

Competition for dead trees between humans and aye-eyes (*Daubentonia madagascariensis*) in central eastern Madagascar

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Received: 12 May 2016 / Accepted: 28 October 2016 / Published online: 15 November 2016
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Abstract The destruction and degradation of forest habitats are major threats to the sustainability of lemur populations in Madagascar. Madagascan landscapes often contain forest fragments that represent refuges for native fauna, while also being used for firewood and timber by local human populations. As undisturbed forest becomes increasingly scarce, understanding resource competition between humans and wildlife in disturbed habitats will be increasingly important. We tested the hypothesis that Malagasy and aye-eyes (*Daubentonia madagascariensis*) compete for the limited number of dead trees in rainforest fragments at Tsinjoarivo, Madagascar. We surveyed 2.16 ha within five fragments (range 5–228 ha) surrounding human settlements to quantify the density of dead trees and traces of both human and aye-aye activity. Neither aye-aye nor human traces were distributed according to the availability of particular trees species, and aye-eyes and Malagasy apparently preferred several different species. Although overlap was recorded in tree species used, human use tended to be positively correlated with a species' desirability as firewood, while a negative relationship was seen for aye-eyes. Both consumers used trees of similar diameter at breast height, but those used by aye-eyes tended to be older, suggesting that human use might precede usefulness for aye-eyes. Finally, the density of dead trees and aye-aye traces were highest in smaller fragments, but

human traces did not vary across fragment size. Although further study is needed to better quantify the aye-aye diet in this region, these data suggest that aye-eyes and local people compete for dead trees, and this competition could constitute a pressure on aye-aye populations.

Keywords Resource competition · Conservation · Habitat loss · Deforestation · Forest degradation

Introduction

Habitat loss is a major threat to the sustainability of natural ecosystems. Deforestation is of particular concern in tropical ecosystems, in which many of the ecosystem goods and services remain unidentified and poorly described to outsiders (Food and Agriculture Organization of the United Nations 2010). Deforestation and habitat fragmentation have had particularly severe consequences on the island nation of Madagascar, which has a highly endemic native flora and fauna. Harper et al. (2006) estimated that forest cover on the island of Madagascar declined by more than 40% between 1950 and 2000, and during this decline has also become more fragmented. Harper et al. (2006) quantified this fragmentation by demonstrating that while small forest patches (<10 km²) comprised 5% of the total forest area of Madagascar in the 1950s, such small patches now make up almost a quarter of the total area. The biodiversity of a series of fragmented patches is expected to be lower than that of a single uniform patch equal in size to the aggregate area (Laurance et al. 2011; Benchimol and Peres 2014), and forest fragments in Madagascar have experienced biodiversity losses in herpetofauna (Vallan 2000; Lehtinen et al. 2003), insectivorous mammals (Goodman and Rakotondravony 2000), birds (Watson et al. 2004) and

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lemurs (Craul et al. 2009; Irwin et al. 2010). Moreover, Bodin et al. (2006) documented reductions in pollination rates of agricultural crops and seed dispersal as a result of habitat fragmentation, illustrating that fragmentation also limits the broader ecosystem goods and services that tropical forests can provide in Madagascar.

Rural Malagasy are intimately tied to the landscape (Styger et al. 2007). Many generations have depended on the forest to provide firewood, material for building homes, and for food. As human populations increase and these resources become limiting, the Malagasy have a larger impact on the limited resources the forests can provide and on the structure and species composition of the natural forest ecosystem (Vallan et al. 2004). Of particular importance to this study, the Malagasy living in rural areas rely on dead trees for firewood, and the abundance of this resource is declining both due to the decline in forest area and the increased cumulative demand for easily accessible firewood (Gade 1996).

