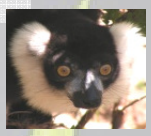
Primary seed dispersal by the black-and-white ruffed lemur (*Varecia variegata*) in the Manombo forest, southeast Madagascar



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ABSTRACT

Seed dispersal is a pivotal ecological process, but remains poorly understood on Madagascar where lemurs are key dispersers. Preliminary data[1] and a suite of behavioural and ecological attributes associated with effective seed dispersal suggest the black-and-white ruffed lemurs (*Varecia variegata*) may be an effective seed disperser, but no studies have investigated this species' dispersal effectiveness. This three-month study investigated primary seed dispersal by two *V. variegata* groups in Manombo forest, SE Madagascar, by describing feeding and ranging behaviour and aspects of dispersal effectiveness using direct feeding observation, faecal analysis and germination trials. The lemurs dispersed seeds of 40 species, most of which were large (>10 mm). The two study groups dispersed an estimated average of 984 seeds/ha/yr within their home range; the Manombo population dispersed up to 55,115 seeds/km2/yr. Gut passage was rapid (4h 26 mins) and generally had beneficial effects on seeds, increasing germination success and reducing latency period, compared to controls. The vast majority of seeds were dispersed away from their parent plant (mean/max distance 180 m/506 m). Dispersal distance is relatively low compared to many anthropoid primates; lemurs are predicted to generally disperse seeds over relatively short distances. Overall, these preliminary results suggest *V. variegata* may be an effective seed disperser in both quality and quantity, and may be critical for large-seeded species. Loss of such large-bodied dispersers may have far-reaching ecological consequences including impacts on tropical forest structure, dynamics and carbon storage capacity.

RESULTS

SEED CHARACTERISTICS

Seed size

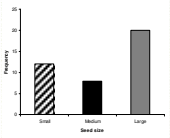


Figure 1. Proportions of average seed sizes of plant species (n=40) dispersed. 'Small' = <5 mm; 'medium' = 5—10 mm; 'large'= >10 mm.

Average individual seed length 14 ±8 mm (N=382); largest single seed 42 mm.

Seed shape

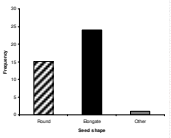


Figure 2. Proportions of seed shapes of plant species (n=40) dispersed.

DISPERSAL DISTANCE AND GUT PASSAGE

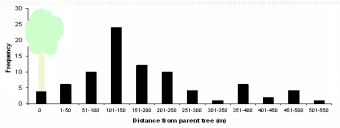


Figure 3. Seed dispersal curve for *V. variegata* (frequency distribution of straight distances seeds were dispersed from parent trees)

95.3% of seeds (N=85) deposited away (>10 m) from parent tree

Average dispersal distance 180 ±127 m; IQ range 103—217 m; max distance dispersed 506 m

Average gut passage time 4 h 26 min ±2 h 0 min (N=77); longest passage time 8 h 27 min

Figure 4. *Varecia variegata* at Manombo forest. Photo courtesy of Daniel Austin.

Figure 5. Lemur food plant (unknown species 3 (Rubicaeae))

Figure 6. Selection of seeds passed by *V. variegata*. Photo courtesy of Daniel Austin.

Figure 7. Lemur food plant *Cecropia peltata* (Cecropiaceae), an invasive species

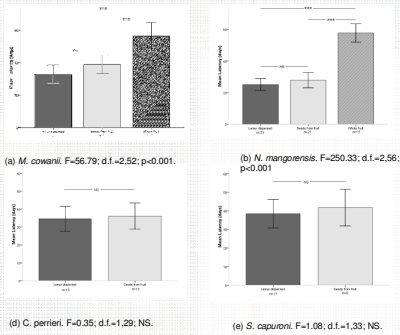
EFFECTS OF GUT PASSAGE

Germination success

Species	*n (per class)*	GERMINATION SUCCESS (%) Lemur dispersed	Seeds from fruits	Whole fruits	χ^2_2	P
Mendoncia cowanii	28	89.3	64.3	42.33	13.38	<0.01
Noronhia mangorensis	23	100.0	91.3	65.2	12.16	<0.01
Chrysophyllum perrieri	21	76.2	71.4	0	30.61	<0.001
Sideroxylon capuroni	28	92.9	32.1	0	50.78	<0.001

Table 1. Germination success (percentage of seeds from which a shoot emerged) of 4 lemur plant foods and chi-squared results for differences in germination success between treatments. 'Lemur dispersed'=defecated seeds; 'Seeds from fruits'=seeds with fruit pulp removed; 'Whole fruits'=seeds within intact, whole fruits.

Latency period



(a) *M. cowanii*. F=56.79; d.f.=2,52; p<0.001.

(b) *N. mangorensis*. F=250.33; d.f.=2,56; p<0.001

(d) C. perrieri. F=0.35; d.f.=1,29; NS.

