Locomotor Flexibility in *Lepilemur* Explained by Habitat and Biomechanics

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ABSTRACT   There are at present few comparable studies of lemur locomotion in the wild. This has unfortunately meant we have little knowledge about locomotor variation, and hence flexibility, with regard to differences in support availability and habitat structure. Here we compare the locomotion of *Lepilemur edwardsi* at Ankarafantsika with that of *Lepilemur ruficaudatus* at Kirindy-Mitea National Park. While data were collected by two individuals, at different times, both studies used the same data collection protocol and are hence highly comparable. Locomotor mode, support diameter and ori-entation, heights, and distances traveled were all collected. We find that locomotor specialization, in this case for vertical leaping, has ensured that some support requirements are independent of habitat. For example, both species used vertical supports most often. However, overall support diameter does indicate a certain degree of flexibility, whereby *L. ruficaudatus* most often used supports ≤5 cm in diameter and *L. edwardsi* >5 cm in diameter. Am J Phys Anthropol 156:58–66, 2015.   © 2014 Wiley Periodicals, Inc.

Locomotion interacts with many ecological and life variables: it enables animals to access food, to avoid becoming prey, and to find a mate (Cant, 1992). Hence understanding an animal's locomotion is vital to knowledge on its ability to survive and reproduce. Primate locomotion is especially interesting, partly as a consequence of being from one of the most ancient mammalian Orders and as one of the least specialized in postcranial morphology, and living primates use an unusually great range of locomotor modes, from terrestrial quadrupedalism through arboreal brachiation, (see e.g., Fleagle, 1977; Fleagle and Mittermeier, 1980). Thus, primate locomotion can tell us much about evolution and niche separation.

Most research on primate locomotion comes out of the captive environment and this is especially good for obtaining well-controlled data. If we examine captive studies on lemurs, we find studies on *Eulemur rubriventer* (Tilden, 1990), *Propithecus verreauxi* (Wunderlich and Schaum, 2007), *Lemur catta* (Demes et al., 2006), and others on multiple species (Terranova, 1996; Demes et al., 1999, 2005). These studies are valuable for obtaining actual pressure and force readings difficult to obtain in the wild, but none of these studies take into account habitat and ecology. An animal's maximum locomotor performance capability is rarely expressed in its daily locomotion, and hence mean recorded displacement tends to fall far short of these maxima. For example, wild *Propithecus diadema* can leap 7 m, but their mean leap length on vertical supports is only 2.3 m (Blanchard, 2007). Thus, a study carried out in captive conditions might well find that *P. diadema* can leap 7 m, but this does not inform us about the leap lengths typically used in the wild during travel or foraging. Thankfully there is a growing body of work on the locomotion of wild lemur species (Dagosto, 1989; Dagosto, 1995; Demes et al., 1996; Warren, 1997; Dagosto and Yamashita, 1998; Razafimanantsoa, 1999; Blanchard, 2007).

The locomotion of *Lepilemur* has long been compared to that of the indriids (Rand, 1935; Petter, 1962) and it was classified by Napier and Walker (1967) as a vertical clinger and leaper alongside the indriids, *Hapalemur, Tarsius, Galago*, and *Euoticus*. While there are observable morphological differences among these genera, they all share elongated hindlimbs, relative to forelimbs, and it is these hindlimbs that power leaping (Napier and Walker, 1967). As one would expect from their locomotor classification, these species are usually observed with a vertical, orthograde, body posture. The most common mode of travel is vertical leaping, and comparing studies that utilize comparable methodology, we see leaping accounts for 66% of all bouts in *Avahi* (Warren and Crompton, 1997) and up to 81% in *Indri* (Blanchard, 2007). Dagosto and Yamashita (1998), using slightly different methods, found even higher rates of leaping for *P. diadema* of 85%. Further, vertical supports are preferred, for example used in 42% of bouts in *Avahi* (Warren and Crompton, 1997) and 55% in *P. diadema* (Blanchard, 2007).

Such primate studies are increasing our understanding of the importance of influences outside of skeletal and muscular adaptations, such as habitat, which affect locomotor behavior. For example, Manduell et al. (2012) found forest structure and support availability strongly

influenced orangutan locomotion. However such studies, examining locomotion in terms of habitat factors such as support availability (see e.g., McGraw, 1996; Youlatos, 2004) are still rare. Even where multiple studies exist on the same genus (e.g., in *Propithecus*: Dagosto and Yamashita, 1998; Razafimanantsoa, 1999; Blanchard, 2007), different methodologies can affect comparability. To this end we compare behavioral locomotor data collected by Warren on *Lepilemur edwardsi* at Ankarafantsika reserve with a study using the same methods on *Lepilemur ruficaudatus* at Kirindy-Mitea National Park (henceforth "KMNP") by Blanchard.

