

The Murphy number: how pitch moment of inertia dictates quadrupedal walking and running energetics

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1 Abstract

2 Most quadrupedal mammals transition from a four-beat walk to a two-beat run (e.g. trot), but some
3 transition to a four-beat run (e.g. amble). Recent analysis shows that a two-beat run minimizes work
4 only for animals with a small pitch moment of inertia (MOI), though empirical MOI were not reported.
5 It also remains unclear whether MOI affects gait energetics at slow speeds. Here I show that a particular
6 normalization of the pitch moment of inertia (the Murphy number) has opposite effects on walking and
7 running energetics. During walking, simultaneous fore and hindlimb contacts dampen pitching energy,
8 favouring a four-beat gait that can distribute expensive transfer of support. However, the required pitching
9 of a four-beat walk becomes more expensive as Murphy number increases. Using trajectory optimization of
10 a simple model, I show that both the walking and slow running strategies used by dogs, horses, giraffes and
11 elephants can be explained by work optimization under their specific Murphy numbers. Rotational dynamics
12 have been largely ignored as a determining factor in quadrupedal locomotion, but appear to be a central
13 factor in gait selection.

14 1 Background

15 Despite their incredible morphological diversity, cursorial quadrupedal mammals typically use stereotyped
16 gaits. As speed increases, mammals commonly transition from a four-beat walk at slow speeds to a two-beat
17 trot or pace (where beats are distinct contact events). We see the 4 → 2 pattern across disparate families,
18 such as equids (horses [1]), canids (dogs [2]), bovids (sheep and gazelle [2, 3, 4]), camelids (dromedaries [5])
19 and antilocaprids [6].

20 This pattern is surprising from an energetic perspective. A simple accounting of energetic losses in gait is
21 to consider leg contacts as collisions acting on the center of mass (COM) [7]. This perspective explains many

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22 phenomena in locomotion, including the pre-heelstrike pushoff in bipedal walking [8], the smooth trajectory
23 of gibbon brachiation [9], why individuals use a flatter running gait in reduced gravity [10], and the leg
24 sequence in transverse galloping [7].

25 The point-mass collisional perspective posits that frequent, evenly-spaced collisions are better than infre-
26 quent, irregular collisions. To optimize work, a quadruped should use as many contacts as possible during a
27 stride; a pronk costs twice as much as a trot, which costs twice as much as a four-beat amble (see supplemental
28 information for a simple derivation).

29 Why, then, do so many mammals trot? It is unlikely that a slow, four-beat running mode is physically
30 impossible for trotters. The “gaited” horses have been bred to exhibit such gaits¹. Notable examples are the
31 tölt of the Icelandic horse [11], the amble of the American Saddlebred Horse, and the running walk of the
32 Tennessee Walking Horse [12]. Given the few morphological differences between gaited and non-gaited breeds,
33 it seems less likely that natural populations are physically constrained from performing a four-beat run, and
34 more likely that they reject it (whether through behavioural, developmental or evolutionary programming;
35 *e.g.* [13]).

36 In a recent article, Usherwood resolved the paradox by considering the energy of pitching the body [14].
37 Assuming ground-contact forces are axial to the leg, then foot contact in a four-beat gait induces pitching,
38 but a two-beat gait can avoid it. The question, then, is when do the energetics of pitching outweigh the
39 energetics of COM translation? When pitching energetics dominate, trotting should be optimal, and when
40 translation dominates, tölting should be.

41 Usherwood [14] showed that the ratio of translational to rotational kinetic energy is related to the
42 dimensionless group

$$\hat{I} = \frac{I}{mL^2}, \quad (\text{The Murphy number}) \quad (1)$$

43 originally defined by Murphy [15] (cited in [16]) with relation to the stability of bounding. In this equation,
44 m is body mass, I body pitch moment of inertia (MOI) about the COM, and L is half the shoulder-hip
45 distance. This dimensionless MOI (called hereafter the “Murphy number” for expediency and in honour
46 of its discoverer), is exactly the ratio of the change in translational to rotational kinetic energy imparted
47 to a free object by a generating impulse perpendicular to L (supplemental information). For $\hat{I} < 1$ more
48 rotational energy is imparted than translational, and the opposite is true for $\hat{I} > 1$ (figure 1).

