

ARTICLE

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Habitat corridor utilization by the gray mouse lemur, *Microcebus murinus*, in the littoral forest fragments of southeastern Madagascar

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ABSTRACT

Habitat fragmentation has reached a dramatic level in Madagascar. As the size of many remaining forest fragments is unlikely to maintain viable animal populations in the long-term, connecting isolated subpopulations by creating corridors is important to support gene flow and the persistence of the endemic fauna, including lemurs. Since restoration with endemic trees is slow, exotic trees may represent a faster alternative to initiate habitats that can be used by animals. Here, we studied whether or not grey mouse lemurs, *Microcebus murinus*, use corridors composed of exotic and native trees of different age and composition to move between littoral forest fragments. For this, we trapped *M. murinus* in four forest fragments and mixed tree plantations between the fragments. One of the corridors was composed of a mixture of endemic and mature exotic *Eucalyptus robusta* trees. The second corridor consisted mainly of an old stand of exotic *Melaleuca quinquenervia*. The third corridor was composed of exotic *Acacia mangium* trees planted in 2009. During four years of study, only one male *M. murinus* used the *Melaleuca* corridor, while several *M. murinus* were caught in the *Eucalyptus* and the *Acacia* corridor in 2013. The density of the corridor under-story appeared to influence the number of individuals captured; the corridor with highest understory density was used most. The captures within the corridors illustrate that exotic trees allow movements of mouse lemurs within less than 5 years after plantation.

RÉSUMÉ

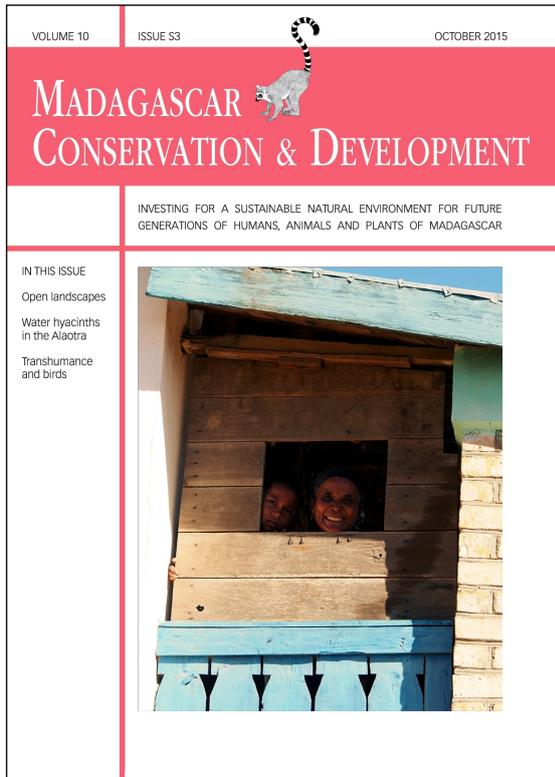
La perte et la fragmentation de l'habitat ont atteint une dimension dramatique à Madagascar. Même si les menaces résiduelles pourraient être atténuées, il est improbable que la taille actuelle de plusieurs fragments de forêts soit suffisante pour maintenir des populations animales viables à long terme. Connecter des sous-populations isolées en créant des corridors biologiques est une stratégie pour restaurer le flux génétique et