While this is an across-species comparison, before genetic studies which split the *Lepilemur* genus (Rumpler and Albignac, 1978; Rumpler et al., 2001; Ravaoarimanana et al., 2004; Andriaholinirina et al., 2005, 2006; Louis et al., 2006; Craul et al., 2007) into at present 27 species (Tattersall, 2013), researchers recognized only a few species based on small variations in cranial morphology and pelage distribution (see e.g., Petit, 1933; Hill, 1953; Petter, 1962). Indeed in the work by Hill (1953) only two species are listed, one of which, *L. ruficaudatus*, includes both species studied in this paper. Louis et al. (2006) molecular study found three genetic subgroups of *Lepilemur*, with *L. ruficaudatus* and *L. edwardsi* both belonging to the western and southern group. Andriaholinirina et al. (2006) used mitochondrial DNA to reconstruct phylogenetic trees and suggest that after *L. mustelinus* split off the remaining species diverged into two subgroups, one containing *L. ruficaudatus*, the other containing *L. edwardsi. Prima facie*, it is reasonable to assume that measurable morphological differences between taxa are more likely to be reflected in locomotor distinctions than are chromosomal or other genetic distinctions.

Both Ankarafantsika and KMNP are dry deciduous tropical forests in western Madagascar. Although a protected forest, KMNP is continuing to undergo deforestation (Whitehurst et al., 2009). At Ankarafantsika, in addition to *Lepilemur* the other nocturnal lemur species are *Microcebus murinus, Microcebus ravelobensis, Cheirogaleus medius* and *Avahi occidentalis*, while the diurnal species are *Eulemur mongoz, Eulemur fulvus*, and *Propithecus coquereli* (Ito et al., 2013). Diurnal lemur species at KMNP are *Propithecus verreauxi* and *Eulemur rufus* and other nocturnal species are *Phaner pallescens, Cheirogaleus medius, Microcebus murinus, M.* cf. *berthae*, and *Mirza coquereli*, but the most ecologically similar genus, *Avahi* (see e.g., Warren and Crompton 1997), is absent.

Lepilemur are broadly classed as vertical clingers and leapers (Napier, 1967). Thus, as congeneric, similarly sized species, *L. edwardsi* and *L. ruficaudatus* locomotor mode choice, support usage (diameter and orientation), distances covered, and height changes should:

Prediction 1a: show no species (habitat) significant differences if locomotion is controlled by physiological adaptations and biomechanics alone,

OR

Prediction 1b: show significant differences if locomotion is affected by habitat, since in this study species can be considered a proxy for location (Ankarafantsika versus KMNP).

METHODS

Field data collection for *L. edwardsi* took place between May 1992 and October 1993 in Jardin Botanique A of Ampijoroa Strict Forest Reserve, now known as Ankarafantsika National Park, Madagascar. Methods for this study can be found in the work by Warren and Crompton (1997). Data collection for *L. ruficaudatus* occurred from June to December 2010 at KMNP National Park, Madagascar, conducted by Blanchard, and methods, following those of the Warren study, can be found below (see also Blanchard and Crompton, 2011 for an overview of methodology).

Study site

KMNP is a dry deciduous forest in western Madagascar that covers approximately 140,000 ha. Data were collected at the Ankoasifaka Research Station in a 1 km^2 trail system at 20°47′17.4″S, 44°10′08.4″E, approximately 21 km east of Belo-sur-Mer, 60 Km south of Morondava (Lewis and Bannar-Martin, 2012). Trails have been cut every 25 m forming quadrats, and within the grid system altitude is 50–100 m. The mean maximum temperature during the study period was 34°C (range 25–41°C), while the mean minimum temperature was 18°C (range 9–25°C) and rainfall totaled 133 mm, falling mostly in December. The study of *L. edwardsi* was carried out at 16°15′S, 46°48′E in Ankarafantsika, 120 km south of Mahajanga (Warren, 1994). The forest is 250 m above sea level. A 300 by 350 m grid of quadrats was set up using forestry flagging tape placed at 10 m intervals, as no paths needed to be cut to allow close following. Total rainfall is between 1,000 and 1,500 mm a year, 95% of this falling between November and April. The mean annual temperature is 26°C, with a maximum of 39.3°C in October and a minimum of 11.4°C in June (Warren, 1994).