Endemic lemurs rely on the forests historically present on the island, and partition forest resources finely to avoid direction competition; for example, Ganzhorn (1989) demonstrated niche separation in the microhabitats and food resources of seven species of lemur in the eastern Malagasy rainforest. The aye-aye (*Daubentonia madagascariensis*) is an extreme example of this niche partitioning. It has adopted a unique diet and feeding adaptations (Erickson 1995; Sterling and McCreless 2006) such as an elongated middle finger with which it can extract insect larvae from beneath the bark of a tree. Although the aye-aye is considered omnivorous, eating flowers, fruit and even small animals, it has evolved a particularly unique foraging mode, termed percussive foraging, in which it drums on the trunks of dead trees with its elongated finger to detect the presence of beetle larvae within. This unique mode of foraging, which requires wood, potentially causes resource competition between aye-ayes and humans, who also rely on dead trees as a fuel source. The limited information available to date suggests that aye-ayes actively select trees with certain acoustic properties (Erickson 1998; Thompson et al. 2016), suggesting that only a small proportion of dead trees in the habitat are actually potential food resources. Further, little is known about how aye-ayes respond to habitat degradation, though Farris et al. (2011) found that feeding sites are less abundant in degraded areas within Ranomafana National Park.

In this study we quantify the use of dead trees as a resource by aye-ayes and humans in fragment and degraded forest habitats in eastern Madagascar, through a census of all dead trees in transects within forest fragments of varying size. Our objectives were to:

1. Quantify the overlap in the tree species used by aye-ayes and humans.
2. Quantify the desirability of different tree species as firewood, and test whether aye-ayes tended to prefer these same species.
3. Quantify the size (diameter at breast height; DBH) of dead trees utilized by both consumer species.
4. Estimate the time since death of dead trees in the sample and quantify whether this differed between those used by the two types of consumer.
5. Quantify changes in resource use across a gradient of fragment size.

Methods

Field site

All the research was conducted at Mahatsinjo, within Tsinjoarivo commune (19°40'56"S 47°45'28"E, elevation 1590 m) in the central eastern rainforest of Madagascar (Fig. 1). The field site is a mosaic of fragments of central eastern rainforest and cleared areas (mostly valleys) containing rice paddies, crop fields, and cow pasture land (Fig. 1). More detailed descriptions of the study site have been published previously (Irwin 2006, 2008).

Field methods

With two local research assistants, we surveyed the distribution of dead trees along five trails in four distinct forest fragments over a 5-day period from 16 to 20 June 2014 (Table 1). The two assistants were present for all surveys. We located all intact or partially removed dead trees (either standing or fallen) within 5 m of the trail on the right-hand side. The cumulative distance censused was 4325 m, corresponding to an area of 2.16 ha.

For each dead tree >5-cm DBH encountered, we recorded species (vernacular name), DBH, distance along the trail (relative to trail markers that were located at 25-m intervals along each trail), the distance from the trail (meters), whether the tree was standing or fallen, and the estimated time since the tree's death. In identifying tree species and estimating time since the tree's death, we relied on local assistants (who have lived locally for >20 years and have extensive experience gathering firewood). Both the assistants had been working with research teams for >10 years and we are confident that their identifications are consistent with previously published work (Irwin 2006). Firewood in this region is typically collected long after the death of a tree, and because species differ considerably in their desirability as firewood, most local residents are skilled in distinguishing tree species, even when trees are dead. Time since death was estimated based on

Fig. 1 False colored satellite imagery of the field site at Mahatsinjo, within Tsinjoarivo commune in the central eastern rainforest of Madagascar. Forest patches with research trails are shown outlined in yellow with the trails marked with yellow letters. Other, non-studied forest patches are shown in the base imagery in red. The trails shown in the map were the ones used for this study. Coordinates are Universal Transverse Mercator Zone 38S (color figure online)

