Chapter 16 Linking Field and Laboratory Approaches for Studying Primate Locomotor Responses to Support Orientation

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Abstract Studies of primate locomotor kinematics typically focus on data conducted in the laboratory setting, with cameras carefully positioned to afford clear views of the focal subjects, and strict control of a range of other variables ranging from light levels, to the travel path and even locomotor velocity of the focal subject. Such studies permit the manipulation of support types, facilitating the collection of a large number of data points relating to specific aspects of animal locomotion, and detailing how an individual responds to differences in arboreal support types. Studies of primate behavior in the field setting provide a completely different window into locomotor behavior. These approaches lend insights into the choices that animals make with regard to support use, providing information on the frequencies of different locomotor behaviors on different locomotor substrates. In this study, we explore the relationship between arboreal support type and forelimb and hind limb kinematics using locomotor data gathered in both the laboratory and natural settings. In the laboratory, we test a biomechanical model generated to explain limb kinematic response to support orientation using a large number of strides obtained from Eulemur individuals negotiating simulated arboreal supports. Next, using techniques that expand laboratory analyses into the field setting, we examine limb movements in Eulemur cinereiceps at the Manombo Special Reserve in southeastern Madagascar. Results suggest that animals tend to protract forelimbs more at touchdown on declines, and retract hind limbs more at lift-off on declines, patterns that generally maintain the line of gravity between the points of contact with oblique substrates. Focal individuals flex the elbow and knee joints more at midsupport on inclined and declined branches, bringing the center of mass closer to oblique supports. Patterns observed in the natural setting accord well with strides collected in the laboratory. This study both documents the effects of support orientation upon strepsirhine primate quadrupedal locomotion and represents the first record of limb kinematics in the natural setting for the critically endangered Eulemur cinereiceps.

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Introduction

Numerous studies have identified primate behavioral and morphological specializations correlated with the use of an arboreal habitat (e.g., Grand 1972; Morbeck 1976, 1979; Oxnard 1976; Fleagle 1979; Ripley 1979; Crompton 1984; Garber 1984; Cant 1988, 1992; Boinski 1989; Larson and Stern 1992; Cannon and Leighton 1994; Larson 1995; Hunt et al. 1996). Studies conducted in the wild have reported on primate strategies for moving on arboreal supports, for example, grasping multiple branches and/or adopting a crouching posture (i.e., flexed and abducted limbs), to move along narrow supports, presumably to improve balance by lowering the center of mass (Fleagle 1977a,b; Fleagle and Mittermeier 1980; Grand 1984; 1988; Dunbar and Badam 2000). Recent decades have seen increased interest in exploring specializations for arboreality, yielding a wealth of experimental kinematic studies aimed at identifying specific locomotor accommodations to different aspects of the arboreal habitat (Rollinson and Martin 1981; Meldrum 1991; Hirasaki et al. 1993; Demes et al. 1995; Schmitt and Larson 1995; Hamrick 1996; Lemelin and Schmitt 1997; Jayne and Irschick 1999; Stevens and Larson 1999; Turnquist et al. 1999; Wunderlich 1999; Schmidt and Fischer 2000; Krakauer et al. 2002: Stevens 2003, 2008).

The Problem of Branch Inclination: Limb Kinematics on Oblique Supports

Angular orientation of supports constitutes one of the most obvious challenges that primates must overcome in negotiating the arboreal habitat. This study focuses strictly on kinematic accommodations to support inclination, using data gathered in the laboratory and natural settings. Oblique arboreal substrates create two primary types of challenges to maintaining balance, namely, increased chances of sliding down or toppling off a support (Fig. 16.1). Sliding and toppling relate to the shear forces that exist between the contact point and the substrate (Hirasaki et al. 1993). A number of animals exhibit well-developed strategies for resisting shear forces, by generating "strong bonds" with the support itself. For example, bats are capable of generating negative pressure along specialized contact surfaces, producing enough suction to remain firmly attached to smooth surfaces (Cartmill 1979). Anurans use both capillary surface tension and viscous adhesion, in order to maintain contact with inclined supports (Barnes 1997). Many animals that use suction and/or adhesive tactics possess an ability to secrete fluids from specialized sweat or mucous glands located in textured toe pads to assist in this process, e.g., tree frogs (Barnes 1997). Those that do not produce



Fig. 16.1 On horizontal branches, the gravity vector is perpendicular to the support. On oblique supports, a surface parallel component of the gravity vector increases with support inclination, increasing the tendency to slide or topple from a support. This component is in the direction of movement on declines, and against the direction of movement on inclines. One way that primates may maintain balance on oblique supports is by altering limb joint angles and protracting and retracting limbs to keep the line of gravity between the points of contact with the substrate

secretions may possess specialized features such as intricate internal tendons that can raise and lower textured surfaces of the contact pads, thereby increasing intermolecular forces between the animal and the substrate via dry adhesion (Cartmill 1979; Haffner 1996).

Another strategy for resisting shear forces on arboreal supports is to find some way to interlock with a branch. One common method employed by small animals is to resist the shear forces via manual and/or pedal claws, which they can imbed into irregularities in tree bark or other surfaces (Cartmill 1974; Haffner 1996; Giannoni et al. 1999). Some rodents that habitually use claws for this purpose have tendon-locking mechanisms that reduce energy expenditure associated with muscle flexion (Haffner 1996). Sloths, dermopterans, and bats also employ tendon-locking mechanisms to interlock with substrates by hooking entire hands and/or feet around the support (Quinn and Baumel 1993; Simmons and Quinn 1994).