appuyer le maintien des faunes endémiques, y compris les lému-riens. Étant donné que la restauration des habitats avec des plantes endémiques est lente, des espèces de plantes allogènes peuvent constituer une alternative rapide et peu onéreuse pour démarrer une restauration ainsi que pour créer des habitats utilisables par les animaux. Dans cette étude, nous examinons l'utilisation de corridors biologiques composés de différentes plantes allogènes par *Microcebus murinus* pour circuler entre divers fragments forestiers dans le Sud-Est de Madagascar. Notre but est de déterminer l'âge et la composition floristique des forêts restaurées qui permettraient la dispersion de *M. murinus* entre différents fragments. Pour cela, nous avons effectué une méthode de capture de *M. murinus* dans quatre fragments forestiers et dans des plantations d'arbres mixtes entre les fragments. Un des corridors biologiques était composé d'un mélange de plantes endémiques et allogènes dont *Eucalyptus robusta*. Le deuxième était principalement un vieux peuplement de *Melaleuca quinquenervia*. Le troisième corridor n'était composé que d'arbres allogènes, principalement des *Acacia mangium*, qui avaient été plantés en 2009. Les résultats montrent que *M. murinus* est abondant dans tous les sites de forêt. Pendant les quatre années d'étude, seul un mâle est passé d'un fragment à l'autre en utilisant le corridor de *Melaleuca*, et seul un mâle *M. murinus* a été capturé dans le corridor d'*Acacia* en 2012. En 2013, 29 individus de *M. murinus* ont été capturés dans deux des corridors suivis dans cette étude, incluant celui composé seulement de plantes allogènes, mais aucun animal n'a été capturé dans le corridor composé seulement de *Melaleuca*. La densité de la strate arbustive du corridor semble influencer le nombre d'individus capturés, le corridor ayant une densité élevée d'arbuste étant le plus utilisé. Ceci montre que les études de capture-recapture avec des *Microcebus*, qui sont des animaux ayant une courte durée de vie, ne sont pas efficaces pour documenter la dispersion de cette espèce dans les forêts littorales et la fonctionnalité des corridors.

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Par contre, les captures dans les corridors et dans les zones avoisinantes en 2013 suggèrent que la probabilité de flux génétique entre les fragments était élevée, et indiquent nettement que les plantes allogènes peuvent encourager les mouvements de *M. murinus*, même dans les peuplements jeunes de moins de cinq ans.

INTRODUCTION

Deforestation and habitat fragmentation, caused by logging and agricultural practices, are the leading causes of biodiversity decline worldwide (e.g., Fischer and Lindenmayer 2007, Habel and Zachos 2012). Fragmentation can result in a series of small subpopulations in the residual habitat, each with a high risk of going locally extinct or suffering from genetic drift (Templeton et al. 1990). This can reduce the ability of the subpopulations to adapt to environmental changes, with lowered fertility and reduced resistance to pathogens and parasites (Schad et al. 2005, Habel and Schmitt 2012).

Madagascar's forests are highly fragmented (Harper et al. 2007). In particular, the littoral forests of Madagascar are a top conservation priority, with the few remaining fragments being mostly smaller than 1,000 ha (Ganzhorn et al. 2001). These habitats are of great biological importance due to their floral diversity. They contain 13% of Madagascar's plant diversity, with at least 40 plant species endemic to Fort Dauphin's littoral forests alongside various endemic and threatened fauna species (Consiglio et al. 2006, Rabenantoandro et al. 2007, Lowry et al. 2008, Wesener 2009). These forest fragments are thought to be too small for the survival of viable populations of most forest-dependent vertebrate species (Ganzhorn et al. 2000, Watson et al. 2004).

Habitat corridors could link isolated populations, and thus mitigate isolation effects (e.g., Hilty et al. 2012). For the implementation of conservation actions, the question remains to understand what vegetation characteristics will allow the movements of animals and thus act as a corridor (Saunders et al. 1991, Hobbs 1992, Fischer and Lindenmayer 2007, Irwin et al. 2010). In Madagascar, natural or facilitated regeneration of natural forests from deforested areas is too slow to counteract forest loss. Non-native plantations can be established faster. This is particularly important in the littoral forests that grow on nutrient-poor sandy soil (Rarivison et al. 2007, Ducouso et al. 2008). Therefore, it is essential to determine the effectiveness of corridors consisting of non-native plant species that would facilitate the movements of species between patches of fragmented habitats (Ganzhorn 1987, Irwin et al. 2010).