Capture

At KMNP two *L. ruficaudatus* were captured during daylight hours from their tree holes using the "ManjaraHazo" method. In this approach the end of a long, straight stick is stripped back, wetted and placed into a tree hole; the stick is twisted to catch the hair, and the stick it is pulled out when the animal grabs the stick. As harsh as this may sound, it was deemed less stressful to the lemur than darting and was overseen by a veterinarian (Fidisoa T. Rasambainarivo, DVM). Once captured, 0.1 ml tiletamine/zolazepam (Telazol, Fort Dodge) was injected intramuscularly and the individual assessed by the veterinarian, before they were weighed and measured. Hand length was taken as the palmar surface from the approximate (palpated) position of the radiocarpal joint to the distal end of the distal phalanx of the third digit. The lemurs were fitted with brass TW-3 radio-tracking transmitter collars (Biotrack, Wareham, UK) weighing a maximum of 18 g, equating to approximately 3% of body weight. There is general agreement that the weight of collars should be kept as possible and Gursky (1998) found that for tarsiers there was no difference in body weight or activity between un-collared animals, and after ~6 months wearing collars weighing between 5 and 7% of their body weight. Our study individuals were captured in late afternoon, held overnight to ensure full recovery, and released early the following day. They were monitored for temperature and given intravenous isotonic water where necessary. The collar of one individual fell off after only two nights of observation, and due to local regulatory problems with capture it was impossible to re-collar a further individual. Technologies available at the time of the previous study

TABLE 1. *Variables recorded with each locomotor bout*

1.	Date
2.	Species and identification
3.	Time
4.	Locomotor mode categories: leaping, vertical climb etc.
5.	Initial support diameter: ≤0.5cm, >0.5 cm to ≤5 cm, >5 cm and ≤10 cm, >10 cm and ≤15 cm, >15 cm
6.	Initial support orientation: vertical (81°–90°), angle (46°–80°), oblique (11°–45°), horizontal (0°–10°)
7.	Terminal support diameter (see 5)
8.	Terminal support orientation (see 6)
9.	Initial height (m)
10.	Terminal height (m)
11.	Horizontal distance travelled (m)
12.	Activity: rest, travel, feed, other

(Warren and Crompton, 1997) did not include such light, strong collars as were available for the present study, and transmitter units had to be hand-assembled from components and embedded in dental acrylic, leading to higher collar weight. While within reasonable limits, weight change *per se* can be assumed to be tolerable as it occurs during pregnancy, since we are dealing with leaping species, stability and position of the center of mass were judged more immediate concerns. Thus, in Warren and Crompton's (1997) study, individuals were fitted with parachute-type backpacks to minimize any effect on collar motion on the position of the subject's center of gravity. However simple neck collars were deemed suitable in the later study as modern purpose built collars are much smaller and lighter and would hence have little effect on altering the center of gravity.

Locomotor data collection

At KMNP, subjects were located before midnight using a Biotrack Sika radio-tracking receiver and flexible yagi antenna, and followed from midnight until dawn and cessation of activity, then the same night they were located at their sleeping trees and followed from the onset of activity until midnight. A red-filtered halogen Petzl head-torch was used during observations. Many researchers chose to use white light with little adverse effect, however while the red-filter does inhibit light in the upper canopy, and can make observing the animal difficult, we follow Nekaris (2003) believing red light minimizes any disruption to the animal. Further, for most of the study, conducted in the dry season, there were few leaves on the trees and the *L. ruficaudatus* was easy to observe. By the time the rains and leaves came, the battery in the radio-collar died ceasing the study. *L. ruficaudatus* exhibited fleeing behavior on the first night of follows, but thereafter could be approached within 5 m without disruption. Un-collared individuals that were observed with the study animal equally showed no adverse behavior and could be easily observed. Data were recorded into a digital voice recorder (Olympus DM-10) and downloaded onto a laptop (HP pavilion dv3) before being transcribed the following day. At Ankarafantsika, individuals were followed all night from dusk to dawn, notes dictated into a tape recorder and transcribed/coded the next day.

Data were collected using *ad libitum* sampling recording each time there is a "bout" of locomotion (following e.g., Blanchard and Crompton, 2011) (Table 1). In this method each leap is considered as a separate bout, but a bout of walking is taken to last from start to end of

walking on each support. Blanchard recorded a total of 200 h of observations at KMNP, 3,124 locomotor bouts, over 29 nights during the six month period. While focusing on a primary individual, locomotion of other individuals were recorded when possible: all data were analyzed together. At KMNP, 2,555 (82%) of bouts originated from the primary individual, 517 (17%) from other adults, and 59 (1.9%) from the collared sub-adult female. At Ankarafantsika, seven *L. edwardsi* were followed for 28 nights, recording 885 bouts of locomotion over the 18 month period.

Although many locomotor modes were recorded in both studies, only three easily comparable modes, each with sufficient bouts (by "sufficient bouts" we mean bouts with enough counts to carry out statistics and avoid having a zero cell count as described below), were used for the statistical analysis in this paper. The definitions below include relevant category codes from Hunt et al. (1996) in parentheses. The categories "fork" and "foliage" in Warren's support orientation data were discarded as not closely comparable to the data collected at KMNP.

- Leaping: hind-limb propelled leaps beginning with a torso-orthograde i.e. upright, clinging posture on a relatively vertical support (L12c in Hunt et al. (1996)).
- Vertical climb: torso-orthograde locomotion up or down a vertical or strongly inclined support, utilizing both fore and hindlimbs, always with the head uppermost. (L8).
- Quadrupedal walk: locomotion above a horizontal or oblique support, including the ground, using all four limbs in a diagonal sequence gait (L1a).