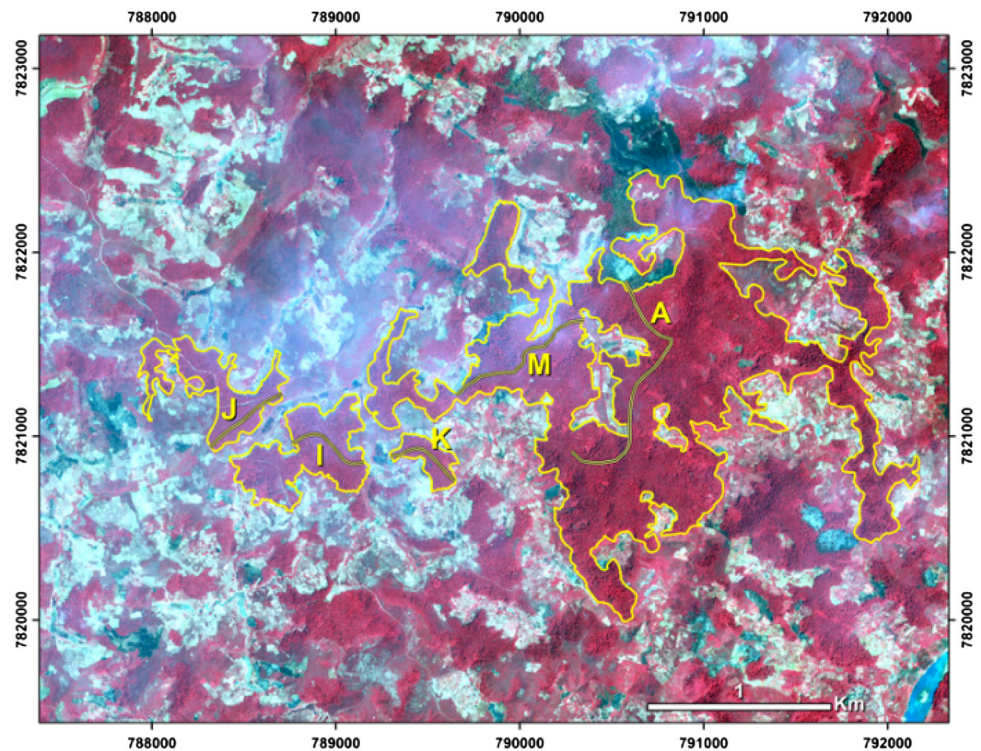


Table 1 Summary of trails surveyed for dead trees during the study. Note that the forest fragments are named based on the trails found within each fragment

Trail name	Forest fragment	Fragment area (ha)	Trail length (m)	Area sampled (ha)
A	A/C/M/AG	228.1	2000	1.0000
M	A/C/M/AG	228.1	975	0.4875
I	I	24.1	500	0.2500
J	H/J	17.6	525	0.2625
K	K	5.3	325	0.1625
Total	–	–	4325	2.1625

appearance and consistency, while species identifications were based on remaining dead leaves (when possible), branching patterns, texture of outer bark, texture and color of inner bark, wood grain properties, and hardness/density. It is possible that the “morphospecies” used in our dataset might have lumped two or more closely related species together.

We also recorded any traces that provided evidence of use by both Malagasy (axe marks, both those that actually cut down trees as well as shallow axe marks) and characteristic aye-aye damage (gnaw marks in the tree made with incisors), and estimated the number of marks of each kind when they were present. Because of the difficulty in determining whether two traces on a tree were part of the same event, we focused simply on the presence/absence of marks rather than using counts of traces on a single tree.

To provide context in understanding patterns of tree use by Malagasy, our Malagasy research assistants collectively assigned a score to 65 common tree species

corresponding to each species’ desirability as firewood [we selected species commonly encountered in the transects supplemented by others common in past botanical inventories (M. T. Irwin, unpublished data)]. We used a 1–10 ordinal scale with 1 being the least desirable and 10 being the most desirable species. Only nine species received a score of 10; twenty-nine tree species received a score of ≥ 5 , and the remaining 35 received a score < 5 . Firewood preferences were not available for three tree species (Rotra mena SL, Tandrokondrilahy, and Kiripika), for which we substituted values available for congeners. Four trees identified as “Malambovony” could have belonged to one of two related species scored separately for firewood desirability; an average score was used for the analysis.

This research complied with protocols approved by Northern Illinois University (IACUC LA12-0011), and adhered to the legal requirements of Madagascar; research permits were issued in Madagascar by the Ministry of

Environment and Forests (no. 131/14/MEF/SG/DGF/DCB.SAP/SCB).

Statistical analysis

We calculated the percent composition by tree species of: (1) all dead trees encountered, (2) the subset of trees with human traces, and (3) the subset of trees with aye-aye traces. To test the hypothesis that the two consumer species (aye-ayes and humans) used different species, we applied a Fisher's exact test to a 2×2 contingency table tabulating whether tree species were utilized or not by the two consumers. To test the hypothesis that each tree species was used in relation to its abundance in the sample (i.e., no species preference), we constructed a contingency table for each consumer species (tree species as rows, and two columns, "count with trace" and "count without trace", respectively). This yielded a 33×2 and a 15×2 contingency table for humans and aye-ayes, respectively. Fisher's exact test with simulated P -values was used to test whether there was non-independence between tree species and likelihood of use. Because the tree species that were encountered may rarely produce a biased signal due to low sample size, we ran each test twice: once with the full dataset, and once only with tree species represented in the sample by five or more individuals.

