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3 Pitch control and speed limitation during overground deceleration in lemurid primates.

4

5 **Short title:** Lemurid pitch control

6

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15

16 **Abstract**

17 An animal's fitness is influenced by the ability to move safely through its environment.
18 Recent models have shown that simple aspects of body geometry - limb length and center
19 of mass (COM) position - appear to set limits for pitch control in cursorial quadrupeds.
20 Models of pitch control predict that the body shape of these and certain other primates, with
21 short forelimbs and posteriorly positioned COM, should allow them to decelerate rapidly
22 while minimizing the risk of pitching forward. We chose to test these models in two non-
23 cursorial lemurs: *Lemur catta*, the highly terrestrial ring-tailed lemur, and *Eulemur fulvus*,
24 the highly arboreal brown lemur. We modeled the effects of changes in limb length and
25 COM position on maximum decelerative potential for both species, as well as collecting
26 data on maximal decelerations across whole strides. In both species, maximum measured
27 decelerations fell below the range of pitch-limited deceleration values predicted by the
28 geometric model, with the ring-tailed lemur approaching its pitch limit more closely. Both
29 lemurs showed decelerative potential equivalent to or higher than horses, the only
30 comparative model currently available. These data reinforce the hypothesis that a relatively
31 simple model of body geometry can predict aspects of maximum performance in animals.
32 In this case, it appears that the body geometry of primates is skewed towards avoiding
33 forward pitch in maximal decelerations.

34 **Key words: Lemur catta, Eulemur fulvus, Deceleration, Pitch, Arboreality**

35

36

37 **Graphical abstract text**

38 Slowing down to a stop, possibly very quickly, is a vital part of primate behavior, but
39 carries risks of tumbling forward ‘over the handlebars’. The body shape of primates,
40 particularly tree-dwelling species, may help to prevent these types of falls.

41

42 **Introduction**

43 The ability to accelerate and decelerate quickly to catch prey or avoid predation is
44 critical to animal survival. Animals must be able not only to generate high speed through
45 muscular effort, but also speed up or slow down without generating excessive pitching
46 moments and causing the body to become unbalanced. The ability to control body pitch
47 appears to be influenced by body proportions, at least in dogs and horses (Williams, Tan,
48 Usherwood & Wilson, 2009). What remains an open question is whether other animals face
49 such limitations, and whether the ability to control pitch is an important factor that
50 constrains animal locomotor behavior, and exerts a selective pressure on limb anatomy.

51 In a defining paper on this topic Williams and colleagues (2009) demonstrated that
52 at relatively slow speeds the need to control pitching moments is the primary limiting factor
53 to maximum accelerations and decelerations in dogs and horses. In both these cursorial
54 species the perils of ‘popping a wheelie’ while accelerating or ‘diving over the handlebars’
55 while decelerating appears to be a greater factor in limiting acceleration and deceleration at
56 slower speeds than the limits potentially imposed by power production by limb extensor
57 muscles (Williams et al., 2009). At higher speeds muscular power production becomes the
58 primary limit to both acceleration and deceleration (Williams et al., 2009). Thus in their
59 model, the key factor determining the theoretical limits of pitching moments is body shape,

60 specifically the ratios of limb lengths to their moment arm around the center of mass
 61 (COM), the latter defined as COM position as a proportion of back length (Williams et al.,
 62 2009, equation 1.1. Figure 1).

$$63 \quad |\bar{a}_x| \leq \frac{gL_{cran}}{Lfore} \quad \text{equation 1.1}$$

64 Where \bar{a}_x is the constraint placed on horizontal acceleration by forward pitch, g is
 65 the acceleration due to gravity, L_{cran} the horizontal distance between the COM and the
 66 glenohumeral joint, L_{fore} the length of the animal's forelimb. This equation explores in an
 67 elegant way the body geometry of animals and the effect of the ability to resist pitch by
 68 incorporating only aspects of limb length, body length, and COM position. When the value
 69 for \bar{a}_x becomes greater than the ratio of gravity and COM position to limb length, forward
 70 pitching moments can no longer be countered, and the animal is in danger of going 'over
 71 the handlebars'. In this expression of the relationship mass would apply to both the \bar{a}_x
 72 (forward acceleration) and g (vertical acceleration) terms, and would therefore cancel out.
 73 The data in Williams et al. (2009) show how effectively this equation predicts pitch limits
 74 for horses and dogs, including demonstration of high pitch in dogs such that they
 75 sometimes miss a forelimb footfall at the beginning of an acceleration event. Thus, under
 76 this model (Williams et al., 2009) the length of the limb and position of the COM have a
 77 profound influence over the range of decelerations an animal can achieve while avoiding
 78 uncontrolled pitch.