49 For short stride times, tölting work is related to trotting work by (supplemental information)

$$W_{\text{tölt}} \approx \frac{W_{\text{trot}}}{2} (1 + \hat{I}^{-1}). \quad (2)$$

¹ Four-beat gaits are desirable as they exhibit less oscillation of the COM, resulting in a smoother ride for the human in the saddle.

50 For large Murphy numbers, the point-mass analysis is justified; no energy goes into pitching, and a tölt is
51 cheaper. For very small Murphy numbers, the rotational term dominates, all the energy goes into pitching,
52 and a trot is cheaper. But when $\hat{I} = 1$, the cost of tölting and trotting are equal. In general, a four-beat run
53 is optimal when $\hat{I} > 1$, but when $\hat{I} < 1$, a two-beat run is optimal.

54 This insight might point to why some mammals deviate from a two-beat run at moderate speeds. Ele-
55 phants and many primates use a four-beat amble at trotting speeds [17, 18]; giraffes and ring-tailed lemurs
56 transition directly from a walk to a canter [6, 19]. $\hat{I} > 1$ implies either that a significant portion of an organ-
57 ism’s mass lies outside its torso, or some mass is positioned a large distance away from the COM (relative
58 to hip-shoulder length). It seems plausible that the large heads of elephants, the long and/or massive tails
59 of some primates, and the long necks of giraffes might push their Murphy numbers beyond unity, but this
60 was not tested by Usherwood [14].

61 While rotational dynamics and the Murphy number would seem to rectify the two-beat running paradox,
62 it raises another question: why is quadrupedal walking typically four-beat? A mammal using a four-beat walk
63 exhibits pitching of the back [20, 21]. If these rotational energies are large, shouldn’t the same arguments
64 for the trotting-tölting tradeoff apply?

65 Four-beat walking benefits from distributed contacts interspersed with passive vaulting phases, where the
66 system dynamics in stance resemble a four-bar linkage [22]. To maintain passive vaulting, a pitching torso
67 is necessary, and the pitching direction must be reversed on each transfer of support. This means angular
68 momentum must be absorbed and resupplied with every step². The orientation of the body at transfer of
69 support is predetermined by the geometry of the four-bar linkage, which is independent of the body’s mass
70 or MOI. Likewise, if step-length and speed are predetermined, then the time between hind and fore transfers
71 of support is independent of MOI. Since the rotational speed is independent of MOI, pitching energy should
72 be *proportional* to MOI— not inversely proportional, as in running (figure 1).

73 We would therefore expect the Murphy number to have the *opposite* effect on the energetics of walking as
74 compared to running. At large \hat{I} , a two-beat walk should be favoured to avoid costly pitching at the expense
75 of larger COM collisions. At low \hat{I} , the optimal strategy should be to distribute contacts in a four-beat walk,
76 but switch to a pitch-free two-beat run at higher speeds— the common $4 \rightarrow 2$ pattern.

77 However, mammals that avoid two-beat running typically do *not* avoid four-beat walking; the walking
78 gaits of elephants, giraffes, and ambling primates appear to be four-beat [17, 23, 18, 24]. It is possible
79 that their gait transition patterns are explained by subtle dynamical effects overlooked by these heuristic
80 arguments.

81 I examine the energetics consequences of changing Murphy number and speed through trajectory opti-

² It is possible that the braking impulse freely transfers some of the rotational energy into translation, though for simplicity this is assumed small.