Most primates lack well-developed claws for interlocking with supports and/ or specialized manual and pedal glands for adhesion. Nonetheless they remain adept at arboreality. Primates are known to make numerous kinematic adjustments in order to counteract balance challenges on inclined branches. Hamrick (1996) and Lemelin (1996) have shown that wrist joint angles and hand placement respectively change with differences in support orientation, and Stevens and Larson (1999) reported that limb joint angles are altered, perhaps to shift the center of mass closer to the substrate. Primates moving along oblique supports exhibit myriad other changes in angular and support patterns (Prost and Sussman 1969; Rollinson and Martin 1981; Krakauer et al. 2002; Stevens 2006).

In addition to the challenges posed for balance, substrate orientation alters the forces necessary for quadrupedal progression. On a horizontal substrate, the weight force or gravity vector acts perpendicular to the surface. When substrates are inclined, the weight force includes a surface-parallel component that increases with inclination. This is a propulsive force (in the direction of movement) when animals walk downhill, and a braking force (against the direction of movement) when animals walk uphill. Therefore, when walking down an inclined branch, the limbs must generate higher braking forces than they would on a horizontal to overcome the tendency to slide down, and conversely, when walking up, the limbs must generate higher propulsive forces. Aligning the limbs with the gravity vector may assist in generating these impulses. Preliminary studies of possums navigating inclines and declines suggest that this is indeed the case (Lammers et al. 2002). One way that a clawless animal may maintain balance while applying necessary braking and propulsive forces is to make accommodations in limb protraction, retraction and flexion. At this point, it is convenient to consider walking up and walking down oblique supports separately.

Incline Predictions

In addition to the use of grasping hands and feet to resist shear forces on oblique supports, it is predicted that elbow and knee joints may become more flexed at midstance in order to bring the center of mass closer to oblique substrates. At lift-off, hind limbs should be more retracted and knees should be more extended on inclines than they are on the horizontal (Fig. 16.1). Because the line of gravity falls more posteriorly along an inclined support, this angular excursion pattern can act to reduce the animal's tendency to topple off of a support by keeping the gravity vector within the line of support defined by the points of contact with the substrate.

Decline Predictions

As an animal walks head-first down declined branches, it is also expected that the elbows and knees will be more flexed at midstance to bring the center of mass closer to the substrate. But in this case, the forelimb should be more protracted and the elbow more extended at touchdown. As the line of gravity falls more anteriorly on a declined support, this excursion pattern should help to maintain the gravity vector near the line of support defined by the points of contact with the substrate, and to control acceleration on the decline to avoid toppling over head-first (Fig. 16.1). Individuals that *are* able to reverse their hind feet, e.g., ruffed lemurs,

may do so, in order to achieve a better grasp on the substrate by placing the hind limb in tension (Laborde 1986; Meldrum et al. 1997). This case may actually result in high hind limb angular excursions on declines. Those that *cannot* reverse their hind feet may take shorter steps, flex their knees in order to lower their center of mass, and be unwilling to walk headfirst down the steepest declines.

Locomotor Kinematics in *Eulemur*: A Case Study for Naturalistic Experimental Research

This study examines a subset of these hypotheses by generating a large sample of strides on horizontal, inclined and declined simulated arboreal supports in a laboratory assembled at the Duke Lemur Center. Importantly, it also extends these hypotheses into the natural setting to examine whether the critically endangered gray-headed lemur, *Eulemur cinereiceps* (until recently known as the white-collared lemur, *E. albocollaris*—see Johnson et al. 2008 for a taxonomic overview), exhibits similar responses to support angulation as the baseline pattern established for its congeners in the laboratory setting.

Eulemur represents a good choice for understanding kinematic accommodations to support orientation, representing an adept arboreal quadrupedal primate that prefers to travel in the continuous canopy (e.g., Sussman 1976), and with welldocumented morphology and positional behavior (e.g. Sussman 1976; Jouffroy and Lessertisseur 1978; Ward and Sussman 1979; Ganzhorn 1985; Jungers 1985; Dagosto 1995; Hamrick 1996; Overdorff 1996). Eulemur cinereiceps, restricted to the low-altitude southeastern coastal rain forests of Madagascar, finds protection only within Manombo Special Reserve, a plot containing 8000 ha of forest located at 22°57'S, 23°08'S latitude and 47°36'E, 47°48'E longitude. In recent years, the Manombo forest habitat has drastically reduced as it has withstood a major cyclone, a natural forest fire, and increasing human pressure through logging and hunting (Ratsimbazafy 2002). Although resilient, this confluence of challenges has rendered *Eulemur cinereiceps* one of the 25 most critically endangered primates in the world, as defined by the IUCN (Mittermeier et al. 2006, 2007). The need for more baseline data on positional behavior and habitat use of this taxon to inform the conservation effort sets the context for its inclusion in this study.

Methods

Focal Subjects

This study adhered to the principles of ethical treatment of nonhuman primates, using noninvasive kinematic data collection protocols approved by the Institutional Animal Care and Use Committees (IACUC) at Stony Brook University, Duke University, and Ohio University. The study sample included one adult male and one adult female of both *Eulemur collaris* and *Eulemur rubriventer* filmed by N.J. Stevens in the laboratory setting, and one adult male and one adult female *Eulemur cinereiceps* filmed in the natural setting of Manombo Forest, Madagascar. Laboratory subjects had regular access to naturalistic supports in their large enclosures. The body mass for *Eulemur* species is ca. 2 kg (Smith and Jungers 1997), and *Eulemur* intermembral indices fall between 68 and 72 (Fleagle 1999). Of the *Eulemur* species examined herein, only *E. rubriventer* has been the subject of long-term research on habitat use (Overdorff 1996). However, all *Eulemur* species with published field data are agile arboreal quadrupeds, similar in body mass and proportions, that travel and forage in the arboreal canopy (e.g., Sussman 1976; Jouffroy and Lessertisseur 1978; Ward and Sussman 1979; Ganzhorn 1985; Jungers 1985; Dagosto 1995; Hamrick 1996; Overdorff 1996; Smith and Jungers 1997; Fleagle 1999), justifying intrageneric comparisons made in this study.