79 Although the role of center of mass placement in introducing pitching moments is
 80 easily understood and imagined (the further back the COM is on the body the more the
 81 body will resist being pitched over the forelimbs), the relationship between limb length and

82 COM position is less intuitive. Although it may seem sensible that long forelimbs would
83 resist pitching, Williams et al. (2009) show that, all else being equal, longer limbs will
84 increase pitching moments around the COM resulting in an animal vaulting over its
85 forelimbs and pitching forward (nose-down) during deceleration. Therefore, the
86 combination of short forelimbs and a posterior COM provides the greatest resistance to
87 forward pitch during deceleration.

88 The model of Williams et al. (2009) appears to apply well to the cursorial mammals
89 studied in acceleration (dogs and horses) and deceleration (horses) and provides important
90 insight into selective pressures on body design. But it remains a question whether this
91 model also applies to other, non-cursorial quadrupedal animals. Here we chose primates
92 because of their adaptations to both terrestrial and arboreal movement. Primates are able to
93 run effectively on the ground and some, including the ring-tailed lemur studied here, do so
94 often. But primates also habitually walk and run on branches that are often small relative to
95 their body size and present a complex and discontinuous substrate. Therefore, being able to
96 avoid forward pitch is especially critical for their survival (even more so than avoiding the
97 backward pitching risked with acceleration), and primates appear to have anatomical and
98 behavioral adaptations for locomotion in an arboreal milieu (see Schmitt (2010) for a
99 review). The ability to quickly stop without tumbling forward is a fundamental problem for
100 all animals, but since it is especially critical for animals moving in trees, we propose to test
101 the idea that primate locomotor behavior and limb proportions will reflect that priority, by
102 avoiding issues of forward pitch during deceleration. Although great strides have been
103 made in understanding how primates cope with challenges of steady state locomotion,
104 decelerating remains a critical behavior which is not yet well studied, despite its

105 implications for a variety of behaviours that require decelerations for both stopping and
106 turning maneuvers. This leaves a gap in our understanding of the selective pressures that
107 influence primate body shape, as well as the factors which limit deceleration potential in
108 primates.

109 Hence we predict that primates should show body proportions that allow them to
110 decelerate over a wide speed range without excessive forward pitch. Primates are known to
111 have anatomical features - including limb length and patterns of force distribution on the
112 limbs - that distinguish them from most other quadrupedal mammals (see Schmitt (2010)
113 for a review). Most non-primate mammals are described as having an anteriorly positioned
114 COM, with greater vertical peak forces and vertical impulses on their forelimbs (See Lee,
115 Bertram & Todhunter, 1999, Witte, Knill & Wilson, 2004, and Henderson, 2006 for
116 examples in dogs, horses and, elephants), while most primates exhibit the opposite
117 condition (Demes, Larson, Stern, Jungers, Biknevivius & Schmitt, 1994; Kimura, 1992;
118 Kimura, Okada & Ishida, 1979; Vilensky & Larson, 1989; Reynolds, 1985), with a more
119 posteriorly positioned COM, as evidenced by the higher weight support by the hindlimbs
120 compared to their forelimbs. Expressed this way, in terms of force distribution, this
121 difference can be seen as a dynamic, rather than strictly anatomical condition (for a
122 discussion of the anatomical issues in primates see Vilensky and Larson 1989), which may
123 be achieved by several possible mechanisms, including limb position, muscle activity, or
124 relative limb compliance (Schmitt, 1999, Schmitt & Hanna, 2004; Larson & Stern, 2009,
125 Raichlen, Pontzer, Shapiro & Sockol, 2009; Young, 2012).