Spearman's rank correlations were used to explore whether the two consumers' use of tree species was linked to that species' desirability as firewood by correlating species-specific usage (percent of censused individuals of that species showing traces) and that species' firewood score. Correlations between fragment size and density of traces (traces per hectare) were explored using Spearman's rank correlations.

All statistical analyses were performed in R studio [cor.test, fisher.test; version 0.98.983, with R version 3.2.3—R (R Core Team 2015)].

Results

We encountered 462 unique dead trees ≥ 5 -cm DBH representing 33 different tree species (Table 2); 230 were fallen trees while 232 were still standing. *Rotra mena* BL (Myrtaceae: *Syzygium* sp.), the most frequently encountered species, accounted for 18.2% of all dead trees recorded, and the top seven species accounted for 73.9% of all dead trees. Twelve species were only recorded once. Among these 462 trees, 52 had aye-aye traces (29 fallen, 23 standing; 12 species) and 94 had human-made marks (51 fallen, 43 standing; 18 species). Among the 33 species, ten species exhibited traces of both humans and aye-ayes (not necessarily on the same tree), two exhibited traces of aye-

ayes but not humans, eight exhibited traces of humans but not aye-ayes, and 13 had traces of neither species. The usage of species by aye-ayes and humans overlapped more than expected by chance alone (Fisher's exact test, 2×2 contingency table, $P = 0.03$); in other words usage by one species meant a higher than expected chance of also being used by the second species.

Fisher tests using all tree species indicated that the likelihood of use by aye-ayes did not vary with species ($P = 0.14$), but that the likelihood of use by people did ($P = 0.012$). However, when the subset of the data was used (including only those 15 species encountered at least five times in the sample), the likelihood of use was shown to vary with species for both consumers (aye-ayes, $P = 0.011$; humans, $P = 0.003$). For eight of the 15 commonly encountered tree species, aye-ayes and humans deviated from expected frequencies in opposite directions; for four, both consumers used the species less than expected, and for the remaining three both consumers used the species more than expected.

Species-specific usage rates (i.e., percentage of trees of a given species showing traces of that consumer) did not show a significant correlation with firewood score for either aye-ayes (Spearman's rank correlation, $P = 0.86$) or humans ($P = 0.70$). However, when the dataset was restricted to commonly encountered species ($n = 15$ species), a trend towards a positive correlation was detected for humans ($\rho = 0.49$; $P = 0.063$) and a trend towards a negative correlation was detected for aye-ayes ($\rho = -0.45$; $P = 0.091$), suggesting differences in the patterns of resource use by aye-ayes and humans.

The distribution of sizes of dead trees >5 -cm DBH in the survey area was unimodal, but positively skewed, with an average size of 16.45 ± 8.82 cm DBH (mean \pm SD) and a median of 14.45-cm DBH (Fig. 2a). Trees with aye-aye traces had a slightly higher average DBH (17.41 ± 12.35 ; Fig. 2b), while trees with human traces had an average DBH similar to the entire sample (16.82 ± 9.85 ; Fig. 2c).

The average estimated time since death for all trees in the sample was 10.7 years; for the trees with aye-aye traces the average time was longer (13.1 years) and for the trees with human traces the average time was shorter (9.1 years). For the ten tree species observed to be utilized by both consumers, the average time since death was shorter for trees with human traces in nine out of ten cases (average difference = 3.95 years). This result is unlikely to occur by chance (binomial test, $P = 0.02$) and suggests that aye-ayes use trees that have been dead a longer time than human-used trees.