Statistical analysis

Statistical testing was carried out using SPSS version 21. The original raw data from Warren's work has been used in all analysis. Following Thorpe and Crompton (2005) and Crompton et al. (2010), we used hierarchical loglinear analyses to explore the relationships between multiple categorical variables (locomotor mode, diameter, orientation; grouped distances and heights are ordered, categorical variables) in the dataset. The loglinear method is in essence an implementation of ANOVA for categorical variables. It is reviewed in the work by Thorpe and Crompton (2005) and our methodology follows that of Crompton et al. (2010). This approach allows us explore the relationship between locomotion and habitat. To find the interactions among variables that best explained the data, loglinear tests were run multiple times with variables (diameter, angles, and distances) separated into different groupings (i.e., ≤1.2/>1.2; ≤1.3/>1.3 etc; see Table 2 for new variable definitions). This ensures we find which combinations of interacting variables exert a statistically significant influence on the data-space; the aim is for the highest "goodness of fit" possible, where a fit of 1 would imply that all the data are fully "explained." This approach is necessary as it is not always apparent which groupings are statistically distinct when comparing multiple variables, and separating variables, for example separating height within the canopy (i.e.. with 10, 15, or 20 m intervals) is by its nature arbitrary (Thorpe and Crompton 2005). Within each significant model, model expressions reaching significance are themselves ranked by the value of the standardized chi-square. While loglinear modeling tells us which variable combinations best

TABLE 2. Substitute variables that gave statistically valid loglinear models

Sp	Species	*L. ruficaudatus/L. edwardsi*
LM	Locomotor mode	Leap/ vertical climb/ walk
ISD2	Initial support diameter 2	≤5 cm/>5 cm
ISO3	Initial support orientation 3	Horizontal & oblique/ angled & vertical
ISO4	Initial support orientation 4	Horizontal, oblique & angle/vertical
HDT9	Horizontal distance travelled 9	≤0.9 m/>0.9 m
HDT12	Horizontal distance travelled 12	≤1.2 m/>1.2 m
HDT20	Horizontal distance travelled 20	≤2.0 m/>2.0 m
EDT16	Effective distance travelled 16	≤1.6 m/>1.6 m
HC	Height change	Down/ no change (horizontal)/up

TABLE 3. Morphometric information for all captured individuals

Species	Individual	Sex	Body weight (g)	Nose to base of tail (mm)	Hand length (mm)
L. ruficaudatus	1	Female	750	340	55
	2	Female	550	260	50
L. edwardsi	1	Female	1156	230	49
	2	Female	838	315	29
	3	Male	728	310	22
	4	Female	837	290	60
	5	male	908	275	50
	6	Female	1108	312	37
	7	Male	552	255	16

explain the dataset, the effects of one variable on another was further explored using a comparison between observed and expected values in two way contingency tables using the nonparametric χ^2, with standardized residuals (SR) indicating the direction and strength of individual associations. Both loglinear and χ^2 require there to be no sampling zeros or low expected cell counts; no more than 20% of expected cells should be under 5, with no cells under one (Tabachnick and Fidell, 1989). Therefore, although non-independence of sequential bout observations is a problem (Dagosto, 1994), we follow Crompton et al. (2010) in using the entire dataset for loglinear exploration and random 25% sampling alongside the full dataset for χ^2 to check for bias from interdependence of observations. Although we include SR values for 100% tests, we only do so for tests with significance in the 25% sample. All reported significances are two-sided and exact. Following a chi-square test of association, the largest standardized residuals were examined, as these indicate which associations contribute substantially to the chi-square value. It is only when the standardized residual is above two, or below minus two, that the relationship is significant as this corresponds to a significance at the 0.05 level. In the results where only one SR is given this is from the 100% of data test, where two are given the first is at the 100% level, the second at the 25% level, although only the 25% χ^2 is given. Heights within the canopy were investigated using the Mann–Whitney *U* statistic on a random 25% sample. The mechanically effective

distance traveled (EDT), taking into account both the horizontal distance and the height change were calculated using Pythagoras theorem.

Take-off angles

We calculated biomechanically optimum take off angles of leaps (assessed in terms of ballistic energetic efficiency) using height change and the horizontal distance traveled, following our previously described methodology (Crompton and Sellers, 2007). In brief, we used the equations of motion of a projectile (Norton, 1982) to calculate the kinetic energy required to leap a specified distance for a specified height change at a specified take-off angle. This allows us to calculate the takeoff angle that requires the minimum kinetic energy and this angle is then taken as the optimal takeoff angle for minimizing the cost of locomotion. This angle can be calculated using the following equation:

$$\text{Optimal takeoff angle in degrees} = (90 + \alpha)/2 \quad (1)$$

α is the angle from the horizontal of a straight line drawn from the takeoff position to the landing position. α is calculated as the *arctan*(height change / horizontal distance). Thus, if both the takeoff and landing are at the same height, α is zero and the optimal takeoff angle is 45°. If the leap causes a height gain of 2 m for a 1 m horizontal distance, α is 63.4° and the optimal takeoff angle is 76.7°. For a 1 m height loss and 1 m horizontal distance, α is −45° and the optimal takeoff angle is 22.5°.