126 These same variables may be critically important for pitch control since pitching
127 moments are created by force application on the ground at some distance from the animal's

128 COM, the position of which is measured using the ratio of peak vertical forces between fore
129 and hindlimbs. Furthermore, lemurid primates have relatively short forelimbs, both
130 absolutely (Napier and Napier, 1967; Fleagle, 2013) and effectively (general observation
131 from video and illustrations and confirmed by data within this paper): lemurid forelimbs,
132 like many other primates, undergo high degrees of elbow flexion and yield during stance
133 phase (Larney and Larson, 2004; Schmitt, 2010), shortening their effective limb length
134 (Larney & Larson, 2004; Larson, Schmitt, Lemelin & Hamrick, 1999; Larson, Schmitt,
135 Lemelin & Hamrick, 1999; Larson, Schmitt, Lemelin & Hamrick, 2001; Fleagle, 2013).
136 There have been a variety of adaptive explanations for this combination of reduced peak
137 loads and limb compliance, including the need to protect relatively gracile forelimbs and
138 the requirements of locomotion and foraging on thin flexible branches (Schmitt & Hanna,
139 2004; Larney & Larson, 2004).

140 Here we suggest an additional adaptive phenomenon: that a more posterior COM
141 and relatively short (absolutely and effectively) and compliant forelimbs compared to the
142 hindlimbs provide lemurs and many other arboreal primates with particularly high pitch
143 limits in deceleration, and therefore greater decelerative potential than other animals. This
144 does not negate other ideas about primate limb form. Rather it suggests that primate limb
145 behavior and anatomy may also be advantageous when decelerating. Although one must be
146 cautious since lemurids do not represent all primates, understanding how their fundamental
147 adaptations may also control pitch would lend additional information and hypotheses about
148 the adaptive origin of primates in an arboreal environment.

149 To test these ideas, we chose two lemurid primate species to examine whether the
150 ability to decelerate rapidly is influenced by body and limb design geometry in a non-

151 cursorial species in the way it appears to be in dogs and horses. This paper focuses on
152 deceleration for both practical and theoretical reasons. First, we were able to collect a large
153 sample of data on these primates slowing down from the maximum speed but considerably
154 less data on acceleration to maximum speed. Secondly, following the models presently
155 available (Williams et al., 2009), we hypothesize that relatively short (absolutely and
156 effectively) forelimbs compared to hindlimbs of many primates and the relatively high peak
157 hindlimb forces on those primates will enhance their ability to decelerate. These very
158 factors may present an inherent tradeoff between deceleration potential and acceleration
159 potential. As such, we see deceleration as a selective factor, particularly for those animals
160 living in trees where changes in direction and discontinuities in substrate make being able
161 to slow down rapidly without pitching over especially important. Therefore we focus on
162 whether control of body pitch during deceleration appears to follow the same rules for these
163 primates as it does for horses.

164

165 **Materials and Methods**

166 Animals: Our subjects were 3 individuals each from two species of strepsirrhine
167 primates from the Duke Lemur Center (DLC) in Durham, NC: *Lemur catta* (Linnaeus,
168 1758) and *Eulemur fulvus collaris* (Geoffroy, 1796). All of the subjects were adult at the
169 time of study, all three *Lemur catta* were male, two *Eulemur fulvus collaris* were male and
170 one was female. The animals were maintained in accordance with United States
171 Department of Agriculture regulations and with the National Institutes of Health Guide for
172 the Care and Use of Laboratory Animals. Protocols were approved by the Institutional
173 Animal Care and Use Committee of Duke University (#A319-10-12). Both species received

174 primarily fruit, vegetables, and monkey chow (Monkey Diet™, PMI Feeds, St. Louis, MO).
175 Water was freely available, and animals were fed daily. The animals were housed socially
176 in small groups of 2–6 animals, in large indoor enclosures (5–15 m² at the base, 5 m in
177 height), which had suitable enrichment and natural light. There is an indoor portion of
178 cinder block and chain link facing a hallway for husbandry staff and an outdoor portion
179 enclosed by chain-link fencing that allowed exposure to the elements. The two portions are
180 separated by a wall with small doors that are open during the day. Animals could enter and
181 exit the indoor portion at will during the day. The enclosures include complex enrichment
182 material. These include ropes, swings, suspended walkways, metal and plastic containers,
183 durable rubber balls and other appropriate primate enrichment. The animals are attended to
184 by DLC staff multiple times a day and thus have regular interactions both with their cage-
185 mates and with humans. They are never handled aside from specific husbandry purposes.
186 During warm months (April through October) animals often have access to large outdoor
187 enclosures of multiple acres. Testing was carried out in a research room on an enclosed
188 runway described below. Animals were captured by hand by DLC staff. Animals are
189 trained for such captures and usually such events invoke minimal stress. They were carried
190 in an appropriate animal carrier to the research room. Animals were never sedated or
191 restrained in any way beyond the manipulation necessary to move them to the experimental
192 area. No animals were sacrificed in this protocol. The experiment itself involved freely
193 chosen movement speeds in a large enclosure and repeated food rewards. The food rewards
194 are small pieces of fruit or nut meats matched appropriately to diet and limited so as not to
195 affect appetite for normal feeding significantly.