For the present paper, we first investigated whether or not, and at what state, corridors with varying exotic tree composition and vegetation structure represent suitable habitat for mouse lemurs (*Microcebus murinus*), a small nocturnal lemur species that is known to use a large variety of forest habitats (Mittermeier et al. 2010). This species was chosen as study species because it can respond rapidly to environmental changes due to its short generation times and high population densities (Ganzhorn and Schmid 1998). In addition, this small-sized species is likely to be vulnerable to predation when passing through areas with inadequate foliage protection (Goodman et al. 1993). Therefore, they are more constrained to forest habitats than larger lemurs, which can occasionally cross open space over larger distances, such as the sympatric *Eulemur collaris* (Donati et al. 2007). In *M. murinus*, males are the dispersing sex (Radespiel et al. 2001, Fredsted et al. 2004). Therefore, we expect more males than females moving through

the corridors. Second, we compared the effectiveness of two different methods to monitor movements of mouse lemurs between forest fragments across an unsuitable matrix consisting of bare sand or heath vegetation.

METHODS

STUDY SITE. This study was conducted in the littoral forest fragments of Mandena, southeastern Madagascar, located at 24° 95'S, 46° 99'E (Figure 1). The study area consists of the forest fragments, M15 and M16 (the Mandena Conservation Zone), the forest fragments M13, M20, and TOK (Antokonlala), and the habitat corridors which link them (abbreviated as CM15-M13, CM16-M20, CM15-TOK; "M" stands for "Mandena" and the number indicates the number of the forest fragment at Mandena; "C" stands for "corridor" linking the fragments; Figure 2, Table 1). "TOK" consists of an old plantation of *Eucalyptus robusta*, planted prior to 1975

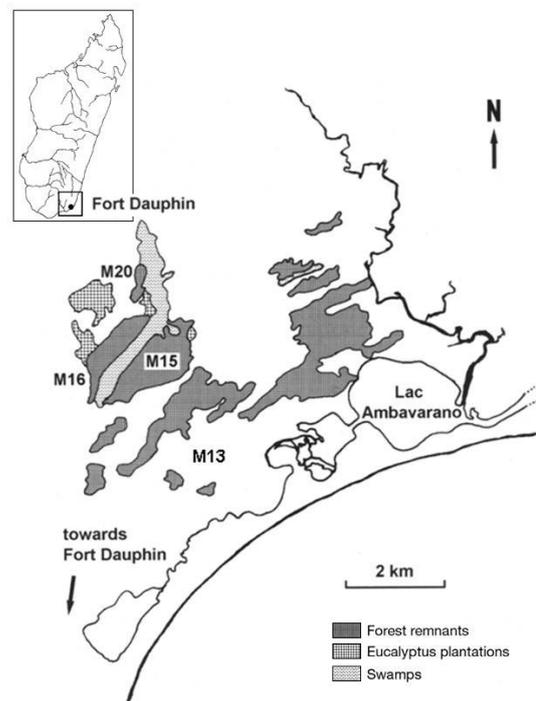


Figure 1. The Fort Dauphin region of south-east Madagascar, with the littoral forest fragments depicted in black (as of 2006) and the area of Mandena highlighted in red (modified from Bollen and Donati 2006).

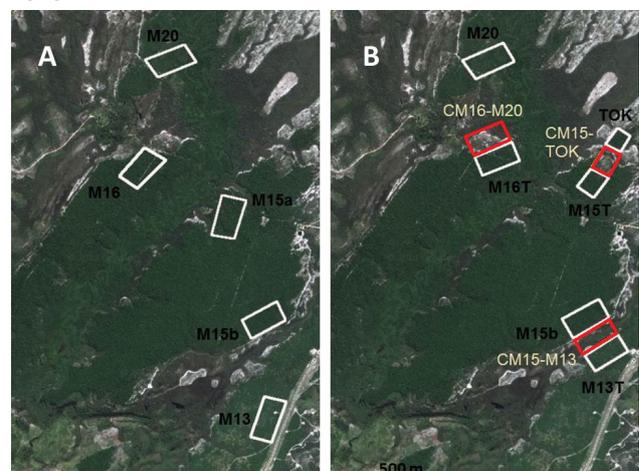


Figure 2. Trapping grid locations in the forest fragments (white) and the corridors (red). A: Trapping grid locations for captures between 2009 and 2012. B: Trapping grid locations for the study in 2013; note that the large distance between the M20 and CM16-M20 trapping grids is due to the presence of a large swamp, which separates them (modified from Google Earth).

