strongly correlated with the presence of large-diameter trees (Grove 2002), and continuous forests are expected to have a greater abundance of large-diameter trees than disturbed forests (Grove 2002; Lachat et al. 2007), we can expect more opportunities for aye-ayes to forage on larvae in a continuous forest than in disturbed habitats. Additionally, invertebrate species richness, likely including species using live trees (i.e., healthy or weakened hosts), is greater in continuous forests (Martikainen et al. 2000; Bishop et al. 2009), so aye-ayes in these continuous forests have access to more types of invertebrates, including those in live trees. Conversely, in disturbed temperate forests, arthropods are more prevalent around deadwood than they would be in a continuous and relatively undisturbed forest (Jabin et al. 2004; Bouget et al. 2013). Therefore, aye-ayes in disturbed habitats such as Kianjavato may need to use deadwood more often to consume invertebrates, whereas in continuous forests such as Torotorofotsy, they have more opportunities to consume invertebrates from living trees.

Alternatively, differences in substrate use could be due to forest composition. For instance, Zeppelin's territory does not contain *Ravenala madagascariensis* trees, while Dera's does. We also know that Dera consumed nectar from *Ravenala* trees (Randimbiharirinirina et al. 2016). It is possible that this additional resource reduces feeding on invertebrates in live trees. However, in Torotorofotsy, both aye-ayes occupy territory containing *Ravenala madagascariensis*, but we have not witnessed either aye-aye consuming nectar. Therefore, it is unlikely that *Ravenala* nectar limits the amount of live tree feeding. Rather, we suggest that *Ravenala* nectar is used to supplement the diet

in a heavily disturbed forest where invertebrate species abundance and richness (i.e., species that depend on healthy or weakened hosts) are potentially lower. It is also possible there is differential availability of deadwood in wetlands such as Torotorofotsy due to an increased rate of decay (Webster and Benfield 1986). However, trees with greater density and diameter, which are more often present in continuous forests (Grove 2002; Lachat et al. 2007), should decay more slowly, so theoretically continuous forests should have more deadwood available for longer periods of time (Chambers et al. 2000). Considering our results and those of Andriamisedra et al. (2015), we are inclined to think that the fact that Torotorofotsy is a wetland has only a minimal effect on substrate use.

Lastly, the type of invertebrates being consumed may have an influence on the aye-eyes' differential use of live trees and deadwood. Although we witnessed aye-eyes using live trees more than deadwood, and were able to occasionally identify the invertebrates removed as larvae, we do not know every resource that was consumed out of either substrate. Based on Sterling's (1993, 1994a, b) research, we know that aye-eyes can consume larvae of various sizes (Fig. 7) as well as adult insects. Not all larvae are created equal, with large and small larvae having different percentages of crude protein, water, and fat content (Sterling 1993). In addition, adult insects are assumed to be less energetically valuable than larvae (Kourimska and Adamkova 2016). It is possible that aye-eyes were removing more adult insects or smaller larvae from live trees while consuming more large larvae in deadwood. This would result in a lower energetic yield from live trees and necessitate more feeding bouts in that substrate.

Given the importance of live tree feeding by aye-eyes, future research on aye-eye feeding behavior needs to re-evaluate current methods for estimating invertebrate abundance. As aye-eyes do not use all available deadwood



Fig. 7 Larvae of various sizes removed from one piece of deadwood in Torotorofotsy

in a given habitat (Thompson et al. 2016), it is likely that excavating invertebrates from pieces of deadwood (Sterling 1993, 1994a; Sterling et al. 1994) or enumerating deadwood (Farris et al. 2011; Sefczek et al. 2012) does not provide an accurate estimation of invertebrates that use dead hosts. In addition, there is no reliable method for identifying dead branches in live trees that contain larvae and enumerating those invertebrates. Moreover, current methods exclude invertebrates that use various other hosts, such as healthy or weakened trees (Hanks 1999). As it appears that aye-eyes remove invertebrates more often from live trees, estimates must be more inclusive of live tree hosts than previous efforts. New sampling methods must be identified for estimating invertebrate abundance, in lieu of damaging living trees to remove invertebrates. We propose estimating invertebrate abundance by conducting monthly sampling along transects to enumerate new traces made in living trees and deadwood, in conjunction with regular observational recording of the number of feeding events and specific substrate an aye-eye uses. Though this methodology will not account for all available invertebrates, such as those contained in dead branches 20+ meters high in a live tree, at a minimum it will provide a more accurate method for recording presence-absence data for invertebrates.

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Appendix

See Table 4.