196 Here we examine the effect of changes in effective limb length and COM cranio-
197 caudal position on pitch limits in two species of prosimian primate – the brown lemur,
198 *Eulemur fulvus*, and the ring-tailed lemur, *Lemur catta*. These two species are very similar
199 in size and morphology (see Fleagle, 2013 and Rowe, 1996 for a review). It is the case that
200 the grasping hands and feet of primates may allow them to counteract some of the pitching
201 moments associated with deceleration on arboreal supports (though see Schmitt & Lemelin,
202 2002 for some reason for caution with respect to hand postures and wrist flexion used by
203 arboreal animals), however, in order to directly compare maximal deceleration abilities of
204 prosimian primates against those calculated by Williams et al. (2009), we collected data
205 using a flat board rather than a raised pole. This model is designed to test the very simplest
206 case, absent other confounding factors, representing a first step towards understanding
207 primate deceleration. We recognize that behaviors on arboreal supports may vary from the
208 flat substrate and look forward in the future to examining those behaviors as well. At
209 present we are asking whether the model of Williams et al. (2009) applies to non-cursorial
210 animals running on the ground.

211 A total of 91 maximally decelerating strides were obtained from 3 adult *L. catta* (n
212 = 32) and 3 adult *E. fulvus* (n = 59). Animals moved freely along a 0.7 m wide x 2.1 m long
213 runway, and were video recorded at 60 Hz using a Sony Handycam (HDR-SR11, Sony,
214 Japan) placed at a distance of 2 meters perpendicular to their path of travel. Animals were
215 encouraged to move at a variety of speeds along a flat runway, and decelerated towards a
216 solid barrier which completely blocked their progress. Animals were allowed to walk and
217 run freely, and were encouraged to decelerate at their maximum comfortable rate from
218 whichever gait they chose. The animals were encouraged to move quickly away from one

219 end of the enclosure and travel toward the barrier. They often hurried away from the
220 investigator when approached, and received food rewards after a complete traverse of the
221 runway. The enclosure gave them room to reach comfortable speeds and take more than
222 three full strides on the straight before encountering the barrier. However, the animals
223 could begin their run at the back of the enclosure, following an elliptical race-track-like
224 path before reaching the straight recording area. Animals were comfortable in the
225 enclosure, having taken part in numerous studies in that environment over a period of
226 several years. Observations of the same animals in this enclosure and in outdoor settings,
227 along with comparison to previous studies on the same species (Franz, Demes & Carlson,
228 2005; O'Neill & Schmitt, 2012), gave us confidence that that animals were using fast
229 walking and running speeds and decelerating near their maximum rate.

230 Initial velocity and deceleration across whole strides were obtained by digitization
231 of the tip of the nose in DLT dataviewer (Hedrick, 2008) over two frames at limb
232 touchdown (to obtain initial velocity) and the next touchdown of the same limb (to obtain
233 final velocity). Total deceleration was obtained by subtracting final from initial velocity,
234 divided by the time between these two events, and lead and trail limbs were assumed to be
235 behaving symmetrically.

236 To examine the decelerative pitch limits for these species a range of limits were
237 calculated using the methods of Williams et al. (Williams et al., 2009, equation 1, table 2).
238 Forelimb and hip-glenohumeral joint length were measured in ImageJ (NIH, Bethesda,
239 MD) from midstance values of both *L. catta* and *E. fulvus* during steady state walking as a
240 conservative estimate of limb length. Two pitch limits were calculated for each species
241 using mid-stance effective limb length values, and estimates of COM position (as a

242 proportion of back length) with either a non-primate-like COM position ‘ D_{COM} ’ (as used by
243 Williams et al. (2009) using values from (Usherwood, Williams & Wilson, 2007), Figure 2,
244 line D_{COM} , for sample curves see Figure 3), and an approximate primate-like COM position
245 ‘ P_{COM} ’ (40% back length, based on dynamic COM values suggested by vertical force
246 distribution in locomotion, Figure 2, line P_{COM}). Relative deceleration magnitudes were
247 also calculated for each empirical data value as a proportion of the conservative dog-like
248 pitch limits (D_{COM}) for each species.