Measuring Locomotor Kinematics in the Laboratory and in the Field

In the laboratory setting, subjects moved upon simulated branches constructed from 2.44 m sections of polyvinyl chloride (PVC) pipes, 1.25 cm in diameter, coated with a nonslip surface and oriented horizontally and at 30° and 60° angles from the horizontal. Individuals acclimated to these substrates in their naturalistic enclosures before data collection, allowing them to become accustomed to the experimental support orientations. Stevens (2003) provides a more comprehensive description of the laboratory experimental setup. In the natural setting, we filmed individuals on oblique supports ranging between 30° and 60° in inclination, and between 1 and 4 cm in diameter. Although some of these branches were flexible, strides analyzed in this study were restricted to supports that oscillated less than 2 cm in the superoinferior plane during the stride cycle. Using standard 2D kinematic techniques in both the laboratory and in Manombo Forest, we positioned cameras on tripods to capture lateral views of the study subjects, placing recording devices at a sufficient distance to reduce parallax, 5 m from the path of movement of the focal subjects. In the laboratory setting, N.J. Stevens used two Panasonic AG-195 VHS professional video cameras, and in the field setting, we used a Sony DCR-HC42 NTSC digital camcorder. In the laboratory, a shutter speed of 1/1000 s was used to reduce motion blur; in the field we used the highest shutter speeds possible in the variably lit settings. Polk et al. (2005) note that error associated with sampling at lower frequencies is most pronounced in animals moving at very high velocity. For both camera types, we optimized frame rates to reduce motion blur by splitting interlaced video fields to achieve 60 Hz, a sampling rate adequate to capture the angular kinematics, shoulder and hip heights, and stride lengths used by Eulemur subjects at the velocities that they traveled in this study.

Using Peak Motus (version 9.1) to import video clips, N.J. Stevens collected 15 strides per individual per substrate that provided unobstructed views of *all* of the anatomical points of interest, with the total number of individuals (n = 4) and support (n = 5) combinations yielding 240 strides in the laboratory setting (notably *Eulemur rubriventer* chose not to walk on 60° declines in the lab). Laboratory-derived data formed a baseline for comparison with a smaller number of strides (n = 19) collected in the natural setting, following field kinematic methods outlined in Stevens et al. (2006). Data collected at Manombo included 10 strides for the adult male (horizontal: 3, 30° incline: 3, 60° incline: 2, 30° decline: 1, 60° incline: 2, 30° decline: 3, 60° decline: 2). In frame-by-frame analysis, we collected kinematic variables by digitizing forelimb and hind limb positions at touchdown and lift-off events. Variables are summarized in Table 16.1.

For the purposes of this study, forelimb angle refers to the angle between the substrate and a line segment connecting the greater tubercle of the humerus with the lateral aspect of the distal end of the fifth metacarpal, such that a larger forelimb angle reflects greater forelimb *protraction*. Hind limb angle refers to the angle between the substrate and a line segment connecting the greater trochanter of the femur with the lateral aspect of the distal end of the distal end of the fifth metacarsal, such

Parameter	Abbreviation	Description
Forelimb angle ^a	FL	Angle made by a line connecting shoulder and hand markers and the substrate
Forelimb excursion	FLEXC	Difference in forelimb angle between touchdown and lift-off
Hind limb angle ^a	HL	Angle made by a line connecting hip and foot markers and the substrate
Hind limb excursion	HLEXC	Difference in hind limb angle between touchdown and lift-off
Elbow angle ^a	Elb	Angle made by the proximal and distal forelimb segments
Knee angle ^a	Knee	Angle made by the proximal and distal hind limb segments
Shoulder height ^a	ShoHT	Perpendicular distance of the shoulder marker from the substrate
Hip height ^a	HipHT	Perpendicular distance of the hip marker from the substrate
Forelimb stride length	FSTRLEN	Distance traveled by the hand marker from one touchdown to the next
Hind limb stride length	HSTRLEN	Distance traveled by the foot marker from one touchdown to the next
Velocity	SPEED	Distance covered in one stride cycle divided by the number of frames

Table 16.1 Kinematic variables considered in this study

^aIndividual angles measured at touchdown (TD, the first frame in which the limb is in contact with the support), midstance (MS, the frame in which the shoulder marker passes over the hand marker/ hip marker passes over the foot marker), and lift off (LO, the last frame in which the limb is in contact with the support).

that a larger hind limb angle reflects greater hind limb retraction. Elbow angle refers to the angle made by the proximal and distal forelimb segments, whereas knee angle refers to the angle made by the proximal and distal hind limb segments, such that for both the elbow and the knee, a smaller angle indicates a more *flexed* limb posture. To account for out-of-plane positions of the elbow and knee joints, 2D angles collected from lateral view were subjected to a trigonometric correction (following Stevens et al. 2006). We measured shoulder and hip heights as the perpendicular distance between the shoulder or hip marker and the substrate. We calculated stride lengths as the distance traveled by the hand/foot marker between consecutive touchdown events for the limb, and velocity as the distance traveled in one stride cycle divided by the number of frames. In the laboratory setting N.J. Stevens placed reflective tape markers on anatomical landmarks on the study subjects, facilitating the collection of a large laboratory data set for each substrate. For data collected in the natural setting, we visually identified anatomical landmarks only for strides that preserved clear and well-lit views of the study subjects moving along supports that had obvious landmarks measured for calibration purposes.

