Do lemurs disperse seeds over relatively short distances? The case for Madagascar's 'spatially restricted seed dispersal'

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ABSTRACT

Seed dispersal is a pivotal ecological process, underpinning the ecology of terrestrial ecosystems and having a significant impact on forest structure and dynamics. In the tropics, up to 90% of seeds are dispersed by fruit-eating animals, whose behaviour greatly influences seed distribution – variations in ranging behaviour and activity patterns, for example, can have significant impacts on dispersal distance. Primates are important seed dispersers throughout the tropics, but are particularly crucial on Madagascar, where lemurs have the greatest biomass and species richness of frugivores on the island. Furthermore, many other seed-dispersing taxa are absent. Previous research[1] had noted relatively low dispersal distances by lemurs. This study aimed to test the hypothesis that seed dispersal by lemurs occurs over relatively short distances in comparison to other primates elsewhere in the tropics. Though only limited dispersal distance data are available (for two lemur species, six New World primate species and three Old World primate species), statistical analysis indicates that seed dispersal by lemurs occurs over significantly shorter distances than by other primate species. This finding supports the hypothesis that seed dispersal on Madagascar is 'spatially restricted'. Possible explanations are that, just as the present-day lemur assemblage represents the vestiges of a once-broader diversity, seed dispersal may also have become restricted with the extinction of the largest-bodied lemurs. An alternative explanation is that prevalent lemur energy conservation strategies, hypothesised to have evolved in response to the low fruit productivity and high unpredictability of resources that characterise Madagascar's forests, are incompatible with long dispersal distances. Two scenarios are presented for how limited seed dispersal by lemurs and fruiting phenology on Madagascar may be related. Furthermore, restricted dispersal processes may be one of the many driving mechanisms influencing the development of local endemism in Madagascar.

METHODS

Dispersal distances by primates were collated form a search of the literature. Mean recorded dispersal distances were found for six New World and three Old World primate species, and two lemur species (*Table 1*). The lemurs' seed dispersal distances were compared with those of the other primates using a Kruskal-Wallis analysis of variance.

RESULTS

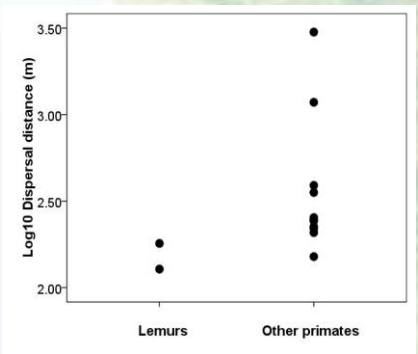

Figure 1. *Mean dispersal distance of lemurs and other primates. Dispersal distances differ significantly (Kruskal-Wallis ANOVA: K = 3.8961; df = 1; p = 0.0484), with lemurs dispersing seeds over shorter distances.*

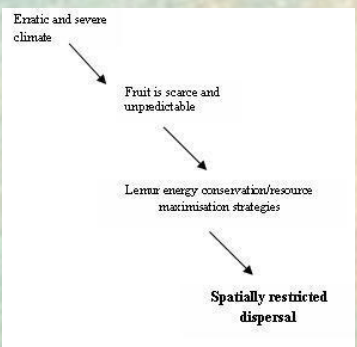

Figure 2. *Possible interaction between Madagascar's abundance and predictability of resources, climate, lemur ecology and seed dispersal. Lemurs conserve energy to cope with unpredictable and scarce resources, caused by the severe and erratic climate of Madagascar. Energy conservation strategies are incompatible with long-distance dispersal, causing dispersal to become spatially restricted.*