249 To further explore the relationship between primate forelimb posture and COM
250 location, the model was then varied for values of COM position between 30% and 80% of
251 measured back length, and limb lengths between 80% and 120% of measured forelimb
252 length values, forming a sensitivity analysis around estimates of potential posture changes
253 (table 1, maximum estimated limit value Figure 2, line Max). Extreme pitch limit values
254 were also calculated for values of COM position between 10% and 90% body length, and
255 50% and 150% limb length for comparison (table 1). This is a very conservative approach
256 and produces a large range of possible values. As a result the pitch limits indicated in
257 Figure 2 represent a broad spectrum of anatomical arrangements that might be considered
258 to characterize the dynamic geometry of primates, with further extreme values available in
259 table 1.

260 Linear regressions of deceleration versus initial velocity, Wilcoxon sum rank tests
261 for differences between both relative and absolute deceleration magnitudes, and all model
262 calculations were performed in MATLAB (R2012a, Mathworks, Natick, MA).

263

264 **Results**

265 Based on the geometric model used here (Williams et al., 2009), both lemur species
266 have pitch limits that are relatively high (more negative) compared to previously published
267 data for horses (Figure 2; Williams et al., 2009), which are the only data available for
268 comparison. In such a direct comparison, without accounting for body size, it appears that
269 lemurid species have the ability to achieve greater decelerations without inducing forward
270 pitch compared to a cursor like the horse. A comparison across species of such significant
271 body size differences should be viewed with caution, so we also compared within our
272 sample; comparing the more cursorial and terrestrial species, the ring-tail lemur, with the
273 more arboreal brown lemur. The calculated pitch limits are greater (more negative) for the
274 more arboreal brown lemur than the ring-tailed lemur. Therefore, while a Wilcoxon sum
275 rank test shows no significant difference in measured deceleration magnitudes between the
276 brown and ring-tailed lemurs ($p = 0.34$), there is a significant difference between the two
277 species in the measured deceleration values relative to the conservative pitch limit
278 calculated from the geometric model ($p = 0.0054$; table 2). Neither species achieves
279 decelerations which cross the conservative pitch limit (D_{COM}) predicted by our sensitivity
280 analyses (Figure 2), though the ring-tailed lemur comes much closer to this limit than the
281 brown lemur. In that context, the ring-tailed lemur exhibits a greater potential to pitch
282 forward and fall than the brown lemur. Deceleration shows a significant increase with
283 increasing speed in both species (table 3).

284

285 **Discussion**

286 The morphological and kinematic data recorded here for two primates, in
287 conjunction with the pitch and muscle power limit model of Williams et al. (2009), suggest

288 that lemurid primates are especially well adapted to the challenges of managing pitching
289 moments, and avoiding falling forward when decelerating. Lemurids share a bauplan with
290 many other quadrupedal primates – relatively short (absolutely and effectively forelimbs
291 compared to their hindlimbs, a relatively long back, and a more caudally positioned COM –
292 that may be well suited to achieving rapid decelerations while avoiding forward pitch.
293 Forward pitch associated with deceleration is inherently more hazardous than backward
294 pitch associated with acceleration in terms of avoiding potentially fatal falls in a complex
295 discontinuous environment. Indeed this body geometry may represent a significant tradeoff
296 between deceleration potential and acceleration potential in arboreal animals, which
297 warrants further study.

298 Conservative pitch limits on decelerative potential were calculated at -7.73 ms^{-2} and
299 -5.74 ms^{-2} for the brown and ring-tailed lemurs respectively. These values are greater than
300 those seen for the much larger horses studied by Williams et al. (2009, -3.89 ms^{-2}). In
301 decelerating horses a parabolic relationship was seen between deceleration and speed, with
302 the inflection point at around 5.0 ms^{-1} , however at equivalent speeds (table 4) the
303 decelerations of both lemur species continue to increase in magnitude (become more
304 negative). Hence it may be the case that neither lemur is limited by the ability to produce
305 the muscle power needed for successful deceleration within the range of speed values
306 observed, as was seen in the horses. This is an area that deserves further study and a
307 broader, size-matched comparative sample.