Owing to the smaller sample of strides obtained in the field setting, we statistically analyzed only the laboratory data set for this study, incorporating field data in more qualitative comparisons. As kinematic variables do not always follow a normal distribution, we rank-transformed laboratory data prior to analysis and replaced original variates with the ranks, breaking ties by assigning mean ranks to tied cases (SPSS version 13.0). Rank transformations permit two-way analysis of variance without loss of power in data sets that are not normally distributed (Iman 1974; Conover and Iman 1981).

Because differences in velocity may themselves constitute a response to branch orientation, we did not attempt to constrain velocity in either the laboratory or the natural settings. To explore substrate-related differences in limb kinematics while taking into account differences in velocity, we subjected data to an analysis of covariance (ANCOVA) (Sokal and Rohlf 1981) with velocity (m/s) as the covariate. ANCOVAs compare kinematic variables collected on two substrates at the mean velocity observed on both substrates. When we found no significant relationships with velocity, we analyzed data using analyses of variance for substrates of differing orientations.

Results

Means and standard deviations for all kinematic variables by individual and substrate type are presented in Table 16.2. Significance levels for ANOVA/ANCOVA analyses of strides collected in the lab are summarized in Table 16.3. Males and females exhibited similar locomotor responses to support orientation in the variables discussed herein, although not all differences in limb kinematics reached significance in both individuals (Table 16.3).

Table 16.2 ⁶	n Mean	(AVG)	and sta	ndard	deviatior	ns (SD)) for kine	matic	variable	s of Eu	lemur cc	ollaris	(labora	tory se	tting)					
	Female									~	Male									
	Н		I 30		I 60		D 30		D 60		E		[30		09 I		D 30		09 C	
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD /	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg. S	D
FLTD ^a	127.73	1.10	124.21	3.10	127.72	2.39	137.94	1.53	143.16	1.60	127.84	2.11	121.31	3.06	123.72	3.87	138.31	1.49	36.88	3.18
FLTO ^a	50.73	1.73	45.18	4.53	46.08	3.39	63.83	3.47	97.58	5.88	54.54	2.52	47.61	3.02	45.42	3.35	59.89	3.67	71.95	6.87
elb MS ^{a,b}	116.04	4.503	99.14	5.64	93.67	4.13	102.08	3.01	87.56	44.57	122.77	4.01	93.34	3.61	90.81	4.92	106.17	5.77	74.36	7.82
HLTD ^a	58.61	0.79	66.37	2.27	76.30	3.03	43.08	1.63	39.27	2.12	63.57	2.85	70.52	2.79	74.26	4.52	43.73	1.65	39.10 1	0.07
HLTO ^a	123.66	1.65	130.73	1.40	133.82	2.38	110.88	2.48	129.79	6.49]	128.30	2.30	134.12	1.91	136.97	2.12	124.71	3.43	18.45	9.87
knee $MS^{a,b}$	105.11	2.81	93.09	3.70	83.20	2.99	67.48	3.76	56.19	8.26	99.98	3.64	86.21	2.30	81.14	3.17	71.39	2.95	60.49	5.24
f str leng c	0.49	2.42	0.60	6.61	0.53	4.63	0.46	3.16	0.32	4.64	0.58	2.27	0.59	4.51	0.56	4.52	0.50	2.86	0.38	5.95
h str leng ^c	0.49	2.55	0.60	6.48	0.51	3.52	0.46	2.89	0.64	7.76	0.57	2.29	0.58	3.75	0.53	7.05	0.50	3.03	0.51	7.69
ShoHt TD ^e	0.15	0.51	0.16	1.06	0.14	0.56	0.13	0.46	0.12	1.17	0.16	0.74	0.15	0.74	0.17	0.67	0.14	0.44	0.12	1.01
ShoHt MS ^c	0.16	0.61	0.16	0.66	0.16	0.68	0.14	0.51	0.14	2.24	0.18	0.76	0.16	0.82	0.18	0.69	0.16	0.39	0.14	1.14
ShoHt LO ^c	0.14	0.70	0.14	0.88	0.14	0.85	0.14	0.56	0.14	1.53	0.17	0.40	0.15	0.82	0.16	0.70	0.15	0.71	0.14	1.05
HipHt TD ^c	0.23	0.63	0.22	1.10	0.20	0.24	0.18	0.47	0.17	1.75	0.23	0.86	0.21	0.36	0.21	0.55	0.19	0.53	0.17	1.31
HipHt MS ^c	0.23	0.97	0.22	1.17	0.21	0.49	0.18	0.71	0.16	2.03	0.23	0.73	0.21	0.45	0.21	0.51	0.18	0.66	0.18	1.10
n = 15 for a	ll variab	oles coli	lected ir	1 labor	atory set	ting. A	bbreviat	ions fc	ollow the	se of T	able 16.	<u>-</u>								
^a Units in de	grees.																			
^b 2D.																				
°Units in me	eters.																			