Table 1. Vegetation characteristics of the study sites in Mandena. Fragment size (in hectares) as of 2005; canopy cover from Vincelette et al. (2007b); density of trees in forest fragments; *based on "Point-centred-quarters" (Ganzhorn et al. (2007b), and **based on "Whittaker plots" (additional sites established in 2013 and corridors, Blanthorn 2013).

Site	Size (ha)	% Canopy cover	Density of trees per ha			Number of tree species			% Exotic species		
			≥ 10 cm	5.0 – 9.9 cm	< 5 cm	≥ 10 cm	5.0 – 9.9 cm	< 5 cm	≥ 10 cm	5.0 – 9.9 cm	< 5 cm
Forest fragments											
M13*	109	≤ 20	81	210				0	0	0	
M13T**			230	800	19000	19	4	18	0	0	
M15a*	95	51 – 70	356	693				0	0	0	
M15b											
M15T**			320	1200	19000	21	5	16	0	0	
TOK	2										
M16*	53	51 – 70	356	693				0	0	0	
M16T**			300	4200	22000	21	3	19	0	0	
M20*	6	≤ 20	156	730				0	0	0	
M20**			170	400	22000	13	2	25	0	0	
Corridors											
CM15-M13**		0	155	600	5000	2	2	2	100	100	
CM15-TOK**		0	230	400	7000	4	2	12	98	100	
CM16-M20**		0	280	200	4500	1	1	7	100	100	

with a rich undergrowth of native trees. It is unclear whether *E. robusta* had been planted within degraded native forest or whether the native forest regenerated after the plantation of *E. robusta*.

The Mandena Conservation Zone is part of Quebec Iron and Titanium (QIT) Madagascar Minerals' (QMM) environmental program that seeks to minimise the impacts of ilmenite mining on the regional biodiversity (Temple et al. 2012). The company is required to restore the mined area after mining. In order to achieve this goal, various long-term studies have been carried out to understand the present biodiversity patterns and ecosystem processes (e.g., Ganzhorn et al. 2007a, Lowry et al. 2008, Temple et al. 2012). As part of its environmental activities, the company has established tree plantations around the conservation zone with much emphasis on the eventual connection of the fragmented littoral forests of Mandena through habitat corridors (Vincelette et al. 2007b). These corridors consist of a mixture of native and introduced plant species (mainly *Eucalyptus*, *Acacia* and *Casuarina*), that will aid in the restoration of the impoverished soil as well as provide a fast-growing matrix for the movement of animals. This will eventually facilitate the dispersal of seeds of native tree species by animal frugivores (Bollen and Donati 2006). Several corridors have been established between fragments M15 and M16 and the surrounding fragments, three of which were included in this study (CM16-M20, CM15-M13, CM15-TOK; Table 1; Figure 3). The two fragments M16 and M20 are connected (CM16-M20) via a swamp with exotic *Melaleuca quinquenervia* that had established itself at least 20 years ago prior to the onset of the restoration activities. The fragments M13 and M15 were connected by *Acacia mangium*, planted in 2009 to create the corridor CM15-M13. Up to the time of study in 2013, this corridor contained next to no undergrowth of native tree species. Fragment M15 and "TOK" are linked by *E. robusta* and some regenerating native tree species (CM15-TOK).



Figure 3. The three types of corridors included in this study. Left: CM15-TOK. Centre: CM16-M20. Right: CM15-M13.