Across the five trails surveyed, the density of dead trees showed a significant negative correlation with fragment size ($\rho = -0.97$; $P = 0.005$). Similarly, the density of

Table 2 Species composition and incidence of aye-aye and man-made marks on 462 dead trees at Mahatsinjo, Tsinoarjoivo, arranged by decreasing abundance within the sample

Local name	Family	Scientific name	No. individuals	Percent of sample	Average time since death (year)	With aye-aye traces		With human traces		Firewood score
						Count	%	Count	%	
Rotra mena BL	Myrtaceae	<i>Syzygium</i> sp. 1	85	18.40	12.3	7	13.46	22	23.40	10
Lalona	Cunoniaceae	<i>Weinmannia rutenbergii</i>	68	14.72	10.6	3	5.77	11	11.70	7
Lanary	Euphorbiaceae	<i>Uapaca</i> sp.	55	11.90	8.0	7	13.46	15	15.96	10
Ramilevina	Asteraceae	<i>Adopoccephala pauciflora</i>	54	11.69	11.8	11	21.15	11	11.70	1
Maka	Cunoniaceae	<i>Weinmannia</i> sp.	28	6.06	10.1	2	3.85	10	10.64	8
Tavolo	Lauraceae	<i>Cryptocarya</i> sp.	27	5.84	16.2	10	19.23	2	2.13	4
Sana lavaravina	Elaeocarpaceae	<i>Elaeocarpus hildebrandtii</i>	25	5.41	9.2	4	7.69	1	1.06	3
Vatsilana tenany	Araliaceae	<i>Polyscias</i> sp.	23	4.98	8.0	4	7.69	2	2.13	1
Lendemilahy	Loganiaceae	<i>Anthocheista</i> sp.	18	3.90	11.2	1	1.92	2	2.13	1
Merapotsy	Asteraceae	<i>Brachylaena merana</i>	11	2.38	14.9	0	0.00	0	0.00	9
Rotra mena SL	Myrtaceae	<i>Syzygium</i> sp. 2	11	2.38	9.8	0	0.00	5	5.32	10
Sily	Euphorbiaceae	<i>Croton</i> sp.	8	1.73	4.2	1	1.92	3	3.19	5
Menahihy	?	?	6	1.30	11.2	1	1.92	0	0.00	7
Angavodiana	Ericaceae	<i>Agarista</i> sp.	5	1.08	11.8	0	0.00	0	0.00	2
Hazombo	?Sapindaceae	?	5	1.08	7.6	0	0.00	2	2.13	10
Malambovony	Erythroxylaceae	?	4	0.87	12.0	0	0.00	1	1.06	6.5
Ravitsakay	Putranjivaceae	? <i>Drypetes madagascariensis</i>	4	0.87	4.3	0	0.00	3	3.19	3
Tandrokondriahy	?Lauraceae	? <i>Ocotea</i>	3	0.65	14.3	0	0.00	0	0.00	6
Valanirandambo	Loganiaceae	<i>Nuxia</i> sp.	3	0.65	3.3	0	0.00	0	0.00	1
Alakamishazo	?Rutaceae	?	2	0.43	12.0	0	0.00	1	1.06	1
Ambora	Monimiaceae	?	2	0.43	19.0	0	0.00	1	1.06	2
Mokaranana	Euphorbiaceae	<i>Macaranga macropoda</i>	2	0.43	7.0	0	0.00	0	0.00	10
Sary	Meliaceae	<i>Astrotrichilia elliotii</i>	2	0.43	1.6	0	0.00	0	0.00	2
Vakoandambo	Pandanaceae	<i>Pandanus</i> sp.	2	0.43	5.5	0	0.00	1	1.06	0
Anjavidy	Ericaceae	<i>Philippia</i> sp.	1	0.22	6.0	0	0.00	0	0.00	10
Hetatra	Podocarpaceae	<i>Podocarpus madagascariensis</i>	1	0.22	2.0	0	0.00	0	0.00	10

Table 2 continued

Local name	Family	Scientific name	No. individuals	Percent of sample	Average time since death (year)	With aye-aye traces		With human traces		Firewood score
						Count	%	Count	%	
Kininina	Myrtaceae	<i>Eucalyptus</i> sp.	1	0.22	1.0	0	0.00	0	0.00	8
Kiripika	Euphorbiaceae	? <i>Croton</i>	1	0.22	22.0	0	0.00	0	0.00	5.5
Marokoditra	?Lauraceae	?	1	0.22	2.0	0	0.00	1	1.06	6
Nato	?Sapotaceae	?	1	0.22	22.0	0	0.00	0	0.00	3
Rebosa	Rutaceae	<i>Melicope madagascariensis</i>	1	0.22	5.0	0	0.00	0	0.00	3
Sana mavoravina	Elaeocarpaceae	<i>Elaeocarpus</i> sp.	1	0.22	8.0	0	0.00	0	0.00	1
Silimainty	Euphorbiaceae	<i>Croton</i> sp.	1	0.22	3.0	1	1.92	0	0.00	6
Grand total/average			462		10.7	52	13.1	94	9.1	