Table 16.2b N	fean (AVC	G) and s	standard d	leviation	ns (SD) fc	or kinem	atic varia	ibles of	Eulemur	rubiven	ter (labo)	atory set	ting)			
	Female								Male							
	H		I 30		I 60		D 30		Н		I 30		I 60		D 30	
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD
FLTD ^a	128.20	1.79	127.08	3.29	118.09	12.66	138.38	2.26	127.17	1.96	120.42	4.99	124.97	3.28	137.46	3.42
FLTO^a	52.75	2.59	49.64	3.62	36.06	1.85	61.22	6.50	54.02	2.97	49.05	3.99	39.84	4.35	62.58	8.43
Elb MS ^{a,b}	125.97	2.60	109.16	5.95	88.86	7.53	104.05	4.66	126.74	3.91	106.00	8.16	90.98	7.57	108.38	6.78
HLTD ^a	57.68	2.71	74.24	4.17	89.11	3.20	37.40	5.14	62.32	2.40	81.61	2.61	82.03	3.51	40.93	2.54
HLTO ^a	125.54	1.82	131.62	1.81	142.16	2.17	111.65	6.80	125.92	1.93	133.85	2.21	141.12	1.72	107.69	96.6
Knee MS ^{a,b}	103.02	2.62	100.07	4.36	87.08	5.92	72.03	6.06	107.70	2.84	90.20	4.60	77.69	5.30	74.67	8.81
f str leng ^c	0.47	1.82	0.54	3.21	0.56	5.43	0.41	3.36	0.47	2.17	0.52	5.51	0.51	7.67	0.40	5.18
h str leng ^c	0.47	1.63	0.54	3.50	0.53	4.55	0.44	7.87	0.47	2.11	0.51	5.05	0.53	7.54	0.40	4.82
ShoHt TD ^e	0.16	0.47	0.14	0.63	0.14	0.71	0.13	0.65	0.15	0.46	0.13	0.88	0.13	0.90	0.13	0.72
ShoHt MS~	0.17	0.47	0.15	0.54	0.14	0.81	0.14	0.52	0.17	0.72	0.14	0.96	0.13	0.65	0.14	1.07
ShoHt LO ^c	0.15	0.73	0.14	0.69	0.11	0.60	0.14	0.82	0.15	0.70	0.14	0.92	0.11	1.03	0.14	1.37
HipHt TD°	0.22	0.61	0.21	0.77	0.21	1.28	0.16	1.55	0.23	0.46	0.20	0.57	0.19	0.63	0.17	0.70
HipHt MS ^c	0.24	0.80	0.21	0.71	0.20	5.59	0.18	1.47	0.24	0.48	0.20	0.54	0.18	0.49	0.17	1.31
HipHt LO°	0.22	0.80	0.20	0.69	0.17	0.73	0.16	1.92	0.22	0.66	0.20	0.57	0.18	0.86	0.16	0.85
n = 15 for all v	ariables co	ollected	in labora	tory set	ting. Abb	reviation	ns follow	those o	f Table 1	5.1.						
^a Units in degre	es.															

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^b 2D. ^c Units in meters.

Table 16.2c	Mean (Avg.) and st	andard deviat	ions (SD) for k	inematic varial	oles of Eulemur	· cinereicep	os (natural settin	(g)		
	Н		I 30		I 60		D 30		D 60	
	4		4		4		4		e	
= <i>u</i>	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD
FLTD	127.19	4.24	123.85	3.02	123.68	2.65	141.01	2.06	142.94	4.48
FLTO	52.79	6.38	43.55	0.66	43.78	3.47	53.68	5.68	98.46	22.99
elb MS	109.89	4.64	98.68	3.70	89.83	4.75	100.82	3.67	92.93	7.25
HLTD	57.98	3.84	69.38	1.29	77.58	3.55	37.14	3.50	40.20	5.52
HLTO	125.04	2.03	132.82	2.38	136.48	1.69	114.69	5.28	125.78	8.02
knee MS	103.63	5.62	87.94	2.66	81.08	3.04	62.81	3.99	53.41	5.67
f str leng	0.55	0.06	0.56	0.03	0.57	0.03	0.47	0.02	0.36	0.17
H str leng	0.55	0.06	0.55	0.03	0.58	0.08	0.47	0.02	0.59	0.10
ShoHt TD	0.17	0.01	0.15	0.01	0.16	0.01	0.13	0.01	0.12	0.01
ShoHt MS	0.17	0.01	0.16	0.01	0.16	0.01	0.16	0.00	0.13	0.01
ShoHt LO	0.16	0.01	0.14	0.01	0.14	0.00	0.14	0.01	0.14	0.01
HipHt TD	0.24	0.00	0.22	0.00	0.20	0.01	0.17	0.01	0.16	0.00
HipHt MS	0.24	0.01	0.22	0.01	0.21	0.01	0.18	0.01	0.16	0.02
HipHt LO	0.23	0.01	0.21	0.00	0.20	0.01	0.17	0.01	0.16	0.02
Abbreviation	s follow those of Ta	ble 16.1.								