Habitat analysis

At Ankarafantsika, diameter at breast height (DBH, taken to be 1.3 m) and maximum crown width of all potential supports (i.e., trees, vine, shrubs etc.) directly on the line were obtained by Warren (1994) along a 1 km long transect. At KMNP, DBH and crown width was measured for all potential supports along six 100 m long transects.

RESULTS

Body size

Two female *L. ruficaudatus* were captured in KMNP. The former was an older adult female (KMNP Individual 1 in Table 3): her right ear was torn, the fifth digit on the right foot amputated at the p2/p3 junction, and her canines highly worn. The latter, smaller, individual (KMNP Individual 2 in Table 3) was a younger female, with teeth in good condition and it is this individual that lost her collar. Both of these body masses are relatively low and given that Ganzhorn (2002) suggested 600 g as an indication of reaching sexual maturity, the latter individual may have been sub-adult. Warren (1994) captured seven *L. edwardsi* in Ankarafantsika (Table 3), only Individual 7 was considered a possible juvenile.

Loglinear locomotor analysis

Model 1. In Model 1 (Table 4; *N* = 2,185), we examined the interactions in the variables of species, ISD2, height change, and HDT20 during leaping (variable definitions can be found in Table 2). The most significant expression from this model was between species, height change, and HDT20 (Sp*HC*HDT20) and an examination of all two-way interactions using cross-tabulation found that species and height change was the most significant interaction even at the 25% level (χ^2 [df = 2, *N* = 556] = 31.664, *P* = 0.000). When

TABLE 4. Models of best fit ($P > 0.05$), their contained expressions and associated standardized χ^2 values

Model	Goodness of fit	Expression	Partial χ^2	DoF	Standardized χ^2
1) Sp/ISD2/HC/HDT20	0.918	Sp*HC*HDT20	16.335	2	8.168
		Sp*ISD2*HDT20	7.495	1	7.495
		Sp*ISD2*HC	7.404	2	3.702
2) Sp/LM/ISD2/EDT16	0.890	Sp*LM*EDT16	140.777	2	70.3885
		Sp*ISD2*EDT16	5.512	1	5.512
		Sp*LM*ISD2	7.567	2	3.7835
3) Sp/ISO3/HC/HDT12	0.860	ISO3*HDT12	9.272	1	9.272
		Sp*HC*HTD12	9.359	2	4.6795
		Sp*ISO3	3.956	1	3.956
4) Sp/ISD2/ISO4/HDT9	0.836	ISD2*HDT9	19.52	1	19.52
		ISO4*HDT9	10.237	1	10.237
		Sp*HDT9	4.697	1	4.697
		Sp*ISD2*ISO4	4.307	1	4.307

L. edwardsi leapt it was horizontal less than expected (SR $-6.1/-2.9$) and down (SR 7.1/4.0) and up (SR 3.4) more than expected; *L. ruficaudatus* leapt horizontally more than expected (SR 3.1) and up less than expected (SR $-3.6/-2.1$). Further, there was significant association between height change and HDT20 at the 25% level (χ^2 [df = 2, $N = 556$] = 9.034, $P = 0.007$): leaps up were more likely than expected to be >2 m long (SR $-3.4/-2.2$). While the association between species and HDT20 was significant at the 25% level (χ^2 [df = 1, $N = 561$] = 7.971, $P = 0.005$) only at the 100% level was there significant SR; *L. edwardsi* leapt >2 m long less than expected (SR -2.2) and *L. ruficaudatus* did not. Within the second most significant expression (Sp*ISD2*HDT20), there was a significant relationship between species and ISD2 observed at the 25% level (χ^2 [df = 1, $N = 561$] = 30.156 p = 0.002). *L. edwardsi* used supports >5 cm in diameter more than expected (SR 9.0/4.0) and those of ≤ 5 cm less than expected (SR $-6.5/-2.9$). Conversely *L. ruficaudatus* leapt from supports >5 cm in diameter less than expected (SR $-4.6/-2.0$) and those over more than expected (SR 3.3). There was no significant relationship between species and HDT20, or ISD2 and HDT20 at the 25% level. From the third most significant expression (Sp*ISD2*HC), the relationship between species and ISD2, and species and height change has previously been described. The relationship between height change and ISD2 was significant at the 25% level (χ^2 [df = 2, $N = 561$] = 7.443, $P = 0.024$) although there were only significant SR at the 100% level: horizontal leaps were less likely than expected, whereas leaps down were more likely than expected (SR 3.6) to start from supports >5 cm in diameter (SR -2.4), and less likely from those of ≤ 5 cm (SR -2.6).