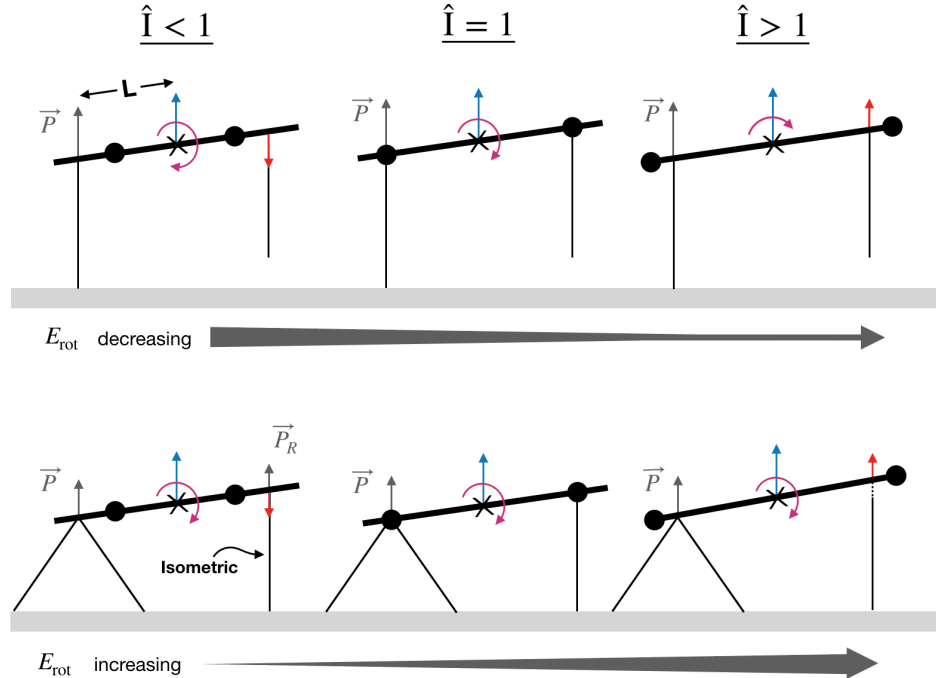


Figure 1: Heuristics showing why Murphy number has opposite effects on walking and running energetics. An impulse \vec{P} is generated at the hindlimbs and produces an equal change in center of mass velocity (blue arrow) and translational kinetic energy (E_{trans}) across all cases. (*Upper row*) In four-beat running as Murphy number increases (left to right), the angular velocity (purple arrow) and rotational energy (E_{rot}) decrease. When $\hat{I} < 1$, $E_{\text{rot}} > E_{\text{trans}}$ and a two-beat gait should be favoured. (*Bottom row*) In four-beat walking, the impulse from hindlimb transfer of support generates a reaction impulse at the forelimbs (\vec{P}_R) for $\hat{I} < 1$, as in this condition the induced forelimb velocity change is downward (red arrow). Because of this, the angular velocity in a four-beat walk does not change as Murphy number increases. However, the rotational energy increases proportionally with MOI. A two-beat gait should be favoured for some $\hat{I} > 1$ when $E_{\text{rot}} > E_{\text{trans}}$. For $\hat{I} > 1$, the impulse \vec{P} causes a positive change in forelimb vertical velocity. However, if forces are not instantaneous, the forelimb can compensate by reducing its applied force, maintaining a constant pitch rate.

82 mization of a simple quadrupedal model with a work-based cost function. I also use published data to test
 83 the hypothesis that Murphy number is a predictor of differences gait choice between quadrupedal mammals.
 84 Finally, using the results of the model, I point to interesting consequences of Murphy number on optimal
 85 ground reaction forces, and why point-mass dynamics are insufficient to explain quadrupedal walking.

86 2 Methods

87 2.1 Computational modelling and optimization

88 The quadrupedal model is planar and based on the methodology of Polet and Bertram [25]. Legs are massless
 89 prismatic actuators; limbs cannot generate torque about their respective attachment points to the torso. For
 90 simplicity, limb lengths are equal to inter-limb spacing ($2L$), and the COM is located halfway between the

91 fore and hind limbs.

92 There are a few noticeable differences between the present simulation methodology and that of [25]. First,
93 I constrain the analysis to symmetrical gaits. I compute optimal gaits using trajectory optimization (direct
94 collocation) over the *half* stride cycle. A full stride cycle can be generated by repeating the solution in the
95 second half of the cycle. Since the body is fully symmetrical about the torso center, torso pitch angle can
96 be as high or low as $\pm\pi$, and I do not impose a limb excursion constraint. Some bipedal solutions emerged
97 as locally optimal on occasion. These were eliminated from the analysis *post hoc*.

98 Following [25], the present model uses an objective combining limb work with a penalty proportional
99 to the integral of force-rate squared and complementarity violation terms. The force-rate penalty smoothes
100 otherwise impulsive work-minimizing solutions, and is otherwise presently not of interest. Its normalized
101 penalty coefficient is 3×10^{-5} , 100 times smaller than the value used in [25].