(e) *S. capuroni*. F=1.08; d.f.=1,33; NS.

Figure 8a—d. Mean latency periods (mean number of days from planting to radicle emergence) of lemur food plants. Horizontal lines represent differences between treatments. NB: As no whole *S. capuroni* and C. perrieri fruits germinated, only comparisons between 'lemur dispersed' and 'seeds from fruit' were possible.

DEPOSITION CHARACTERISTICS

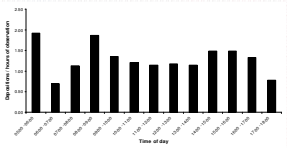


Figure 9. Temporal distribution of depositions (n=445 depositions). Frequency of depositions made was corrected for the uneven spread of observation hours across the day.

Droppings contained on average 11.6 ±26.4 seeds/dropping (range 0—201) and 1.2 ±0.9 species/dropping (range 0—6)

DIET AND FEEDING

- Consumed fruit of 34 species (total food plants 57)
- 79% eaten ripe
- Seeds of 88% of species swallowed, 22% unknown

DISPERSAL QUANTITY

- 40 species dispersed
- On average, 9 depositions/day; 11.6 seeds/deposition
- Individual lemurs: 104 seeds/day; 37,960 seeds/yr
- Lemur groups: 364 seeds/day; 132,860 seeds/yr; 4 seeds/ha/day; 1,444 seeds/ha/yr
- Manombo population: (pop density 1.45 ind/km^2) 151 seeds/day/km^2; 55,115 seeds/yr/km^2

DISCUSSION

- Evidence that the black-and-white ruffed lemur may be an important and effective disperser of seeds, in both quality and quantity and particularly for large seeds, at least at this study site and at this time of year
- Brief study period and small sample sizes present limitations but important ramifications of results nevertheless
- Seed shadows generated by *V. variegata* are characterised by low occurrence of defecations beneath parent tree crowns, and a majority transported over 100 m, with seeds deposited in low-density defecations in a scattered distribution. These characteristics may minimise inter- and intraspecies seed competition and density-dependent mortality factors[6,7,8,9]
- Lemurs habitually swallowed fruits whole, very rarely damaged seeds or dropped them beneath parent plants, and gut passage provided beneficial effects – capable of dispersing large quantities of seeds and providing a reliable dispersal service
- Unripe fruit often consumed however – could destroy/disperse immature seeds, reducing quality of dispersal service
- Most dispersed species were large (>10 mm). Biggest seeds swallowed by the next largest frugivorous lemur (*Eulemur* spp.) are 20 mm[10]. Five species dispersed by *V. variegata* were >20 mm. This suggests that the largest-seeded tree species at Manombo may depend exclusively upon ruffed lemurs for dispersal – critical ecological role
- Dispersal distance was relatively low compared to other primates. Results may underestimate year-round dispersal patterns, or may be of typical magnitude for lemurs. In the case of the latter, this 'spatially restricted dispersal' on Madagascar may be related to prevalent lemur energy conservation strategies[11] that are incompatible with long dispersal distances.
- As a potentially critical disperser of large seeds, loss of *V. variegata* may result in plant communities altered in diversity, structure and dynamics, through shifted selection for small-seeded and/or non-zoochoric dispersed species.[12,13,14,15,16]

METHODS

Study site: Manombo – highly disturbed coastal lowland forest, SE Madagascar. Study conducted Sep—Dec 2009: moist-cool, hot-dry and the hot-rainy seasons

Study species: *V. v. editorium* subspecies. Two study groups: Group one consisted of one adult male, one adult female, and one juvenile), group two had one adult male, one adult female and two juveniles.

Data collection and analysis:

Diet and feeding: continuous focal observation (total 345 h 37 min of observation, avg observation periods 9 h 36 min ±2 h 26 min); GPS points of feeding trees and deposition sites recorded; faecal samples collected (445 in total). *Faecal analysis:* seeds removed from faeces, identified, counted, measured and categorised for size and shape. *Dispersal quantity:* number of seeds dispersed estimated by extrapolation[2,3,4,5]. Depositions/observation period/individual used as an estimate of depositions/day/individual. *Germination trials:* three treatments: lemur-dispersed (from faeces) plus two controls: C1= seeds from fruits, pulp manually removed; C2= seeds within whole fruits; trials run for 10 weeks; % germination compared between treatments with 3x2 chi-squared & pair-wise comparisons; latency period between treatments compared with one-way ANOVAs and post-hoc Tukey tests.

Dispersal distance: defecated seeds from known parental trees used as markers[4]; straight dispersal distances between deposition sites and parent trees calculated using Garmin Mapsource software.

Gut passage time: average time between start of feeding bout and appearance of seeds in depositions

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