

Locomotor Ecology of *Propithecus verreauxi* in Kirindy Mitea National Park

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Key Words

Seasonality · Support use · Leaping · Intergroup differences · Lemur · Madagascar · Verreaux's sifaka

Abstract

The locomotor behaviour of 2 groups of *Propithecus verreauxi* (Verreaux's sifaka) was studied over an 8-month period in Kirindy Mitea National Park (KMNP), Madagascar. This paper assesses the major characteristics of their locomotion, focusing on the extent that seasonal variation in climate and habitat, and local variation in habitat, is reflected in changes in locomotor behaviour. *P. verreauxi* is a committed leaper with a strong preference for vertical and angled supports. We found clear between-group differences in support orientation and diameter suggesting local variation in habitat. During the dry season, *P. verreauxi* utilizes smaller-diameter supports than in the rainy season. While this difference cannot yet be ascribed to any single cause, we discuss the factors which may contribute to this result.

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Introduction

The locomotion of small-bodied, nocturnal strepsirhines [Crompton, 1983; Crompton and Andau, 1986; Demes et al., 1996; Warren and Crompton, 1997; Blanchard et al., 2015] and larger, diurnal species [Dagosto, 1995; Demes et al., 1996; Dagosto and Yamashita, 1998; Blanchard, 2007] has been studied in the wild and in captivity [Gebo, 1987; Tilden, 1990; Demes et al., 1995, 1999]. Marked contrasts in locomotion are evident between wild and captive studies, and such distinctions likely relate to the inevitable impoverishment of the captive, compared to the natural,

environment [Crompton, 1980]. Contrast between studies suggests the possibility that locomotor variation may exist between populations of the same species, and indeed between groups within the same locale, where animals encounter differently structured habitat, each with their own support availability, distribution of resources and threats. For example local differences have been reported for individual *Galago moholi* at Mosdene, South Africa [Crompton, 1980] and species are able to adapt their locomotion to different habitats, for example *Colobus badius* [Gebo and Chapman, 1995] and *Pongo pygmaeus wurmbii* [Manduell et al., 2011, 2012]. Further, as discussed most recently by Crompton et al. [2010], differences in data collection protocols mean comparability between studies cannot be assumed and consequently there is need for further locomotor studies using a standard protocol. In this paper we contribute to this goal for the specialist vertical leaper [Napier and Walker, 1967] *Propithecus verreauxi*, a mid-sized diurnal indriid, inhabiting the southern and western dry deciduous forests and spiny forests of Madagascar.

Seasonal variation in locomotion has been previously reported for *Galago* and *Otolemur* [Crompton, 1983]. Factors such as rainfall, temperature and day length vary seasonally, and in turn affect the abundance and distribution of food resources [Crompton, 1983; Nash, 1998]. Kirindy Mitea National Park (henceforth KMNP) is a deciduous forest, displaying marked seasonality, characterized by a long dry season when resources are scarce. Hence we would expect seasonality to be expressed in the locomotion of *P. verreauxi* at KMNP. In this study we report (a) seasonal changes in locomotion as well as (b) distinctions in locomotion between 2 study groups.

Methods

Data were collected between May 2010 and January 2011 in KMNP located in western Madagascar. KMNP is one of the largest continuous tracts of remaining dry deciduous forest in Madagascar that covered 101,031 ha in 2006 [Whitehurst et al., 2009]. The area is marked by seasonality, characterized by a hot rainy season from December to March and a cooler dry season between April and November [Lewis and Kappeler, 2005; Rasoazanabary, 2006].

The Ankoasifaka Research Station, established by R. Lewis, lies approximately 21 km east of Belo-sur-Mer (20°47.9177' S, 44°10.0771' E) and consists of a 1-km² grid system, with trails every 25 m running east/west and north/south. Lewis habituated 8 groups of *P. verreauxi* in 2005; individuals are captured and measured on a yearly basis, ensuring all individuals are tagged with identification collars and at least one member of each group is radio-collared [Lewis, 2009; Lewis and Rakotondranaivo, 2011; Rasambainarivo et al., 2014]. The sifakas are followed throughout the year by Lewis and coworkers.