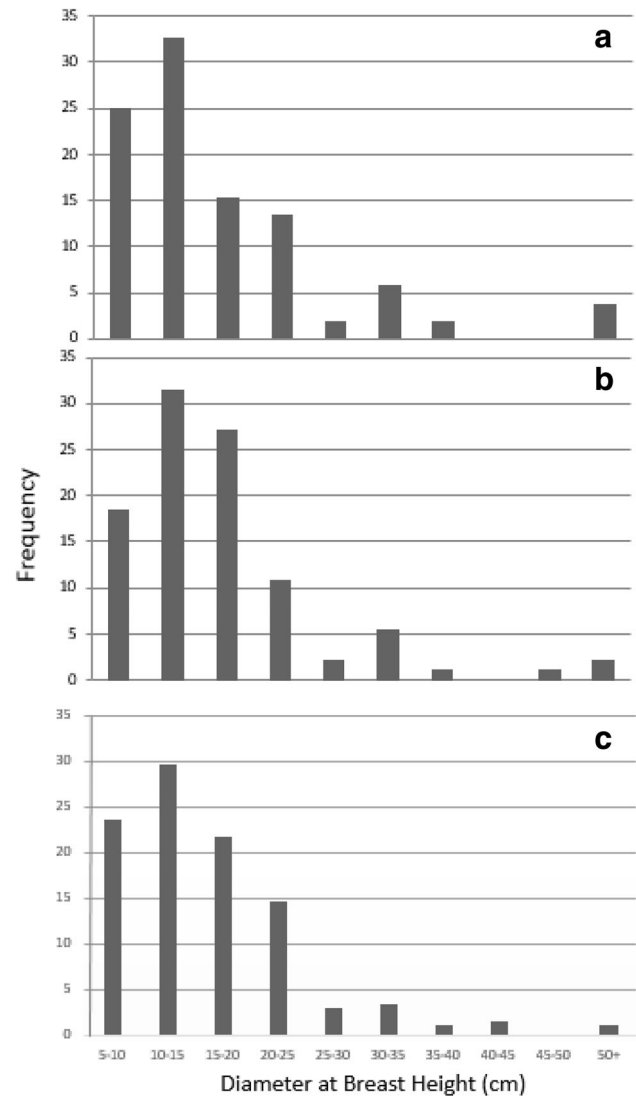


Fig. 2 Distribution of tree diameter at breast height (cm) for **a** the subset of trees with indications of use by aye-aye, **b** the subset of trees with indication of use by Malagasy, and **c** a sample of 462 dead trees surveyed within forest fragments at Mahatsinjo, eastern Madagascar

aye-aye traces was highest in the smallest fragments (Fig. 3), and the effect was marked (although not statistically significant, $\rho = -0.87$; $P = 0.054$). In contrast, human traces were found at a similar density in all fragments ($\rho = 0.05$; $P = 0.93$).

Discussion

Our analyses detected signs of niche separation between aye-ayes and humans in terms of tree species utilized, as well as some indication that these two types of consumer use some tree species more or less frequently than expected based on their abundance. However, extensive overlap exists between the tree species used, and we believe that