308 These results provide a new perspective on primate adaptations and open up areas
309 for future investigation. Since the only available comparative model to date is the horse, a
310 large, terrestrial animal likely operating at the opposite extreme to primates – prioritizing

311 acceleration abilities over deceleration since it habitually runs on flat ground – future work
312 is needed to calculate values for intermediate species in both ecology and body size. It
313 would also be remiss to ignore another primate feature - grasping hands and feet. The
314 ability to use prehensile hands and feet to grip arboreal substrates may also play a large part
315 in maintaining a primate's on-branch security, and may allow primates to counteract some
316 of the pitching moments associated with deceleration. However, it is also possible that such
317 a mechanism, relying on the coordination of incredibly fast reflexes and enough time for
318 each footfall to transmit a sufficient quantity and direction of force, would be of limited
319 effectiveness when coming to a sudden stop in such a precarious environment.

320 Finally, although not the main focus of this study, it is worth speculating on the
321 effect of habitual substrate use in these two primates and the implications of these data for
322 future studies. The brown lemur is almost exclusively arboreal, while the ringtail is the
323 most terrestrial of all the prosimian primates, and exhibits gait mechanics that are more
324 similar to those of a dog than those of the brown lemur (O'Neill & Schmitt, 2012). Though
325 both lemurs exert higher peak forces on their hindlimbs compared to their forelimbs, the
326 disparity is also more extreme in the brown lemur (Franz et al., 2005). The geometry of the
327 brown lemurs, particularly their shorter forelimbs, gives them greater potential for
328 deceleration without approaching the point where they are likely to fall forwards. Hence,
329 while their absolute deceleration magnitudes are equal to those of the ring-tailed lemurs,
330 their decelerations relative to their pitch limits are significantly smaller, potentially
331 decreasing their chances of risking a fall. These data may hint at further evidence that
332 arboreal animals may choose to 'play it safe' when it comes to locomotion, avoiding
333 extreme behaviors which might cause perturbations on thin branches, destabilizing their

334 locomotor substrate and increasing their visibility to predators (Schmitt et al., 2006). We
335 propose here that this anatomical arrangement and mechanism of increasing safety while
336 decelerating may well be an important contribution to primates' success in arboreal
337 locomotion, and their adaptation to and radiation in an arboreal environment. This study
338 combined with that of Williams et al. (2009) suggest a productive area for further study in
339 other primates and cursorial and non-cursorial animals.

340

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342 Data are archived at Duke University on servers maintained by the Evolutionary
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347

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424 **Tables**

425

426 **Table 1.** Pitch limits and pitch limit ranges. Calculated using equation 1.1, as derived from
 427 equation 1.1 of Williams et al. (2009). * denotes values displayed on Figure 2. D_{COM} ,
 428 measured limb length and dog-like COM position (identical to the calculations of Williams
 429 et al., 2009), P_{COM} , measured limb length and primate-like COM position (based on, Max,
 430 maximum reasonable limit from COM position values between 30-80% back length, 80-
 431 120% limb length, with the minimum reasonable limit calculated from the same range of
 432 values. Maximum and minimum extreme limits as calculated from COM position values of
 433 10-90% back length, 50-150% limb length.

	Brown lemur (ms^{-2})	Ring-tailed lemur (ms^{-2})
Dog limit (D_{COM}^*)	-7.73	-5.74
Primate limit (P_{COM}^*)	-10.54	-7.83
Minimum reasonable limit	-2.93	-2.17
Maximum reasonable limit (Max*)	-15.37	-11.41
Minimum extreme limit	-1.17	-0.87
Maximum extreme limit	-31.62	-23.48

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436 **Table 2.** Means and standard deviations of decelerations. Deceleration means and standard
 437 deviations, both absolute magnitudes and as proportions of the conservative pitch limits
 438 calculated for each species. Sd, standard deviation, n_{a-f} , sample sizes from each individual.

		Mean	Sd
Absolute	<i>E. fulvus</i> (n = 59) (ms ⁻²) (n = 59; n _a = 16; n _b = 29; n _c = 14)	-2.07	1.20
	<i>L. catta</i> (n = 32) (ms ⁻²) (n = 32; n _d = 6; n _e = 10; n _f = 16)	-2.41	1.38
Relative	<i>E. fulvus</i>	0.27	0.15
	<i>L. catta</i>	0.42	0.24

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443 **Table 3.** Linear regression equations, coefficients of determination (R^2) and sample sizes
 444 (n) for the two datasets of deceleration (negative acceleration) values with respect to
 445 velocity (V_0). In both species the slope of the regression line is significantly different from
 446 zero (t statistic) and the fit of the datapoints to the regression line is significant (f statistic).