LONG-TERM STUDY ON LARGE-SCALE DISPERSAL. First, the question of whether or not corridors between forest fragments would be effective was studied using long-term study plots established in the littoral forest fragments M13, M15a, M16, and M20 between 1998 and 2000 (Ramanamanjato and Ganzhorn 2001, Ganzhorn et al. 2007b, Figure 2A). M20 is located about 450 m north of M16. M16 and M15a are about 550 m apart and connected via littoral forest and native swamp vegetation. M15b is a newly established trapping grid some 550 m south of M15a; both are located within the continuous littoral forest of M15. M15b served as control to estimate whether or not dispersing individuals can be found in two trapping grids, spaced at the same distance within a fragment as the distance between trapping grids in different fragments. M15b was separated from M13 by open sand, with forest restoration activities starting between these two fragments in 2009.

We set up Sherman Traps baited with banana in these five permanent trapping grids (in M13, M15a, M15b, M16, and M20) for four nights every three months from February 2009 to August 2012. Each trapping grid consisted of 40 trapping stations with one trap on the ground and one trap in trees or bushes. Trapping stations were spaced 25 m apart in parallel transects, which were also 25 m apart (Ramanamanjato and Ganzhorn 2001). While designed originally to study population dynamics of small mammals, data collected during this period were also used to assess how far the mouse lemurs dispersed in the area and whether or not standardized trapping can be used to monitor movements between fragments.

SHORT-TERM CORRIDOR-CENTRED CAPTURES. As we never caught the same individual *Microcebus murinus* in both of the two trapping grids within M15 (M15a and M15b), we questioned whether or not the original design was suitable to assess the effectiveness of corridors. We therefore started trapping directly in the corridors. First, traps were set in the corridor plantation adjacent to M15b towards M13 in August 2012 (= CM15-M13). Subsequently, we set up a study designed explicitly to assess whether or not the corridors were used by *M. murinus* (Blanthorn 2013). For this, new trapping grids were created in May 2013 in three habitat corridors (CM16-M20, CM15-TOK and CM15-M13) (Figure 2B) and right next to the corridors in the forest fragments they link (M16T, M15T, TOK, M13T; M20 and M15b were the same trapping grids as used in the long-term study) with the aim to see whether the mouse lemurs were using the habitat corridors to move. The new trapping grids in the forest fragments were positioned contiguous to the habitat corridors to enhance the chance of recapturing marked animals.

Between May and July 2013, four days were spent trapping at each site. In the corridors, traps were set for another four days

(i.e., eight days in total). Captured animals were marked with Trovan transponders (2.1 x 11.5 mm; Trovan ID 100). An animal's movement across the trapping grids was noted when it was recaptured in a different fragment to where it had initially been captured. The distance moved by an individual was measured as the distance between trapping points of capture and recapture.

VEGETATION DESCRIPTIONS. We established botanical plots in the forest fragments and connecting corridors to quantify the vegetation characteristics (species richness, canopy height and tree density) at each site. These variables have been found to be related to habitat utilization of lemurs in previous studies (e.g., Ganzhorn et al. 1997, Lahann 2008, Sehen et al. 2010). The vegetation of each plot used for the long-term study had been described between 1998 and 2004 based on the point-centred quarters method (Ganzhorn et al. 2011), centred on the 40 trapping stations (Ganzhorn et al. 2007b). For the study sites used for the corridor study in 2013 (Blanthorn 2013), the horizontal and vertical vegetation structures were measured using a modification of the Whittaker plot (Shmida 1984). Our modification involved creating a 50 m by 20 m plot for trees larger than 10 cm dbh (diameter at breast height), with two smaller plots at the centre, one measuring 10 m x 5 m for trees with 5–9.9 cm dbh, and one measuring 5 m x 2 m for trees under 5 cm dbh (Supplementary Material). This was done to incorporate a measurement of the understory plants as *Microcebus* are small primates and likely to utilise such habitats (Lahann 2008). A total of 13 vegetation descriptions were carried out: two in each corridor, one in each fragment (except for TOK) and one in each swamp. The height estimation, dbh and local name were recorded for each plant in the plot. Plants were identified to their vernacular name and the majority to their scientific names, following nomenclature in Randriatafika and Rabenantoandro (2007) and the knowledge of the QMM fauna team.