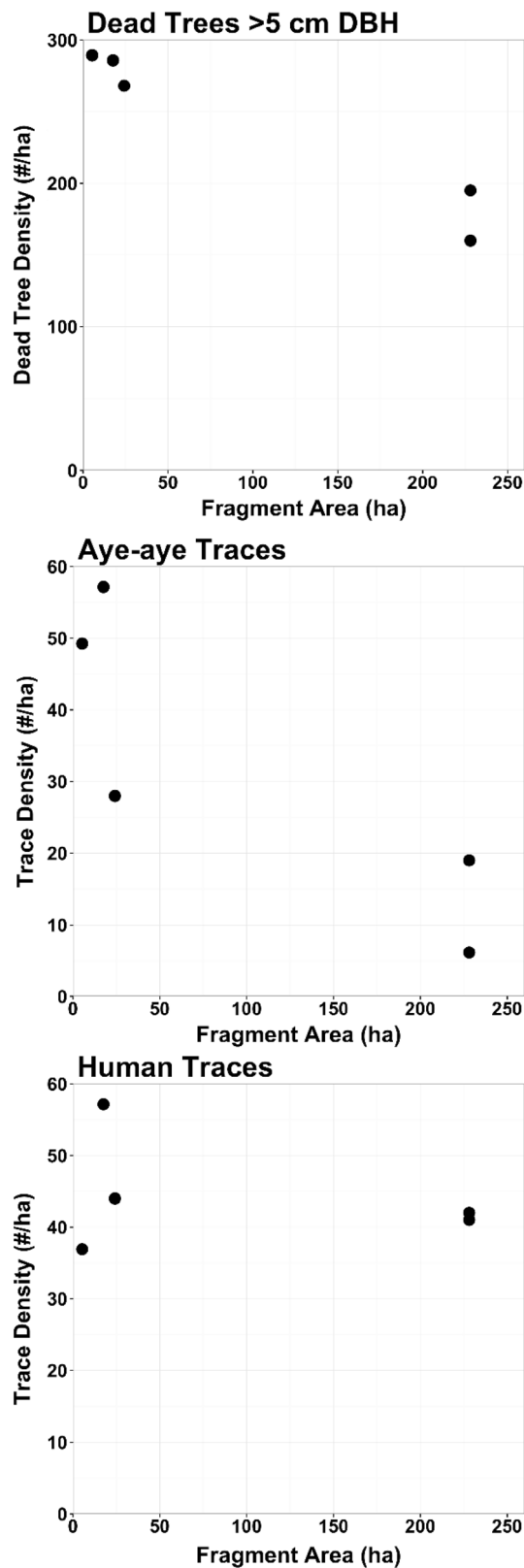


Fig. 3 Relationship between fragment size and density of dead trees >5-cm diameter at breast height (*DBH*), density of aye-aye traces, and density of Malagasy traces

usage may be more extensive than our sample indicates. Our sample contained many species that were only rarely encountered (18 of the 33 species were represented in the sample by four or fewer individuals); many among these had been observed previously to have aye-aye traces (M. T. Irwin, personal observation), and aye-ayes have even been observed to extract prey from arborescent bamboo at Tsinjoarivo (M. T. Irwin, personal observation) and elsewhere (Duckworth 1993). Of the 15 most commonly encountered species in this sample, 11 were utilized by aye-ayes and 12 by people. This suggests that the larvae consumed by aye-ayes are not restricted to a few tree species, and that there is a significant potential for resource overlap between aye-ayes seeking larvae and humans seeking firewood.

Our firewood rankings allowed us to more finely assess the likelihood of resource competition. Our analysis rested on the assumption that humans were harvesting dead wood rather than actively cutting living trees, which was in line with our assistants' description of local practices. When only the most commonly encountered species were considered, the likelihood of a dead tree showing human traces tended to be positively correlated with its firewood score, as expected, while the opposite relationship was shown for aye-aye traces. Both relationships, while not significant, demonstrated a reasonable effect size. Thus, although the list of species utilized overlaps considerably, aye-ayes may tend to focus on less-preferred firewood species, such as *Ramilevina*, *Tavolo* and *Sana lavaravina* (Table 2), in their foraging for larvae.

In terms of the timing of resource competition, the average estimated time since death of the trees in our sample was quite long (10.7 years). Since this age was only estimated, we must consider the possibility that it is an overestimate. However, the research assistants were able to provide specific examples of older dead trees, including one standing dead tree within sight of our camp that had already died when the camp was established in 2002 (the assistant further assessed that tree was still not quite dry enough to be useful as firewood). Therefore, we believe these estimates are reasonably accurate. These assistants further stated that trees of some species are not good as firewood until they have been dead for 17–25 years.

If the estimates of time since death are accurate, the lower value for trees utilized by people suggests that trees may generally become useful for firewood before they are useful for aye-ayes (through housing larvae of Coleoptera). This suggests humans may have an advantage in this particular form of resource competition, and that harvesting for firewood may directly remove dead wood from the environment that would otherwise have been useful in providing food resources for aye-ayes.

Commensurate with the fact that Mahatsinjo is a fairly disturbed forest and has suffered extensive timber extraction by local people (Irwin 2006), the average DBH for all dead trees, and those used by both consumer species, was <20 cm. Presumably larger dead trees would be a richer resource for both consumers (and possibly had been for past populations in this region), but are less prevalent today.