	n	Linear regression equation	Coefficient of determination (R^2)	P-value (t statistic)	P-value (f statistic)
Brown lemur	59	$y = -1.87x + 2.06$	0.44	<0.01	<0.001
Ring-tailed lemur	32	$y = -1.82x + 1.66$	0.57	0.02	<0.001

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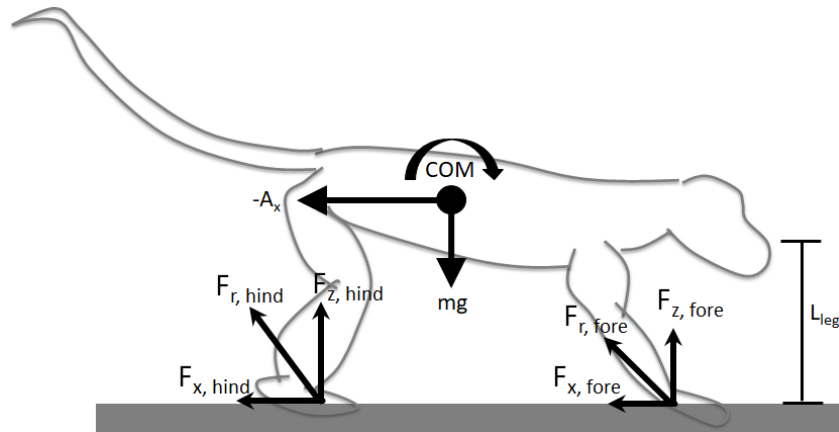
449 **Table 4. Body parameters used in pitch limit modeling, and equivalent speeds for the**
 450 **brown lemur, ring-tailed lemur and horse.** 3.0 ms⁻¹, the upper limit of speeds observed
 451 in the slowest animal, a brown lemur, was used to calculate Froude numbers based on both
 452 brown lemur hindlimb and forelimb length: a Fr of 2.1 for the hindlimb and 2.5 for the
 453 forelimb. For comparison between brown and ring-tailed lemurs and the horse values
 454 reported in Williams et al. (2009) equivalent speeds in ms⁻¹ were back calculated from
 455 these Fr values using limb lengths for the ring-tailed lemur and horse. Hence a brown lemur
 456 travelling at 3.0 ms⁻¹ is travelling at roughly the same relative speed as a ring-tailed lemur
 457 moving at 3.7 ms⁻¹, and a horse moving at 7.6 ms⁻¹.

	Back length (m)	HL length (m)	Speed (ms ⁻¹) HL (Fr 2.1)	FL length (m)	Speed (ms ⁻¹) FL (Fr2.5)
Brown lemur (average)	0.26	0.20	3.0	0.14	3.0
Ring-tailed lemur (average)	0.32	0.32	3.7	0.24	3.8
Horse (Williams et al., 2009)	1.22	1.32	7.6	1.31	9.0

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461 **Figure Legends**

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463 **Figure 1.** Modified from figures 1 and 2c of Williams et al. 2009 to show the effects of
 464 deceleration (rather than acceleration) on the COM (center of mass) of a generalized
 465 primate. More negative horizontal forces (F_x) will direct the GRF (ground reaction force)
 466 behind the COM and produce nose-down pitch. F_x , F_z and F_r represent horizontal, vertical
 467 and resultant ground reaction forces respectively, mg represents the vertical effect of
 468 gravity on the COM, $-A_x$ the negative acceleration of the resultant deceleration, and L_{leg} ,
 469 the length of the forelimb.