102 Like the model of [25], the present trajectory optimization setup uses complementarity constraints to
103 allow the optimizer to determine the stepping sequence. Optimizations were carried out with *hp*-adaptive
104 quadrature in GPOPS-II (v. 2.3) and the NLP solver SNOPT (v. 7.5).

105 I define a non-dimensional stride length and mean horizontal speed as $D' = D/L_H$ and $U' = U/\sqrt{gL_H}$
106 respectively, where L_H is hindlimb length (equal to $2L$ in the model). These correspond to a common
107 normalization seen in the literature [26]. I use the prime superscript $(\cdot)'$ and the hat diacritic $\hat{(\cdot)}$ to denote
108 variables normalized by hindlimb length or half inter-limb spacing respectively.

109 D' was determined from U' through an empirical relationship for walking cursorial mammals [26]:

$$D' = 2.4 (U')^{0.68} \quad (3)$$

110 Grid points were selected between $0.25 \leq \hat{I} \leq 10$ and $1.5 \leq T' \leq 4$. The latter represents the lowest and
111 highest stride times observed by [26] among cursorial mammals. $T' = D'/U'$ was used as target inputs to the
112 model, as it determines running energetics more directly than speed (see analytical analysis in supplemental
113 information).

114 An initial search took place at grid points on $T' = 0.25$ intervals, and $\hat{I} = 0.25, 0.5, 0.75, 1, 1.25, 2,$
115 $5,$ and 10 . Afterwards, grid points were added close to identified transition zones between gaits. 50 initial
116 guess were used for each $T' > 2.5$ condition, while 100 initial guesses were used for $T' \leq 2.5$. Convergence
117 was difficult at the slowest speeds ($T' = 4$), and several outliers were identified as isolated gaits of a certain
118 number of beats surrounded by solutions with a different number of beats. To these solutions, another 50
119 guesses were added to better converge to the optimal solution. Initial guesses were formed by selecting from
120 a uniform random distribution across each variable's range at 16 uniformly-spaced grid points.

121 For a given parameter combination, the lowest-cost solutions were selected among all local minima dis-
122 covered. The beat number was determined *post hoc* by looking at peak negative power during the stride.
123 Defining a beat as peak negative power is consistent with the collisional gait perspective, which points to
124 mechanisms of energy loss and approximates them as impulsive events [7, 27]. Setting normalized (negative)
125 power as

$$P_{N_{\text{tot}}}(t) = \frac{-P_{\text{tot}}(t)}{\max(-P_{\text{tot}}(t))}, \quad (4)$$

126 where P_{tot} is instantaneous net power from all actuators, the number of beats were the number of local
127 maxima in $P_{N_{\text{tot}}}(t) > 0.3$. If two maxima were less than $0.03 T$ apart, the greater maximum among them
128 was counted as a single beat. This method eliminated some noise while selecting only the largest events of
129 energy loss as a “beat”. However, it is somewhat arbitrary and the shape of gait “zones” changes to some
130 extent depending on tolerances (see supplemental information for results using other tolerances).

131 Limb contact for a given limb was defined as its GRF $> 0.01 mg$. Walking was defined as having duty
132 factor > 0.50 in at least one pair of limbs (fore or hind), with running being all other cases. Although this
133 distinction aligns with Hildebrand’s use of the terms “walk” and “run” for symmetrical gaits [12], there are
134 examples in nature of “grounded running” where the COM bounces as in a run, but duty factors exceed 0.5
135 [28, 17].

136 2.2 Calculations of empirical moments of inertia

137 The relevant pitch moments of inertia (MOI) about the COM were taken during standing, and were derived
138 from values reported in the literature (Supplementary table S1). Alexander [29] measured whole body MOI
139 for an Alsatian dog directly and reported the normalized value along with body mass. The reference length
140 (not reported by the author) was derived from figure 12 in [2], which Alexander used as a reference [29].
141 Whole body MOI for the Dutch Warmblood was calculated from [30] using figure 1 from that study as a
142 guide for limb and head orientation.