Our study showed that the smaller the fragment, the greater the density of dead trees; this mirrors investigations elsewhere in the tropics indicating that edge effects increase tree mortality (Laurance et al. 2011). Interestingly, the density of aye-aye traces showed a similar trend, with higher densities in the smallest fragments [opposite to the trend reported by Farris et al. (2011)], while human traces showed little variation across fragment sizes. This suggests that human populations (which were relatively evenly spread across our study area) utilized all fragments at roughly equal intensities. However, the variation in aye-aye traces could have several different explanations. First, it is possible that aye-aye traces were more easily detected in the smaller fragments (e.g., if trees were shorter or more likely to have fallen, traces would be nearer to the ground and easier to detect). Second, it is possible that aye-ayes exist in higher densities in smaller fragments. It is unlikely that this is the sole explanation, however, as the three smaller forest fragments (5–25 ha) are smaller than the recorded home ranges of aye-ayes [females, 30–40 ha; males, 125–215 ha (Sterling 1993)]. The degree of isolation of the fragments may also be important. Further research is needed to quantify aye-aye home range size at Tsinjoarivo, but it seems likely that some crossing between patches (at least the smaller ones) occurs. Third, the varying trace density may indicate that aye-ayes are using a broader landscape, but concentrating their foraging in smaller patches, perhaps due to higher dead tree density resulting in a higher density of larvae. Finally, it is possible that local aye-aye densities or patterns of patch use are not biased towards smaller patches, but simply that larvae contribute a greater proportion of their diet in smaller patches; when foraging in the larger patches, aye-ayes might show a higher reliance on other resources that were not detected in this study.

There are several confounding factors that might have influenced our results. First, because of time constraints we used plots adjacent to trails. These trails were set up as research trails, and along most of their length are not heavily used by people; however, they could have provided easy access for wood-cutting activities. Thus, human traces may be somewhat more prevalent near the trails than in the environment at large. Aye-aye traces are likely not biased because trails are rarely used by people at night.

Additionally, because dead trees persist in the environment for so long, it is hard to gauge whether we were detecting very recent or old traces. This makes it hard to gauge whether we were detecting signals that no longer reflected the current situation. However, humans have lived in the area for at least 30 years, and aye-ayes have presumably been continuously present, so there is no obvious reason to suspect that drastic recent changes in resource use have occurred.

Despite the results we report here, much remains to be learned about the ecology and viability of aye-ayes in this human-dominated landscape. Although our analyses provide information on both resource use and range, focal animal studies are a necessary next step to quantify diet and resource use (including resource overlaps with those of the human population), as well as aye-aye density, population dynamics and landscape-use patterns.

Deforestation and habitat degradation continue to be of concern for aye-ayes (Farris et al. 2011), with regard to both their global status in the wild, and particularly that at Tsinjoarivo (which currently is not a protected area). We documented the use of tree species by aye-ayes in an area used by the Malagasy, but we have no insight on whether the realized niche of aye-ayes may have shifted in response to the use of the forest by Malagasy. Degraded and fragmented forests generally have a lower canopy height, tree density, and species diversity (Irwin 2006; Laurance et al. 2011). Highly species-rich forests, such as those found in Madagascar, are the most vulnerable to human impacts (Brandon, 2014). Given the extent of deforestation and habitat fragmentation in Madagascar it would be challenging to find a field site that has not been impacted by the Malagasy's use of the forest. Thus, it is perhaps unlikely that we will ever know the fundamental niche of aye-ayes, but understanding their realized niche in human-impacted landscapes will be crucial in efforts to sustain viable aye-aye populations.

Acknowledgements The authors thank the community of Tsinjoarivo, Madagascar for their assistance and support throughout this project, including the local assistants and the associations Maitsoanala and Taratra. We thank the government of Madagascar, CAFF/CORE and the Ministry of Environment, Ecology, Oceans and Forests for research permissions. This work was conducted as part of a Study Abroad program run by SADABE, Northern Illinois University and the University of Massachusetts in partnership with the Department of Paleontology and Biological Anthropology, University of Antananarivo. R. T. M. thanks P. J. Perry for introducing her to the lemurs of Madagascar.

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