Model 2. Model 2 (Table 4; $N = 3570$) examined the interactions in species, locomotor mode, ISD2, and EDT16. Only three locomotor modes could be included in a loglinear analysis due to low bout counts for other modes: leaping, vertical climbing and walking. From Model 2, expression Sp*LM*EDT16 was the most significant. Examining this expression, the most significant association was found to be between locomotor mode and EDT16 even at the 25% level (χ^2 [df = 2, $N = 864$] = 72.892, $P = 0.000$), where effective distance of leaps were more often than expected >1.6 m (SR 10 at 100%; 4.6 at 25%), whereas vertical climbs (SR 6.8/3.0) and walking (SR 4.5 at 100%) were more often than expected ≤ 1.6 m. There was no significant association at the 25% level between species and locomotor mode or species and EDT16. The second most significant expression was

Sp*ISD2*ETD16, and the most significant association was between species and ISD2, even at the 25% level (χ^2 [df = 1, $N = 864$] = 70.172, $P = 0.000$). *L. edwardsi* used supports of >5 cm in diameter more than expected (SR 10.9/6.1) and those of ≤ 5 cm less than expected (SR $-7.5/-4.3$). Conversely, *L. ruficaudatus* used supports ≤ 5 cm in diameter more than expected (SR 4.1/2.2) and those over less than expected (SR $-6/-3.2$). Further, there was a significant association between ISD2 and ETD16 even at the 25% level (χ^2 [df = 1, $N = 864$] = 27.035, $P = 0.000$) where locomotion from a support of >5 cm in diameter was more likely than expected to result in travel >1.6 m long (SR 5.4/3.6) and locomotion from ≤ 5 cm supports in diameter more likely than expected to result in travel ≤ 1.6 m long (SR 2.4). From the third most significant expression, Sp*LM*ISD2, we have previously discussed the relationship between species and ISD2 and there is no significant association between species and locomotor mode, or locomotor mode and ISD2.

Model 3. In Model 3, we examined the interactions in species, ISO3, height change, and HDT12 during leaping (Table 4: $N = 2,185$). There was no significance at the 25% level in the first expression (ISO3*HDT12) of Model 3. In the second most significant expression (Sp*HC*HDT12), there was a significant relationship between height change and HDT12 at the 25% level (χ^2 [df = 2, $N = 561$] = 9.945, $P = 0.007$): leaps up were more likely than expected to be ≤ 1.2 m (SR 2.9/2.1) and less likely than expected to be >1.2 m long (SR $-2.9/-2.0$). The relationship between species and height change has been previously discussed in Model 1 and there was no significant association between species and HDT12. Further, there was no significant association between the third most significant expression (Sp*ISO3).

Model 4. In Model 4, we examined the interactions in species, ISD2, ISO4, and HDT9 during leaping (Table 4: $N = 2,185$). There was no significance at the 25% level in the first most significant expression (ISD2*HTD9). In the second most significant expression (ISO4*HTD9), there was significance between ISO4 and HTD9 at the 25% level (χ^2 [df = 1, $N = 561$] = 7.058, $P = 0.008$) although there were only significant SR at the 100% level: leaps ≤ 0.9 m long were more likely than expected to be on horizontal supports (SR 2.3) and less likely than expected on vertical (SR -2.3). In the third most significant expression, there was significance between species

and HDT 9 at the 25% level (χ^2 [df = 1, N = 1,023] = 10.024, P = 0.000), whereby for *L. edwardsi* leaps ≤0.9m were less likely than expected (SR −2.6) and those >0.9 m were more likely than expected (SR 2.9). In the fourth most significant expression (Sp*IS-D2*ISO4), the relationship between ISD2 and ISO4 was significant at the 25% level (χ^2 [df = 1, N = 561] = 17.047, P = 0.000): leaps from supports >5 cm in diameter were less likely to be from horizontal/oblique/angled supports (SR −4.4/−2.4) and more likely than expected from vertical supports (SR 4.4/2.4), and leaps from supports ≤5 cm in diameter were more likely to be from horizontal/oblique/angled supports (SR 3.2) and less likely than expected on vertical supports (SR −3.2). The significant relationship between species and ISD2 was discussed in Model 1, and there was no significant association found between species and ISO4.

Leap take-off angle

Using this methodology the take-off angle for all horizontal leaps is 45°, for leaps down (N = 537) the mean angle was 30° (±8) and for leaps up (N = 303) it is 60° (±8.5). A random 25% *T*-test (following a check for normality of data) between the two species indicated a significant difference in mean take-off angle (P = 0.034 2-tailed with no assumption of equal variance): *L. edwardsi* (N = 121) had a mean optimum take-off angle of 41.3° and *L. ruficaudatus* (N = 420) of 43.9°.