143 For the elephant and giraffe, no direct MOI measurements are available, but some studies report estimates
144 using 3D models. [17] provide measured masses and estimated moments of inertia for elephants. The
145 shoulder-hip length was calculated by scaling their reported limb lengths to figure 1 in [31]. Estimated MOI
146 was also derived for a horse and giraffe from [32]. Shoulder and hip locations were estimated by comparing
147 their figure 1 to skeletal drawings or mounts. COM position was assumed to lie along the shoulder-hip
148 line, and its bias towards the forelimbs (m'_F in [25]) was determined from calculations using [30] for the
149 horse ($m'_F = 0.50$) and ground reaction forces from [23] for the giraffe ($m'_F = 0.65$). The horse MOI was
150 used to ground-truth the estimate from [32], and yielded $\hat{I} = 0.80$, similar to the empirical value of 0.82

151 (supplementary table S1).

152 3 Results and Discussion

153 Figure 2a shows optimal gaits at parameter combinations of \hat{I} and U' . Optimal gaits generally fall into
154 four large regions. At high \hat{I} , four-beat runs and two-beat walks are optimal. At low \hat{I} , the reverse is true.
155 While the cutoff between two- and four-beat runs is approximately $\hat{I} \sim 1$, as predicted by equation (2), the
156 transition \hat{I} for four-beat to two-beat walking increases from about $\hat{I} = 1$ at the highest walking speeds to
157 $\hat{I} = 2$ at the slowest speeds examined.

158 These findings support the hypothesis that Murphy number has opposite effects on the optimality of gait
159 in walking and running. In both walking and running, there is a tradeoff between distributing collisions
160 between multiple contacts (favouring four-beat gaits) and avoiding work to pitch the body (favouring two-
161 beat gaits). During running, the possible energetic losses from pitching increase as Murphy number *decreases*,
162 while in walking, these losses increase as Murphy number *increases*.

163 For dogs and horses ($\hat{I} \sim 0.8$), the tradeoff means it is optimal to use a four-beat walk and two-beat
164 run, as these animals typically do. Indeed, even a quadrupedal robot with a small Murphy number finds the
165 same $4 \rightarrow 2$ beat transition to be optimal [33]. For elephants, which have $\hat{I} \sim 1$, the tradeoff seems to favour
166 a four-beat gait regardless of speed. In reality, these animals only use four-beat gaits, and it is difficult to
167 distinguish their transition from walking to running [17].

168 A four-beat run is predicted for dogs and horses right before the transition to two-beat running. The
169 optimal solution is borderline between walking and running: the ground reaction forces exhibit the double-
170 hump profiles characteristic of walking, and the duty factor is slightly less than 0.5. Increasing the force-rate
171 penalty extends the duty factor at the walk-trot transition comfortably into the walking range, and better
172 matches empirical data [25], highlighting that minimizing limb-work alone does not fully explain gait choice.

173 The giraffe has the most extreme Murphy number by far of all the mammals investigated here. It also
174 has unusual gait patterns, exhibiting only two gaits, the walk and the gallop³, with no intermediate trot
175 [34, 6, 4]. However, figure 2a predicts that giraffes should have *three* distinct gaits: a four-beat walk at
176 slow speeds ($U' < 0.34$), a two-beat walk at higher speeds ($0.3 < U' < 0.7$) and a four-beat run at higher
177 speeds ($0.8 < U'$). The walk-run transition point appears sensible, as Basu *et al.* [35] report a walk-gallop
178 transition speed⁴ of $U' \approx 0.8$.

179 Walking giraffes exhibit a mean hind-fore phase offset of 0.14 (range 0.09-0.2) [21, 23], above the 0.0625

³ There is some debate whether the canter, also used by giraffes, is a distinct gait or merely a slow gallop. ⁴ As $U' \approx 0.8$ was the slowest running gait observed, and the authors did not report on walking gaits in that study, it is unclear if this is truly the transition speed.