RESULTS

VEGETATION DESCRIPTIONS. CM15-TOK had the lowest proportion of exotic plant species, and the highest diversity and density of understory trees (Table 1). The corridor between M15 and M13 (CM15-M13) had the highest proportion of exotic trees (100% for all plant dbhs) and the lowest species diversity (two species for each tree size category; Table 1).

LONG-TERM STUDY ON LARGE-SCALE DISPERSAL OF *MICROCEBUS MURINUS*. According to the long-term mark-recapture study carried out from 2009 to 2012, mouse lemurs are abundant in all forest fragments (Figure 4). Only one animal was caught in more than one trapping grid. This male had moved from M20 to M16 between February and August 2010. No individual was recorded to have moved between the three trapping grids (M15a, M15b, M16) located within the continuously forested fragments M15 and M16.

SHORT-TERM CORRIDOR-CENTRED CAPTURES OF *MICROCEBUS MURINUS*. We captured 2–17 *M. murinus* individuals in the forest fragments within a single capture session lasting for four nights. No *M. murinus* were caught in the corridor CM16-M20 that consists mainly of *Melaleuca* with sparse undergrowth due to the swampy nature of the ground and the inhibiting effect of *Melaleuca* on the regeneration of other plant species. In corridor CM15-M13, 2 and 8 *M. murinus* were caught per trapping ses-

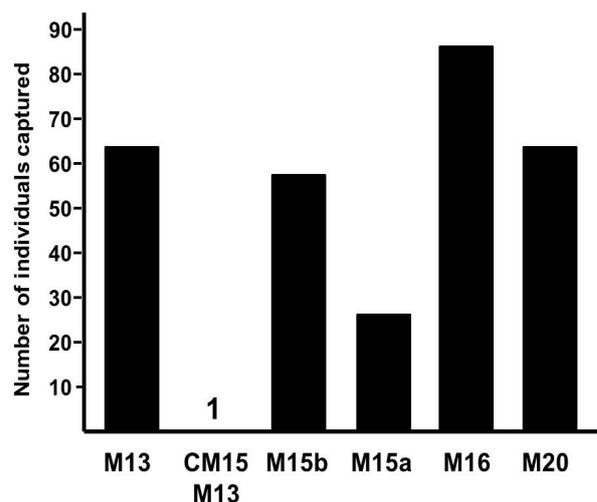


Figure 4. Number of individuals captured in the different permanent trapping plots between 2009 and 2012. In the corridor (CM15-M13) traps were set only in 2012.

sion in 2013. In 2012 only one *M. murinus* had been caught in this corridor. Seven and 12 different individual *M. murinus* were caught in corridor CM15-TOK in 2013. This corridor had the highest density of regenerating trees and shrubs.

The number of animals captured in the forest fragments per trapping session was significantly higher than the numbers captured in the corridors (data for 2013 from the first capture session: Mann-Whitney-U test: $U = 1.5$, $p < 0.05$). There was no significant difference between the sex-ratio of the animals captured in the forest to those captured in the corridors (Fisher's exact test: $p = 0.16$). Around half of these animals were then recaptured in a different habitat area. A higher number (nine out of 13) of these were males (not significant). The distance they moved between trapping sites ranged from 25 m to 200 m, with females moving on average further (100–200 m; mean 169 m) than males (25–175 m; mean 114 m). The difference was not significant.

DISCUSSION

As large areas of continuous habitats continue to shrink, linking populations in remnant habitats and facilitating the survival of species in anthropogenic habitats has become a prime initiative around the world. Some examples of this include creating a network of connected habitats in Europe through the program "Natura 2000" (Ostermann 1998), connecting forest fragments of the Mata Atlantica in South America (Tabarelli et al. 2005), and facilitating animal migrations in Africa (Bartlam-Brooks et al. 2011) or wildlife in Asia (Wikramanayake et al. 2004, reviewed by Gardner et al. 2010). While restoration with native plants is certainly desirable (Hollaway 2003, Birkinshaw et al. 2009), plantations with non-native plants may sometimes provide alternatives as they often are faster growing and may provide benefits for humans, thus becoming more attractive and acceptable for local people (Gérard et al. 2015). In Madagascar, the study of the role of anthropogenic habitats for the native fauna has a long history (e.g., Petter et al. 1977, Ganzhorn 1987, Goodman et al. 1996, Irwin et al. 2010, Martin et al. 2012), but plantations are rarely used as a tool to mitigate fragmentation effects. Thus, our experience and knowledge of the possibilities of plantations for restoration and conservation action in Madagascar is limited.