Height usage

The median height of initial observation for both *L. edwardsi* (mean 5.04 m; N = 885) and *L. ruficaudatus* (mean 5.17, N = 3124) was 5.0 m: not significant (Mann–Whitney U = 1,371,187.500, P = 0.713). No significant difference was found for terminal height (Mann–Whitney U = 1,342,272.500, P = 0.187), whereby the median for *L. edwardsi* was 4.8 m (mean 4.9 m, N = 885) and 5.0 m for *L. ruficaudatus* (mean 5.1 m, N = 3124).

Habitat differences

A significant difference (Mann–Whitney U = 109,269.0, P = 0.000) was found in the median diameter at breast height (DBH) between KMNP (median = 1.0 cm, mean = 2.04 cm, N = 1013) and Ankarafantsika (median = 3.0 cm, mean = 4.7 cm, N = 432). Note DBH does not only sample trees, but also vines, shrubs, and saplings at the appropriate height. A significant difference at 25% (Mann–Whitney U = 44,050.0, P = 0.000) was also found for median crown diameter, whereby tree crowns at Ankarafantsika (median = 3.0 m, mean = 3.7 m, N = 432) were larger than at KMNP (median = 1.0 m, mean = 1.2 m, N = 623).

DISCUSSION
Between-site differences

While examining all locomotion and leaping, one of the strongest associations was found between species and initial support diameter; *L. edwardsi* commonly used larger supports than *L. ruficaudatus*. A link between body size/mass and support size has been documented, often resulting in niche differentiation between sympatric species. For example, Fleagle et al. (1981) found that *Cebus apella* (tufted capuchin: ~3.9 kg for males) in Surinam used larger supports than the smaller *Saimiri sciureus* (squirrel monkey: ~741 g for males)

with which it forms mixed species groups. Similarly, smaller *C. jacchus* (0.35 kg) preferred supports under 10 cm, whereas larger *Cebus* sp. (~3 kg) had a tendency to use supports over 10 cm (Cunha et al., 2006). This pattern is found outside the primate clade by Cunha and Vieira (2002) where a positive relationship between body size and support use size amongst didelphid marsupials in Brazil was found. It must be noted that these relationships are linked to body mass, with the species under comparison being a magnitude bigger/smaller in size (i.e., 350 g compared to 3 kg). While the two *Lepilemur* species in this study have different mean body weights, with the larger bodied species (*L. edwardsi*) most frequently using larger supports, the body weights of the two *L. ruficaudatus* largely fall within the range of *L. edwardsi* (Table 3). Further, hand lengths overlap between the two species, and we would expect this to result in a similar grasping ability. Hence we feel that weight differences between the two species, in this case, are probably insufficient to explain such a dramatic difference in support diameters.

It is known that niche separation can contribute to the differences in support diameter usage. Different support sizes are found at different heights and sympatric species may utilize separate niches based on height in the canopy (Peres, 1993; Lopes and Ferrari, 1994). Hence we should consider the effects of differences in sympatric nocturnal species between the two sites, *Microcebus* and *Cheirogaleus* are present at both sites; however at Ankarafantsika, *L. edwardsi* is sympatric with the nocturnal *Avahi*, while at KMNP *L. ruficaudatus* is sympatric with *Mirza* and *Phaner*. *Avahi* is the most similar to *Lepilemur*, both are folivorous, saltatory species (Warren and Crompton, 1997) and it is therefore possible that the absence or presence of *Avahi* affects support usage within *Lepilemur* species. However, it is unlikely here that niche separation can be attributed to the support diameter usage differences, as there was no significant difference in canopy height usage between the two *Lepilemur* species.

Therefore we look to variation in habitat structure being the cause of the observed differences in support diameter use. The west coast of Madagascar is often protected from the worst cyclone damage, but on January 21, 2009, Cyclone Fanele made landfall in the vicinity of Belo with sustained winds of 185 km/h. This study commenced 18 months following this cyclone, while its effects were still evident. Lewis and Bannar-Martin (2012) studied its effects on forest structure at KMNP, where *L. ruficaudatus* lives. They found that over 95% of trees experienced some damage, with 8.5% mortality. Unfortunately, their main sample only included trees greater than 15 cm in DBH. Within this sample, DBH was a significant predictor of death or damage; trees with larger DBH were most likely to be damaged or killed as they would be more exposed above the canopy. Stem density and biomass were also greatly decreased. They also report that 69% of food trees of sympatric *P. verreauxi* sized 10–14 cm were damaged and 3.4% died. This dying off of large trees allows re-growth of smaller saplings, shrubs, and vines, making the understory more impenetrable than before (Lewis pers. comm.). Whatever the cause, the median DBH in the range of *L. ruficaudatus* at KMNP was significantly smaller than that in Ankarafantsika for *L. edwardsi*.