								adding only	2					
	Eulemur	collaris			Eulemur	rubivente	r		Eulemur	collaris			Eulemur 1	ubiventer
	Female		Male		Female		Male		Female		Male		Female	Male
	H-I 30	09 I-H	H-I 30	09 I-H	H-I 30	09 I-H	H-I 30	09 I-H	H-D 30	H-D 60	H-D 30	H-D 60	H-D 30	H-D 30
FLTD	0.000	I	0.000	0.001	I	0.007	0.000	0.044	0.000	I	0.000	0.000	0.000	0.000
FLTO	0.001	0.000	0.000	0.000	I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HLTD	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HLTO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	I	0.001	I	0.000	0.000
elb MS	I	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
knee MS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
FL str leng	I	I	I	I	I	I	I	I	0.000	0.000	0.009	0.000	0.000	0.000
HL str leng	I	I	I	I	I	I	I	I	0.000	I	I	0.003	0.000	0.000
ShoHt TD	I	0.000	0.000	I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ShoHt MS	I	I	0.000	I	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.000
ShoHt LO	I	0.014	0.000	0.000	0.000	0.000	0.000	0.000	I	I	0.000	0.000	0.000	0.011
HipHt TD	I	0.000	0.000	0.000	0.047	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HipHt MS	I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HipHt LO	I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
All significa	nt differen	ices in tab	ole indicate	e lower va	lues for o	blique sur	port relat	ive to hor	izontal EX	CEPT in F	ILTD and	HLTO COI	nparisons	on inclines
(H-I 30, H-I	60), AND	in FLTD a	ind FLTO (comparison	ns on decl.	ines (H-D	30, H-D 6	0); regula	r text indic	ates ANOV	/A results;	bold italics	s indicate r	elationship
with speed,	hus ANCC	JVA resul-	ts; .000 de	notes p <<	; 0.001; bl	anks indic	ate nonsig	gnificant d	lifferences.					
Kinematic a	breviation	ns follow t	those in Ta	ble 16.1.										

 Table 16.3
 ANOVA/ANCOVA significance levels for kinematic variables on oblique supports

In the laboratory setting, both *Eulemur collaris* and *E. rubriventer* exhibited significantly more protracted forelimbs (larger forelimb angles) at touchdown on declined supports than either did on the horizontal branches (Fig. 16.2a). These patterns were present throughout the stride cycle, with larger forelimb angles also observed at lift-off on declines. Hind limb angles were generally smaller, reflecting in this case that hind limbs too, tended to be more protracted at touchdown and lift-off on declined supports (Table 16.3).

On inclines, both *Eulemur* species examined in the laboratory utilized more retracted hind limbs (larger hind limb angles) at both touchdown lift-off events (e.g., Fig. 16.2b). Similar patterns were observed for the forelimbs, typically less protracted on inclines at touchdown and lift-off events (Table 16.3). *Eulemur cinereiceps* in Manombo Forest used similar kinematic patterns, e.g., exhibiting larger forelimb angles at touchdown on declines (Fig. 16.3a), and larger hind limb angles at lift-off on inclines (Fig. 16.3b).



Fig. 16.2 Limb protraction and retraction on oblique supports in the laboratory. (a) Forelimb protraction at touchdown on declines. (b) Hind limb retraction at lift-off on inclines. Heavy lines in these and subsequent boxes represent median values



Fig. 16.3 Limb protraction and retraction on oblique supports in the field. (a) Forelimb protraction at touchdown on declines. (b) Hind limb retraction at lift-off on inclines

With regard to limb flexion during locomotion, in the laboratory setting, *Eulemur* species tended to exhibit smaller elbow and knee angles at midsupport on oblique substrates (Fig. 16.4a, b), a pattern also observed for *Eulemur cinereiceps* in the field (Fig. 16.5a, b). On simulated arboreal supports, focal subjects tended to take relatively shorter forelimb strides on declines (Fig. 16.6a), and carried their center of mass closer to oblique branches, as evidenced by lower shoulder and hip heights. For example, hind limb kinematics reflected lower hip heights at throughout the stride on both inclines and declines (Table 16.3). Although the Manombo rain forest habitat provided a greater variability in support types than was present in the laboratory, *Eulemur cinereiceps* exhibited kinematic responses to substrate orientation consistent with its congeners (e.g., Table 16.2; Fig. 16.6b).



Fig. 16.4 Limb flexion at midsupport on oblique supports in the laboratory. (a) Elbow flexion on inclined supports. (b) Knee flexion on declined supports



Fig. 16.5 Limb flexion at midsupport on oblique supports in the field. (a) Elbow flexion on inclined supports. (b) Knee flexion on declined supports



Fig. 16.6 Forelimb stride lengths on declined branches. (a) *Eulemur collaris* and *E. rubriventer* in the laboratory setting. (b) *Eulemur cinereiceps* in the natural setting

Discussion

Laboratory studies offer clear benefits for the collection of kinematic data, utilizing sophisticated camera setups and/or cineradiographic approaches in well lit spaces specifically designed to capture and accurately document limb movements and postural adjustments with large samples of strides collected in a repeatable manner (e.g., Schmidt and Fischer 2000; Polk 2001). In addition, lab based studies allow us to isolate different characteristics of arboreal substrates, permitting the examination of their separate and combined effects upon locomotion (e.g., Stevens 2003, 2006, 2008).

Yet, the laboratory setting necessarily limits locomotor choices available to study subjects. By design, substrate complexity in experimental studies rarely approaches that available in the natural environment. Captive animals may never be inspired to move as rapidly as they do when faced with a predator, competitor, or potential mate in the wild; they may not ever reach so far to select that perfectly ripe fruit (Stevens and Carlson 2008). An even more fundamental problem arises from the fact that laboratory experimental subjects are often housed in small cages, and often lack regular access to natural supports and enclosures of sufficient size to enjoy the daily path lengths and overall activity levels reflective of their wild counterparts (Chang et al. 1999; Stevens and Carlson 2008). Food provided at regular intervals obviates the need for physically demanding travel necessitated by foraging, and often renders captive individuals less able to be active and exhibit behaviors similar to individuals of their species in the wild.