Two groups (groups 3 and 4 in Lewis [2009], although group composition has changed), whose ranges fell entirely within the grid, were chosen for study. As of June 2010, group 3 contained 7 individuals (3 females, 4 males), and group 4 contained 5 individuals (3 females, 2 males). Data were collected from all adult and subadult individuals within the group regardless of sex or whether any adult female was carrying an infant. Dominant females, the least likely to emigrate [Lewis, pers. commun.], were darted and fitted with brass radio collars (model No. TW3SM, Biotrack, Dorset, UK). SIKA radio-tracking receivers (150–153.99 MHz) combined with Yagi flexible element antennae (Biotrack) were used to locate groups. Darting formed part of Lewis' regular darting process and followed her methodology and protocols [Lewis, 2009; Lewis and Rakotondranaivo, 2011]. Animals were captured by an experienced Malagasy darter using a blow gun that delivers disposable non-barbed darts with a 3/8-inch needle. Darts were loaded with Telazol™ at a dosage of 25 mg/kg, and no top-up doses were administered. Darted individuals were caught in a large cotton cloth. Animals were monitored during processing for

temperature, had eye drops added for lubrication and the wound site cleaned. Individuals were returned to their social group within 2–4 h after capture when they had recovered from the anaesthesia, and during the recovery period they were kept in a cloth bag in a shaded area close by. Each of the target females was successfully darted, and no animal was otherwise injured during the procedure.

Groups were followed on 2 consecutive days, from initial contact in the morning until locomotion ceased and all individuals had begun to rest; on the third day, data were collated and transcribed. A total of 41 days were sampled and 9,192 locomotor bouts recorded: 6,941 in the rainy season (November 16, 2010, to January 27, 2011) and 2,251 in the dry season (May 24 to October 18, 2010); 4,795 bouts were recorded for group 3 over 21 days and 4,397 bouts for group 4 over 20 days.

Data collection followed Blanchard and Crompton [2011], itself based on earlier work [Crompton, 1983; Warren and Crompton, 1997] whereby ad libitum, continuous scan sampling is used to record data from any observed locomotor bout from any individual. A bout is defined as any occurrence of locomotion in a given mode that has an obvious beginning and end. For each bout the following was recorded: date, time, locomotor mode, initial and terminal support diameter (i.e. the supports on which a bout begins and ends), initial and terminal support orientation, initial and terminal height, distance travelled and activity. Distance travelled, heights, diameters and orientation were estimated by eye, and to aid accuracy practice sessions were carried out in which estimations were made and actual measurements taken and compared.

Locomotor mode was broken down into 10 categories modified from Hunt et al. [1996]:

- Leaping: a hindlimb-propelled leap beginning with a torso-orthograde clinging posture on a relatively vertical support (L12c)
- Vertical climb: a torso-orthograde locomotion up or down a vertical or strongly inclined support, utilizing fore- and hindlimbs (L8)
- Quadrupedal walk: locomotion above a horizontal or oblique support, including the ground, using all 4 limbs in a diagonal sequence gait (L1a)
- Quadrupedal run: a fast locomotion, similar to quadrupedal walking, but involving a period of free flight (L5)
- Bipedal walk: locomotion utilizing only the hindlimbs to bear body weight along a horizontal or oblique support (L3)
- Terrestrial bipedal hopping: torso-orthograde bipedal movement, where hindlimbs push off and land roughly together, involving an aerial phase (L4), described as a 'bipedal gallop' by Wunderlich and Schaum [2007]
- Arboreal hopping: both bipedal hopping along a horizontal or oblique support where only the hindlimbs are involved in take-off and landing, and hopping where the hindlimbs are involved in the take-off phase but all 4 limbs contribute to the landing phase, normally observed on vertical or angled terminal support (L8e)
- Two-limb suspension: orthograde movement beneath a horizontal or oblique support using only the forelimbs (L9)
- Four-limb suspension: pronograde movement beneath a horizontal or oblique support using all 4 limbs (L10a)
- Foliage crossing: a torso-pronograde movement where a pair of limbs are used to grasp an initial support, whilst the other limbs reach across a gap to grasp the terminal support (L11a); also includes other, less stereotyped, 'aerial-phase'-lacking methods of crossing discontinuities in the substrate

Support diameters were categorized as less than 0.5, 0.6–5, 5.1–10, 10.1–15 and greater than 15.1 cm and orientations as horizontal (0–10°), oblique (11–45°), angled (46–80°) and vertical (81–90°). The behavioural context of locomotor activity was broken down into rest, feed, travel and other. No attempt was made to distinguish non-food-directed travel from travel in search of food (foraging) and none to use this variable to generate activity budgets.

All research was approved by the Malagasy authorities: Madagascar National Parks and CAFF/CORE committee (i.e. Commission Tripartite). Darting and radio tracking were deemed necessary in order to facilitate observations, and the welfare of the individual was paramount.