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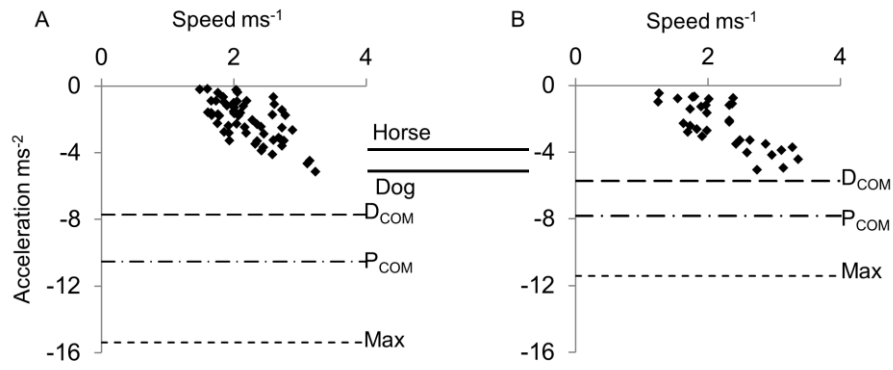
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478 **Figure 2.** Deceleration versus velocity in brown and ring-tailed lemurs. A brown lemurs (N
 479 = 59) and B ring-tailed lemurs (N = 32). Pitch limits (D_{COM} and P_{COM}) are calculated using
 480 Williams et al. (2009, equation 1) using the measured forelimb length for each primate
 481 species (brown lemur in A, ring-tailed lemur in B, Table 4) and either a dog-like center of
 482 mass (D_{COM}) or primate-like center of mass (P_{COM}); Max, the maximum possible pitch
 483 limit defined by the conservative model; and for comparison: Horse, the pitch limit
 484 predicted for the horses used in Williams et al. (2009); Dog, the pitch limit predicted by the
 485 model of Williams et al. (2009) for a dog of average body geometry, calculated from
 486 published values (Usherwood et al., 2007).

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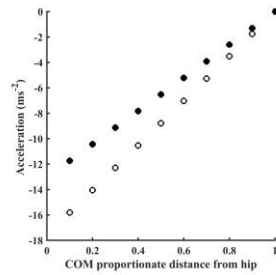
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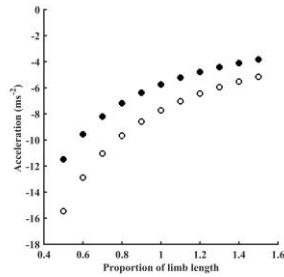
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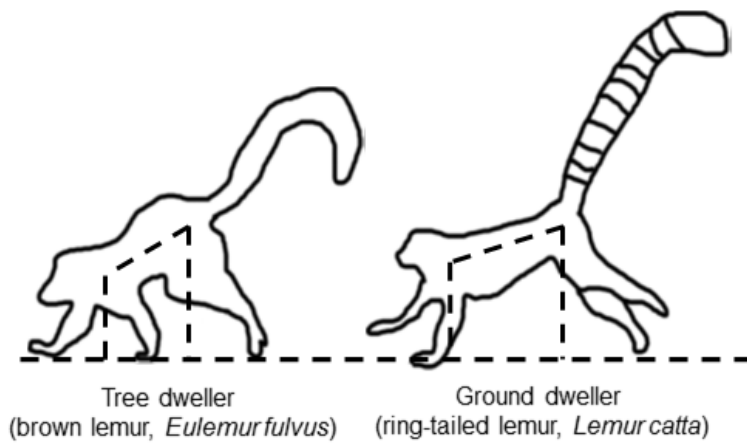


495 **Figure 3.** Sample sensitivity analyses. A. Sensitivity of deceleration limits calculated from
 496 equation 1.1 to changes in COM position for a measured limb length (Table 4). In the
 497 brown lemur (open circles), an animal with shorter forelimbs, there is a proportionately
 498 greater effect on pitch limits in deceleration when the COM is placed closer to the hip
 499 (where the left of the x-axis is closer to the hip, and right closer to the shoulder) as
 500 compared to the ring-tailed lemur (filled circles). B. Sensitivity analysis of deceleration
 501 limits calculated from equation 1.1 to changes in limb length for a given COM position
 502 (taken here as the ‘non-primate-like position’ of 56% Williams et al., 2009; Lee et al.,
 503 1999). Brown lemur values are seen in open circles, the ring-tailed lemur in filled circles.
 504 Shorter limbs have a proportionally greater effect on pitch limits (where the left of the x-
 505 axis shows shorter limbs, and the right longer limbs). Hence more crouched postures, those

506 seen often in quadrupedal primates (Schmitt, 1999) and stealthily walking cats (Bishop, Pai
 507 & Schmitt, 2008) increase pitch limits in deceleration. This effect is also seen in
 508 greyhounds during high accelerations (Williams, Usherwood, Jespers, Channon & Wilson,
 509 2009).

510

511 Graphical abstract and graphical abstract text



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513 Slowing down to a stop, possibly very quickly, is a vital part
 514 of primate behaviour, but carries risks of tumbling forward
 515 'over the handlebars'. The body shape of primates,
 516 particularly tree-dwelling species, may help to prevent these
 517 types of falls.

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