Hence the collection of detailed kinematic data in the wild can offer some clear advantages for capturing postural and locomotor strategies that quadrupedal primates actually employ to maintain balance on arboreal supports. Yet, field studies are not without their challenges. Visibility of moving subjects in the leafy arboreal setting restricts the sample sizes of strides available for detailed kinematic analyses. Sunny days provide filming challenges in variable lighting and backlighting of study subjects, rainy days for maintaining lens clarity and protecting delicate electronic equipment from the weather. Navigation of natural terrain with cumbersome cameras and tripods is complicated by additional limitations imposed by camera battery life. Whereas some kinematic variables remain fairly robust to the challenges of field data collection, even in the best of natural conditions, object-observer positioning is expected to be more variable than in the laboratory, contributing to a realistic expectation of lower precision and/or accuracy for field kinematic data (Stevens et al. 2006). Linking approaches ex situ, capable of assembling large sample sizes of strides with strategic kinematic data collection in the field provides a compromise to explore the potential and actual locomotor niches in concert (Stevens and Carlson 2008). In this way, one can take advantage of the best of both laboratory and field data collection worlds, altering one substrate parameter at a time in the laboratory and recording precise kinematic responses. Lab-derived biomechanical models can be tested in the wild, to explore whether larger and more diverse sample sizes of animals make similar accommodations in their more complex natural habitats.

Exploring Kinematic Patterns in Experimental and Natural Conditions

This study revealed that the highly arboreal genus *Eulemur* exhibits limb kinematic responses to support orientation that are consistent between the laboratory setting and the rain forest habitat. Such observations are significant for documenting the utility of laboratory studies for documenting ecologically relevant behaviors. Given the greater variability in substrate orientations observed in the natural setting, taken together with variability in substrate diameter, flexibility, texture, and connectivity, these results are particularly compelling. Had we found different limb kinematic responses in *Eulemur* species between the laboratory and natural settings, additional data would be required to determine whether discrepancies might reflect differences between the substrate environments or whether they might reflect distinctive aspects of the species themselves.

To counteract shear forces, subjects traveling along oblique arboreal supports were expected to make a host of kinematic accommodations. For example, because the line of gravity falls more posteriorly along an inclined support, *Eulemur* was predicted to exhibit more retracted hind limbs at lift-off (e.g., Stevens and Larson 1999; Stevens 2003; Lammers et al. 2006). Conversely, as the line of gravity falls more anteriorly along a declined support, it was predicted that *Eulemur* would exhibit more protracted forelimbs at touchdown on these supports (e.g., Stevens and Larson 1999; Stevens 2003; Lammers et al. 2006). These excursion patterns were expected to improve balance on inclines and declines by keeping the gravity vector within the line of support defined by the placement of the hands and feet on the branch. Such adjustments may also be beneficial in generating greater propulsive

forces to overcome gravity during forward progression on inclines, and enabling the application of greater braking forces to limit the tendency to accelerate out of control on declines. Finally, it was predicted that *Eulemur* would flex elbows and knees more on oblique supports to bring the center of mass closer to the support.

Each of these predictions was upheld in both the laboratory setting and in the wild. Eulemur individuals exhibited more protracted forelimbs at touchdown on declines (Figs. 16.2a, 16.3a), more retracted hind limbs at lift-off on inclines (Figs 16.2b, 16.3b), and more flexed elbows and knees at midsupport (Figs. 16.4, 16.5), resulting in significantly lower shoulder and hip heights on oblique supports (Table 16.3). Lorisids and cheirogaleids have been shown to exhibit similar limb excursion patterns on arboreal inclines and declines in the laboratory setting (e.g., Stevens 2003). Moreover, consistent patterns have been observed in the laboratory setting in New World monkeys (inclined treadmills: Vilensky et al. 1994; inclined poles: Stevens and Larson 1999; rope treadmills: Nyakatura et al. 2007), Old World Monkeys (inclined poles: Rollinson and Martin 1981), as well as in nonprimate mammals (Monodelphis on trackways and simulated arboreal supports: Lammers et al. 2002). Taken together, these observations suggest a common solution in limb alignment among quadrupedal mammals faced with the problem of an increased tendency to topple off of or slide down an oblique support. This study is the first to document kinematics of *Eulemur* in the natural setting, revealing consistent patterns in forelimb and hind limb touchdown and lift-off angles in the laboratory and the wild. This correspondence suggests that laboratory-based approaches can prove useful in the formulation of kinematic hypotheses about locomotion in the wild.

Why is this important? Clearly, primates have a myriad of possible responses to mechanical challenges, not limited to those related to limb flexion and excursion measured for this study, such as by altering locomotor mode altogether, e.g., descending feet-first, hopping or leaping, or by refusing to negotiate steep supports entirely as did Eulemur rubriventer on the steepest declines. Body mass, relative limb segment lengths, and joint configurations may each play a role in defining the range of potential options an individual may choose among in responding to locomotor challenges. In short, collecting basic kinematic data on Eulemur made it possible to test more explicitly whether locomotion observed in the simplified laboratory setting offers a valid window into natural behavior in the face of a frequently encountered mechanical challenge. Of course, comparisons in this study were necessarily restricted to reflect measurable kinematic variables on a particular set of support types, and likely many significant differences in oblique support kinematics remain between the laboratory and field settings. In short, this study focused on measuring variables relating to clear mechanical predictions for coping with inclines and declines. Should lab and wild observations differ greatly for those variables, there would be no reason for expecting this particular laboratory setting to effectively simulate natural locomotor conditions for the study of kinematics on oblique arboreal supports.