Table 1. Frequency of locomotor modes combined, and in both groups, of *P. verreauxi* (sifaka) at KMNP

Locomotor mode	Both groups		Group 3		Group 4	
	freq.	%	freq.	%	freq.	%
Leap	6,974	75.9	3,573	74.5	3,401	77.3
Vertical climb	988	10.7	534	11.1	454	10.3
Arboreal hop	423	4.6	229	4.8	194	4.4
Foliage cross	419	4.6	226	4.7	193	4.4
Quadrupedal walk	167	1.8	92	1.9	75	1.7
Four-limbed suspension	98	1.1	56	1.1	42	1.0
Terrestrial bipedal hop	78	0.8	52	1.1	26	0.6
Two-limbed suspension	24	0.3	19	0.4	5	0.1
Bipedal walk	20	0.2	13	0.3	7	0.2
Quadrupedal run	1	0	1	0	0	0

All statistical analysis was performed in SPSS version 17. Associations between non-parametric, categorical data were tested using Pearson's χ^2 test, and where significant associations were found, standardized residuals (SR) were examined; only SR greater than 2 (or less than -2) are considered significant. Significant SR can be viewed as more, or less, than expected compared to the finding if the distribution was random [Tabachnick and Fidell, 1989]. The non-parametric Mann-Whitney test (U) was used to examine differences in median heights between variables. Significance values reported here are all 2-tailed.

Results

Leaping was the most utilized mode of locomotion (table 1) accounting for 75.9% (6,974 from a total of 9,192) of all bouts, whilst the bottom 7 locomotor categories accounted for only 4.2% of bouts. A significant intergroup difference was found in locomotor mode choice ($\chi^2 = 23.388$, d.f. = 9, n = 9,192; $p < 0.05$); however, no SR were significant. There was a significant seasonal difference in locomotor mode ($\chi^2 = 149.795$, d.f. = 9, n = 9,192; $p < 0.001$): in the dry season (n = 2,251) quadrupedal walking (SR = -2.1) and arboreal hopping (SR = -4.9) were observed less frequently than expected, but in the rainy season (n = 6,941) leaping (SR = -2.5) occurred less than expected. It must be remembered that 'more or less than' refers to the SR values and not percentages and therefore can be read as more/less than expected if the distribution was random'.

Locomotor bouts were most often used for travel (43.4%), while 26.1% resulted in resting and 27.6% in feeding. There was a significant intergroup difference in activity ($\chi^2 = 8.738$, d.f. = 3, n = 9,192; $p < 0.05$), although no SR were significant. A significant seasonal difference was found in activity ($\chi^2 = 356.634$, d.f. = 3, n = 9,192; $p < 0.001$): in the dry season the sifaka rested more often than expected (29.8%, SR = 6) but travelled less often than expected (39.1%, SR = -5.5), while in the rainy season rest was observed less often than expected (14.7%, SR = -10.6) and travel more often than expected (56.8%, SR = 9.6).

Table 2. Seasonal differences in initial support diameter (ISD) in 2 groups of *P. verreauxi* (sifaka) at KMNP

ISD	Dry		Rainy	
	freq.	%	freq.	%
<0.5 cm	83	1.2	4	0.2
0.6–5 cm	2,695	38.8	418	18.6
5.1–10 cm	2,075	29.9	686	30.5
10.1–15 cm	1,558	22.4	952	42.3
>15 cm	530	7.6	191	8.5

There were significant intergroup differences in usage of both initial ($\chi^2 = 16.918$, d.f. = 4, $n = 9,192$; $p = 0.002$) and terminal ($\chi^2 = 27.322$, d.f. = 4, $n = 9,192$; $p < 0.001$) support diameters. Group 3 ($n = 4,795$) used 0.6 to 5 cm diameter initial and terminal supports less often than expected (initial SR = -2.2; terminal SR = -2.3) and group 4 ($n = 4,397$) more often than expected (initial SR = 2.3; terminal SR = 2.4). Further, group 3 used terminal supports >15.1 cm more often than expected (SR = 2.7) and group 4 less often than expected (SR = -2.8).

P. verreauxi used vertical supports for half of all recorded bouts and angled supports for 35%. Significant between-group differences were found for initial ($\chi^2 = 21.185$, d.f. = 3, $n = 9,192$; $p < 0.001$) and terminal ($\chi^2 = 28.190$, d.f. = 3, $n = 9,192$; $p < 0.001$) support orientation: group 3 utilized horizontals more often than expected (initial SR = 2.2; terminal SR = 2.7) and group 4 less often than expected (initial SR = -2.3; terminal SR = -2.8). Significant seasonal differences in orientation were found for initial ($\chi^2 = 24.472$, d.f. = 3, $n = 9,192$; $p < 0.001$) and terminal supports ($\chi^2 = 20.955$, d.f. = 3, $n = 9,192$; $p < 0.001$). In the rainy season oblique (initial SR = 2.9; terminal SR = 2.1) and horizontal (initial SR = 2.7; terminal SR = 2.9) initial and terminal supports were used more often than expected.