Table 4 List of live trees used by aye-eyes at Kianjavato and Torotorofotsy

Tree	Genus	Species	Family
Afotra	<i>Dombeya</i>	sp.	Maluaceae
Ambavy	<i>Ambavia</i>	<i>capuronii</i>	Annonaceae
Ambora	<i>Tambourissa</i>	<i>cf. thouvenotii</i>	Monimiaceae
Ambovitsika	<i>Craspidospermum</i>	<i>verticillatum</i>	Apocynaceae
Ampali	<i>Artocarpus</i>	<i>heterophyllus</i>	Moraceae
Anjananjana	<i>Leptolaena</i>	<i>gautieri</i>	Sarco-laenaceae
Bedoda	<i>Dypsis</i>	sp.	Arecaceae
Ditimena/Sitimena	<i>Abrahamice</i>	sp.	Anacardiaceae
Famelona	<i>Chysophyllum</i>	<i>biovinianum</i>	Sapotaceae
Fandramanana	<i>Aphloia</i>	<i>theaeformis</i>	Aphloiaceae
Fanjana	<i>Cyathea</i>	<i>gigantea</i>	Cyatheaceae
Fanjavala/Hazopoza	<i>Begnea</i>	sp.	Sapinoaceae
Fantsikahitra	<i>Carissa</i>	sp.	Apocynaceae
Faralaotra	<i>Colubrina</i>	sp.	Rhamnaceae
Farimany	<i>Craterispermum</i>	<i>laurinum</i>	Rubiaceae
Fotona	<i>Leptolaena</i>	<i>multiflora</i>	Sarco-laenaceae
Gavoala	<i>Eugenia</i>	<i>cf. gavoala</i>	Myrtaceae
Hafibato	<i>Dombeya</i>	<i>megaphylla</i>	Maluaceae
Hafitainakoho	<i>Grewia</i>	<i>thouverrotii</i>	Euphorbiaceae
Harina	<i>Bridelia</i>	<i>tulasneana</i>	Phyllanthaceae
Harongana	<i>Harungana</i>	<i>madagascariensis</i>	Hypericaceae
Hazombary	<i>Orfilea</i>	<i>coriacea</i>	Euphorbiaceae
Hazompasika	<i>Eugenia</i>	sp.	Myrtaceae
Hazondomoina	<i>Domohinea</i>	sp.	Euphorbiaceae
Hazonto	<i>Oncostemum</i>	sp.	Myrsinaceae
Hazotokana	<i>Brachylaena</i>	<i>ramiflora</i>	Asteraceae
Hazoxidrano	<i>Ilex</i>	<i>mitis</i>	Aquifoliaceae
Hovana ^a	<i>Dypsis</i>	<i>linea</i>	Arecaceae
Karambitro/Taolambitro	<i>Begnea</i>	<i>apetala</i>	Sapinoaceae
Kijy	<i>Symphonia</i>	<i>fasciculata</i>	Clusiaceae
Lalona	<i>Weinmannia</i>	sp.	Cunoniaceae
Lavaka	<i>Dypsis</i>	sp.	Arecaceae
Lendemy	<i>Anthrocleista</i>	<i>madagascariensis</i>	Gentianaceae
Longotra	<i>Cryptocarya</i>	<i>fulva</i>	Lauraceae
Menahy	<i>Campylospermum</i>	sp.	Ochnaceae
Menavahatra	<i>Scolopia</i>	sp.	Salicaceae
Merana	<i>Brachylaena</i>	<i>merana</i>	Asteraceae
Mokaranana	<i>Macaranga</i>	<i>cuspidate</i>	Euphorbiaceae
Molopangady/Molotriangaka	<i>Homolliella</i>	<i>sericea</i>	Rubiaceae
Nanto	<i>Mimusops</i>	sp.	Sapotaceae
Potsimavo	<i>Xylopi</i>	<i>buxifolia</i>	Annonaceae
Ravenala	<i>Ravenala</i>	<i>madagascariensis</i>	Strelitziaceae
Rotra	<i>Eugenia</i>	<i>bernieri</i> or <i>grossepunctata</i>	Myrtaceae
Tafanala	<i>Terminalia</i>	<i>tetrandra</i>	Combretaceae
Tavia ^a	<i>Rhopalocarpus</i>	<i>crassinervius</i>	Rhopalocarpaceae
Tavolo	<i>Cryptocarya</i>	<i>acuminata</i>	Lauraceae
Tsilaitra	<i>Noronhia</i>	sp.	Oleaceae
Tsirika	<i>Dypsis</i>	sp.	Arecaceae

Table 4 continued

Tree	Genus	Species	Family
Tsitrotroka	<i>Dichaetauthera</i>	<i>squamata</i>	Melastomataceae
Vahivahy	<i>Secamone</i>	<i>angustifolia</i>	Apocynaceae
Vakoka	<i>Trema</i>	<i>orientalis</i>	Celtidaceae
Vakona	<i>Pandanus</i>	<i>utilis</i>	Pandanaceae
Vanana	<i>Sloanea</i>	<i>rhodantha</i>	Elaeocarpaceae
Varongy	<i>Ocotea</i>	sp.	Lauraceae
Vatsilana	<i>Polyscias</i>	sp.	Araliaceae
Voapaka	<i>Uapaca</i>	<i>bojeri</i>	Euphorbiaceae
Volomborona	<i>Albizzia</i>	<i>gummifera</i>	Fabaceae
Vonitra	<i>Dypsis</i>	sp.	Arecaceae

^a Kianjavato trees

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