Examining results found by Nash (1998) for *L. leucopus* at Beza-Mahafaly in southern Madagascar, we find

a preference for <5 cm supports, in agreement with the preference shown by *L. ruficaudatus*. However as *L. leucopus* are found most between 5 and 15 m (Nash, 1998), much higher than the mean heights of either *L. ruficaudatus* or *L. edwardsi*, both found on average around 5 m, this is not surprising as we may assume that the support diameters are smaller higher in the canopy. Considering the DBH of trees in the wetter soil near the river at Beza, where this study was carried out, we find that 88% of trees were <10 cm, 6% 10–25 cm, and 8% >25 cm (Sussman and Rakotozafy 1994). As most stratum at which the lemurs were found (5–15 m) was much higher than breast height in Nash's study, and as they reportedly tended to use small supports, an assumption that support diameter usage was small due to the lemurs being high up in the canopy is further supported. However in the present study, while the lemurs were found at similar heights in the canopy, so that one would expect support diameter usage to be similar, this was not the case: we can most probably attribute this to the effects of cyclone Fenele.

Not only has the cyclone reduced the number of large supports at KMNP, but understory regrowth has likely increased the number of small supports. We therefore propose that that the observed significant differences in support diameter can be attributed to differing support availability between the two forests. While we can only speculate based on present knowledge, we consider the effects of Cyclone Fanele on the forest structure in KMNP a probable cause for the differences in support diameter usage between the two species.

L. edwardsi were more likely than expected to leap over 2.51 m. This would be predicted as *L. edwardsi* were also more likely than expected to leap from supports >5 cm and for reasons we discuss below, linked to support stability, leaps >1.2 m were more likely to occur on supports >5 cm. Hence the longer leap length seen in *L. edwardsi* would appear to be linked to habitat differences.

Species differences were observed in the height change of leaping; *L. edwardsi* were more likely than expected to leap up or down and less likely to leap horizontally, whereas *L. ruficaudatus* most commonly leapt horizontally and less commonly down. Since Cyclone Fanele, *L. ruficaudatus* lived in a tangled environment, due to the understorey and canopy levels becoming denser as mentioned before, and hence needed to avoid collision with supports while leaping. The easiest way to achieve this was to use a more controlled low angled trajectory, resulting in no height change while leaping. However, this would also mean that to change height in the canopy *L. ruficaudatus* would have to resort to other locomotor modes like vertical climbing, which were most likely more energetically inefficient than leaping (Crompton et al., 1993). This could also explain why *L. edwardsi* leapt up and down more than *L. ruficaudatus*, as it was likely using high trajectory leaps to achieve height change. Indeed there has been an assumption that leaping primates will adopt high-trajectory ballistic paths (45°) which minimize energy costs and loads applied to the body and where this is not the case, ecological factors, not solely energy, may be a primate's main consideration (Crompton et al., 1993; Crompton and Sellers, 2007). Demes et al. (1996) examined leaping trajectories in four wild indriid species and found a range of 30°–70°, with the means centered around the 45° optimum. Here we see that although 61% of leaps were at the ballistically

optimal 45°, 25% of leaps had take-off angles less than this (hence were downwards leaps) and 14% of leaps were above this (leaps up); although even leaps at 45° can achieve height gain if the leap is landed short. Although the difference was slight, *L. edwardsi* had significantly lower take-off angles compared to *L. ruficaudatus*.

Biomechanics of leaping

There was an association with distances traveled and locomotor modes ($\chi^2 = 72.892$, $P = 0.000$): leaps were most often over 1.61 m, vertical climbs and walking under 1.6 m, indicating the importance of leaping during travel as we would expect for these specialist leapers.

Leaps from horizontal supports were most commonly ≤1.3 m long and less likely to originate on supports >5 cm in diameter. Shorter leaps in general were associated with smaller diameters, most likely due to the stability requirements of long leaps discussed above.

We also see that leaps with a positive height change were more likely to be short (≤1.2 m) and less likely to be long (>1.2 m and >2 m). Considering leaping trajectories as a ballistic curve, a subject leaps up at an angle (30° to 60°), reaches a peak and then descends. If a lemur lands the leap at the peak it achieves height gain, or it can follow the ballistic curve to lower than its starting point to achieve height loss. Further, leaps down were more likely from supports >5 cm in diameter and less likely from supports ≤5 cm, suggesting increased stability requirements.

CONCLUSION

Prediction 1a stated "show no species (habitat) significant differences if locomotion is controlled by biomechanics alone." This is upheld for distances traveled for each locomotor mode (Model 2: LM*ETD16) and for height change and leap length (Model 1: HC*HDT20).

However, *Prediction 1b*, "show significant differences if locomotion is affected by habitat, where species can be considered a proxy for location (Ankarafantsika and KMNP)" is upheld for initial support diameter usage (Model 1: ISD*Sp) and whether leaps are horizontal, up or down (Model 1: Sp*HC): variables that appear strongly linked to support availability and habit structure.

Hence we have shown that while this specialist leaper does have requirements for specific supports (e.g., stiff near verticals) it can adapt its locomotion to local conditions.

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