The mean initial and terminal heights were 4 m, ranging from the ground up to a maximum of 14 m. There were no significant between-group differences with regard to initial ($U = 10,474,893.5$, $n = 9,192$; $p = 0.595$) or terminal height ($U = 10,523,653$, $n = 9,192$; $p = 0.885$). A significant difference was found in the initial ($U = 6,485,215.5$, $n = 9,192$; $p < 0.001$) and terminal ($U = 6,481,449.5$, $n = 9,192$; $p = 0.000$) heights of *P. verreauxi* between the rainy and dry seasons. The median height in the dry season was 4 m (mean 4 m), while in the rainy season the median height was 3 m (mean 4 m).

Discussion

In dry seasonal tropical forest such as that of the KNMP, mammals are predicted to require activity adjustments to cope with seasonal scarcity [Stoner and Timm, 2011] and seasonal changes are clearly evident in *P. verreauxi* activity: rest decreasing by 15%, but travel increasing by 18% during the rainy season. Vasey [2005] found a similar pattern in *Varecia rubra*, where the lemurs moved less during times of food scarcity, but did not spend significantly more time feeding. In

P. edwardsi, travel increases in the rainy season [Hemingway, 1998], and in the dry season the frequency of rest is increased. Hemingway [1998] attributed this to the availability of primarily mature, less energy-rich leaves. While there is not a single identical response by primates to the challenge of seasonality, reduction in energy expenditure during times of shortage may be a common response.

In this study we demonstrated clear between-group differences in support use (table 2). Group 3 used 0.6 to 5 cm diameter initial and terminal supports less than group 4, but terminal supports >15.1 cm more often, and group 3 used horizontal supports more, and vertical supports less than group 4. Crompton [1980] found parallel differences in orientation in 2 sites at the same location for *G. moholi*. While differences in body size have previously been linked to support diameter usage, with larger species using larger supports [Fleagle et al., 1981; Cunha et al., 2006], no difference in body weights occurred between group 3 and group 4; individuals from both groups weigh on average 2.8 kg. While further discussion would be premature, this suggests that fine distinctions in habitat structure may be reflected in variation in locomotor behaviour, and that future studies should examine this further.

One of the most striking findings is the clear evidence for less frequent use of larger support categories in the rainy season than the dry: specifically that in the rainy season supports >5 cm diameter were used less often and supports 10.1–15 cm in diameter more often. There are a number of possible explanations. In a highly seasonal dry tropical forest such as in the KMNP, the moisture content in wood might be expected to be low in the dry season. Low moisture content reduces the elasticity and compliance of wood [Cannell and Morgan, 1987]. Conversely, in the rainy season an increase in humidity and moisture content might be expected to increase the compliance of supports. *P. verreauxi* might therefore be expected to use larger supports in the rainy season, since the greater effective compliance of moist wood implies a greater disadvantage of smaller supports because of excessive bending, both increasing the cost of locomotion, because of greater loss of energy to the take-off support, and by increasing instability. This interpretation is consistent with the significant reduction in leaping in the rainy season, which suggests a concern with support stability. In addition, wet supports may result in a higher likelihood of the sifaka slipping, and hence it may choose smaller supports it can grasp more effectively.

An alternative (but not mutually exclusive) suggestion is that greater leaf cover might obscure landing sites and hence make it necessary to utilize a lower part of the tree. This might explain our finding of a decreased height of observation in the rainy season. In addition, *P. verreauxi* are folivore-frugivores with a strong dietary preference for young leaves [Irwin, 2008], and much of the new growth which characterizes the early part of the rainy season at KMNP occurs at lower heights [pers. observation]. Indeed, Chouteau [2006] found a decrease in visibility at a height of 1.5 m during the rainy season in nearby Kirindy Centre de formation professionnelle forestière, primarily due to new leaves. This new growth might encourage *P. verreauxi* to lower its feeding height and thus to encounter larger supports during the rainy season. The possible interactions are complex, and this issue demands a more detailed multivariate analysis of leap characteristics season by season with reference to leap length, substrate availability and leaf phenology.

Conclusions

The term vertical climber and leaper [Napier and Walker, 1967] is certainly an apt description of the locomotor behaviour of *P. verreauxi*. Typical for the indriids, leaping frequencies are high and *P. verreauxi* uses high-angled supports most often. While we do not have time budgets, it does appear that periods of food scarcity elicit a change in the context of locomotor activity. Higher frequencies of resting are typical, suggesting that *P. verreauxi* attempts to conserve energy during times of food scarcity, rather than ranging further in search of nutrition. Between group differences in support usage appear to reflect local variation in support availability. Height within the canopy, and tree moisture content, are probable causes of the strong seasonal variation in support diameter.

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