Within large-scale restoration obligations after a mining operation (Vincelette et al. 2007a, Temple et al. 2012), various corri-

dors were planted to link isolated remnants of littoral forest fragments in southeastern Madagascar (Rarivoson et al. 2007, Vincelette et al. 2007c). These plantations offered the possibility to study the efficiency of restoration activities for native plants and animals. Apart from one mouse lemur that had moved from M20 to the permanent trapping grid of M16, no other individual was found to have moved between any of the permanent trapping grids, neither within the continuous forest block M15/M16, nor through the vegetation between forest fragments. Since the continuous forest of M15/M16 does not provide a physical barrier for *Microcebus murinus*, and these lemurs are known to move over several hundred meters (Radespiel et al. 2003, Schliehe-Diecks et al. 2012), we conclude that this method was not sensitive enough to assess movements over distances of several hundred meters.

In the second approach, trapping grids were installed directly in the corridor and at either side of the corridor in the natural forest fragments. This design revealed that several *Microcebus murinus* used the corridors as well as the bordering natural forest and actually moved repeatedly between these different portions of habitat. Though none of these animals actually used the corridor to cross the matrix and move from one forest fragment to the other, the results show that planted woody vegetation can provide useful habitats at least for *M. murinus* within about four years. This should contribute substantially to the connectivity of the remaining forest fragments. Our preliminary habitat characterization indicates that structural features of the vegetation were more important than plant species diversity, though small sample size prohibited statistical analyses. More data is necessary to investigate this aspect in more detail.

While it is encouraging that plantations with fast growing trees are used by arboreal lemurs, it should be kept in mind that *Microcebus murinus* is not a habitat specialist, but occurs in a wide range of different habitats (Petter et al. 1977, Irwin et al. 2010, Mittermeier et al. 2010). Therefore, this species may be less hesitant to use non-native vegetation than other lemur species. Except for *Avahi meridionalis*, all the other lemur species occurring in Mandena (*Cheirogaleus* spp., *Hapalemur meridionalis* and *Eulemur collaris*) use the *Melaleuca* stands to feed on nectar when trees are flowering and for travel and resting (e.g., Lahann 2008, Eppley et al. In press). *E. collaris* are known to cross bare ground or heath vegetation between forest fragments (Donati et al. 2007) and *H. meridionalis* is feeding intensively on grass on the ground (Eppley and Donati 2009). None of these species has been seen during visual inventories of the corridors (Blanthorn 2013). Therefore, we cannot speculate whether or not these planted corridors provide the habitat characteristics required by these lemur species.

Many non-native plant species, including *Melaleuca quinque-nervia* and *Acacia mangium* can be invasive (Gérard et al. 2015). This should be considered when using exotic plants for habitat restoration, buffer zones or corridors (Simberloff et al. 2013). For the time being, *Melaleuca* remains restricted to swamp areas and *Acacia mangium* has not shown any signs to move into the natural littoral forests (J. Rabenantoandro, pers. comm.).

In conclusion, our findings suggest that habitat corridors composed of exotic, or mixtures of exotic and native, plant species can facilitate the movement of gray mouse lemurs. The density of the understory appears to be more important to these small lemurs than the presence of native plants. The presence of individuals in corridors only 3–4 years after they had been planted sug-

gests that the likelihood of genetic flow across the fragments via the corridor is high, and likely to improve as the corridors mature and become more established.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

S1. Schema of modified Whittaker plot.