The Role of Kinematic Approaches in the Wild

The application of kinematic questions in the natural setting has become increasingly important for understanding locomotion in an ecologically relevant context. This study has demonstrated consistency between laboratory and field results for a number of forelimb and hind limb kinematic parameters. Other studies demonstrate a more complex reality. For example, whereas theoretical and laboratory biomechanical studies predict an increase in the use of diagonal sequence gait patterns in the terminal branch setting (e.g., Cartmill et al. 2002), Dunbar and Badam (2000) found quite the opposite in the wild, in that juvenile bonnet macaques in the natural setting actually utilized a lower proportion of diagonal sequence gaits in the terminal branch milieu than they did on more stable supports closer to the tree trunks. Interestingly, Isler and Grüter (2006) also reported the incorporation of lateral sequence gaits during vertical climbing in wild snub-nosed monkeys. Whereas many studies assume that animals optimize travel distances to minimize costs of locomotion, Dunbar and Badam (2000) note that given the choice, bonnet macaques may travel greater distances rather than crossing directly among terminal branches to avoid utilizing unstable supports. The use of unstable supports has been modeled in the laboratory as more energetically costly (Alexander 1991; Demes et al. 1995), yet, Thorpe et al. (2007) suggest that in the wild at least some primates increase energetic efficiency of locomotion through the use of compliant branches. In addition, although most laboratory studies utilize cylindrical simulated branches, Eulemur cinereiceps individuals, like the bonnet macaques examined by Dunbar and Badam (2000), often grasped small supports perpendicular to the path of motion on oblique supports, improving balance by spreading their body support over a broader area, and suggesting that more information about balance strategies may be gleaned in a more complex setting. Studies of red slender lorises in the natural setting have also documented a surprising array of unpredicted behaviors including the use of rapid arboreal quadrupedal locomotion at velocities far outstripping those collected for lorises in the laboratory setting (Nekaris and Stevens 2007). Whereas laboratory studies offer the opportunity to break down the natural environment into individual components for study, it is important to recognize that this simplification necessarily limits the choices available to focal subjects. In the laboratory setting, it may not be possible or even desirable to replicate the complexity of locomotor options available to animals in the wild. Field kinematic approaches provide complementary approaches to the study of primate locomotion, pivotal for addressing questions related to how individuals select among and use arboreal supports for locomotion in an ecologically relevant setting.

Challenges and Solutions for Integrating In Situ and Ex Situ Data

Clearly, it is far simpler to configure a kinematic data collection system in the laboratory setting than in the wild. As in any field study of positional behavior, visibility of the focal subjects in a forest setting often presents an issue. Individuals can move great distances over the course of just a few hours, sometimes appearing only for a moment in a particular camera view before moving on. To maximize the chance of collecting usable locomotor sequences, we restricted kinematic data collection to habituated individuals at Manombo Forest in Madagascar, with the assistance of graduate students and expert field guides well versed in their travel patterns. This provided the additional advantage of having data on the morphometrics of focal individuals, recorded in previous captures for behavioral studies. To minimize the impact of growth-related changes, we considered only subjects recorded as adults during previous captures in this study. This, along with the fact that these primates are critically endangered and quietly cryptic at Manombo, necessarily limited the sample size of strides in this analysis. We compensated for these challenges by maximizing the number of hours spent in the field each day, and by streamlining as much as possible the kinematic data collection setup.

Traditional kinematic setups can be heavy and cumbersome to move about within the field, not to mention the delicate and expensive nature of electronic equipment in terms of transport/repair. Designing a portable setup that could record locomotor kinematics in a remote setting required taking a large supply of lithium ion batteries and sufficient protection of the camera from rain. The solution outlined here utilizes a single rugged, lightweight and inexpensive camcorder/tripod setup for the field, with the potential for collecting 3D kinematic data using a simple trigonometric correction described in Stevens et al. (2006).

Future Directions for Linking Laboratory and Field Techniques

Despite a growing number of laboratory kinematic studies examining different aspects of primate arboreality, we still have relatively little information about the kinematic solutions primates employ to navigate their complex three-dimensional natural arboreal habitats. Merging data on "how often" primates employ different locomotor behaviors with specifically "how" they utilize natural substrates promises to be a significant avenue of research for biological anthropologists and primatologists. Melding laboratory and field approaches offers the hope of unraveling specific contributions of life history to both potential and actual locomotor behavior, e.g., in exploring the effects of ontogeny/aging, dimorphism, and gestation upon the solutions that primates have for solving problems posed by their ever-shrinking habitats. Quantifying the ways that habitat alteration can affect substrate use and locomotor energetics of different species will be particularly critical for informing conservation efforts. Preliminary work in rainforests of southeastern Madagascar suggests abundant opportunities exist for clear filming of habituated primates moving at will and at their own pace during their daily activities. Although animal visibility varies from site to site and season to season, it becomes increasingly evident that prospects are quite good for developing a larger bank of detailed, ecologically-relevant, kinematic data for primates engaging in their daily activities in the wild.

Conclusions

This study documents the effects of support orientation upon quadrupedal locomotion in *Eulemur*, and represents the first quantitative record of limb kinematics in the natural setting for the critically endangered *E. cinereiceps*. In both the laboratory and natural settings, forelimbs tend to be more protracted at touchdown on declines and hind limbs tend to be more retracted at lift-off on inclines. Moreover, individuals flex the elbows and knees more at midsupport on oblique branches, bringing the center of mass closer to the support, as evidenced by lower shoulder and hip distances from the substrate. This study represents a good test case for the integration of experimental and naturalistic data collection in the study of arboreal primate locomotor kinematics.

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