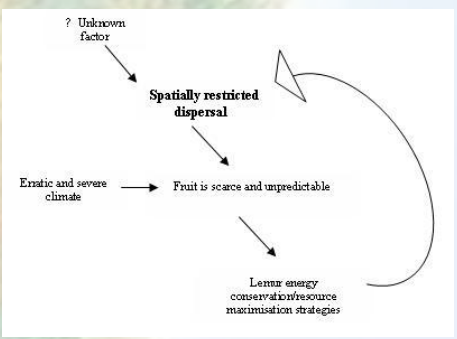

Figure 3. *Alternative scenario of possible interaction between Madagascar's climate, abundance and predictability of resources, lemur ecology and seed dispersal. An unidentified factor(s) causes lemur seed dispersal to be spatially restricted which, along with the severe and erratic island climate, results in fruit scarcity and unpredictability. Lemur strategies to cope with scarce resources are incompatible with long-distance dispersal and act to further limit dispersal.*

DISCUSSION

- Results suggest that seed dispersal by lemurs occurs over significantly shorter distances than seed dispersal by other primate species
- It may be expected that other lemurs on Madagascar disperse seeds over even shorter distances than the two species used in this study – two of the largest-bodied extant lemurs - due to their smaller body sizes and home ranges[2], which may be proportional to dispersal distance capabilities[3].
- These findings support the hypothesis that seed dispersal on Madagascar is 'spatially restricted'.
- Possible explanations are that, just as the present-day lemur assemblage represents the vestiges of a once-broader diversity, seed dispersal may also have become restricted with the extinction of the largest-bodied lemurs. It is possible that the seeds of Madagascar's forests were once transported greater distances by the now-extinct Mega-Lemuridae, in their presumed larger home ranges or territories[4]. Limited distribution and dispersal of some Malagasy tree species have been attributed to the loss of large-bodied seed dispersers on Madagascar[4,5]. The relationship between body mass and home range size is confounded by numerous variables, however, such as energy requirements, diet and social structures[6,7] and body size does not necessarily correlate with daily travel distances among primates[8].
- Alternatively, prevalent lemur energy conservation strategies (increased resting, limited ranging, increased intake of non-fruit resources), hypothesised to have evolved in response to the low fruit productivity and high unpredictability of resources that characterise Madagascar's forests[9,10,11], are incompatible with long dispersal distances.
- Two scenarios are presented for how limited seed dispersal by lemurs and fruiting phenology on Madagascar may be related (*Figures 2 and 3*).
- Spatially restricted dispersal could have significant implications for plant population genetics. Population genetic theory predicts that the more spatially restricted seed dispersal is, the more likely plant populations are to develop local genetic differentiation[12]. Local endemism (and therefore local genetic differentiation) is prevalent on Madagascar[13], possibly lending further support to the hypothesis. It is possible that ecological (such as seed dispersal) and evolutionary (such as speciation) processes on Madagascar in general are spatially restricted, perhaps as a result of the isolation (due to e.g. rivers[14] or watersheds[15] of populations, which has been proposed as a mechanism driving local endemism, which may have restricted the movements of animals and the seeds carried in their guts. Conversely, spatially limited dispersal may have been involved in the evolution of local endemism on the island; patterns of endemism in Madagascar are consistent with multiple potential driving mechanisms rather than one unifying explanation[16] and dispersal processes may have been a contributing factor in their evolution.
- The current dearth of data on seed dispersal patterns on Madagascar presents a major barrier to testing such hypotheses; further studies are needed to confirm dispersal distances in other lemur species.

Species	Mean dispersal distance (m)	Reference
New World primates		
Cebus apella	390	Zhang and Wang (1995)
Cebus capucinus	208	Wehncke et al. (2003)
Alouatta seniculus	225	Julliot (1996)
Ateles paniscus	151	Russo (2003a)
Ateles paniscus	254	Zhang and Wang (1995)
Ateles belzebuth	246	Dew (2001)
Lagothrix lagotricha	355	Stevenson (2000)
Lagothrix lagotricha	243	Dew (2001)
Old World primates		
Cercopithecus ascanius	1,178	Lambert (1997)
Hylobates muelleri x agilis	220	McConkey (2000)
Pan troglodytes	3,000	Lambert (1997)
Lemurs		
Varecia variegata	180	Moses and Semple 2011
Eulemur fulvus rufus	128	Spehn and Ganzhorn 2000

Table 1. *Mean dispersal distances for New World primates, Old world primates and lemurs*

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