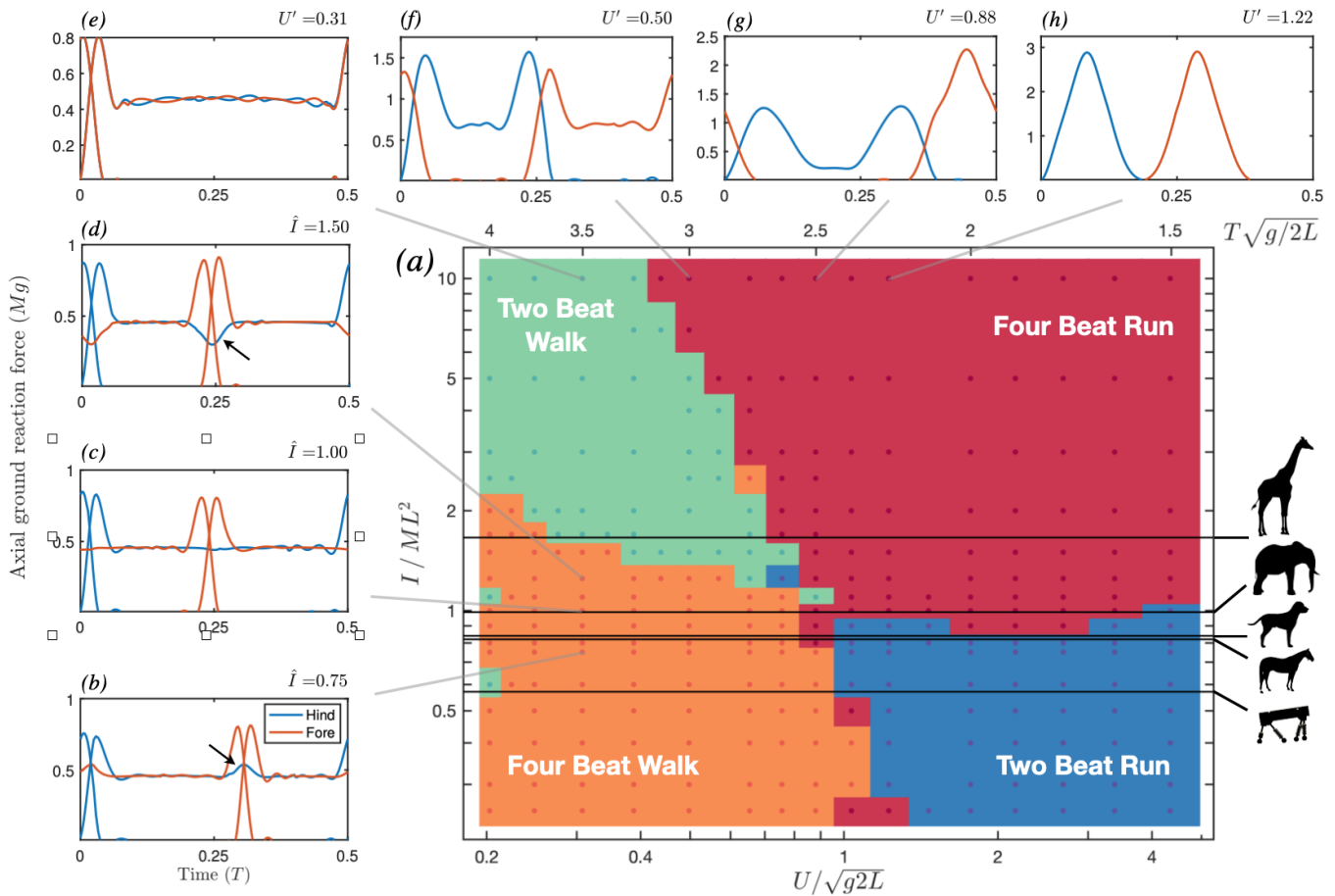


Figure 2: Optimal gaits for parameter combinations of \hat{I} and U' . (a) Gaits largely fall into four main regions. At high \hat{I} , four-beat runs and two-beat walks are optimal. At low \hat{I} , the reverse is true. Dogs and horses have $\hat{I} < 1$, and exhibit a four-beat walk and two-beat run, as predicted. Likewise, a robot with low \hat{I} finds $4 \rightarrow 2$ beat transition to be energetically optimal [33]. Elephants, with $\hat{I} = 1$, exhibit a four-beat gait regardless of whether walking or running [17]. Giraffes have the most extreme \hat{I} examined here and do not use a two-beat run [34]. Despite their large \hat{I} , a four-beat walk remains optimal at slow speeds. (b-h) Limb-axial ground reaction forces (GRF) for a number of optimal solutions (animated in supplemental videos 1 and 2). A half-cycle is shown in each case; the solution is repeated during the second half-cycle, but mirrored in the sagittal plane. (b-d) Transfer of support in one pair of limbs during four-beat walking induces a vertical reaction force at the other pair. (b) When $\hat{I} < 1$, the vaulting limb exhibits an increase in GRF (arrows) to cancel the negative reaction force and maintain its length. (c) At $\hat{I} = 1$, the vaulting limb does not exhibit a change in force. (d) At $\hat{I} > 1$, the vaulting limb sees a reduction in midstance force. (e) At slow speeds and high \hat{I} , a two-beat walk is optimal. (f) As speed increases with $\hat{I} = 10$, a four-beat “running” solution emerges, with single limb vaulting swapping between fore and hind limbs. (g) At higher speeds, the optimal gait is a hybrid between vaulting in hind and bouncing in front, reminiscent of the slow tölt [11]. (h) At still higher speeds, a typical fast tölt pattern emerges.

180 limit for a pace given by Hildebrand [12]. These observations of a four-beat gait are for an extremely slow
181 normalized speed ($0.14 < U' < 0.30$), matching the region where the work-minimizing model predicts a
182 four-beat walk (figure 2a). Is there any evidence of giraffes using a two-beat walk at intermediate speeds?

183 The walk of the giraffe has been described in two-beat terms, including “rack-like” [34] or as a pace [36].
184 However, without quantifying the phase relationship or speed at which these observations were made, it is
185 not clear whether these represent the same gait quantified as four-beat in other studies [23, 21]. It seems
186 difficult to elicit walking speeds above $U' = 0.3$ for giraffes in captivity [37, 23]. Indeed, Innis [34] reports
187 that wild adult giraffes seem to use only two modes; a “leisurely” walk or a fast run. This leaves a large
188 gap ($0.3 < U' < 0.8$) where giraffe gait has not been quantified, approximately where figure 2a anticipates
189 a transition to a two-beat walk.

190 We should not place too much weight on the model’s exact quantitative predictions in this case. Giraffes
191 occupy a region of \hat{I} - U' space where subtle changes in MOI can have profound changes on $4 \rightarrow 2$ walk
192 transition speed. Added to the fact that \hat{I} is highly sensitive to L (a 5% change in L can lead to a 10%
193 change in \hat{I}), the predicted four-beat to two-beat walk transition could vary substantially with measurement
194 error. The walk-run transition speed, however, is less sensitive to choice of \hat{I} .

195 While the model correctly predicts the absence of a two-beat run, giraffes do not use the predicted
196 symmetrical four-beat run either, instead opting for a three-beat canter or four-beat gallop. While the
197 present symmetrically-constrained model could not reproduce these asymmetrical gaits, a collision-based
198 analysis predicts that a canter should be optimal at intermediate running speeds for a long-limbed animal
199 with a high Murphy number, such as a giraffe [14].

200 3.1 Changes in walking strategy with Murphy number and speed

201 An interesting effect in walking can be observed as Murphy number increases. During transfer of support
202 on one set of limbs (*e.g.* the hind pair), the leg at the opposite end of the body (*e.g.* forelimbs) will exhibit
203 increased reaction force if $\hat{I} < 1$ and decreased reaction force if $\hat{I} > 1$ (figure 2b-d). Why does this occur?

204 An impulse at the hindlimbs simultaneously causes the body to translate upwards and pitch down.
205 Depending on how much the impulse causes rotation *vs* translation, the net effect at the instant of the
206 impulse may be to push the forelimbs up or down. For $\hat{I} < 1$, an impulse at the hips cause the shoulders
207 to *descend*; at $\hat{I} > 1$, the same impulse causes the shoulders to *ascend*; and at $\hat{I} = 1$ the shoulders remain
208 (momentarily) stationary (figure 1).

209 During walking, it is advantageous for the vaulting limb to maintain its length; a change in length while
210 providing axial force implies that the limb is performing work. The strategy, then, is for the vaulting limb

211 to cancel the force it feels from the limbs undergoing transfer of support. For $\hat{I} < 1$, double-stance contact
212 induces a downward force on the vaulting limb, which can respond by increasing its applied force so as to
213 maintain its length and perform no work (figure 2b).

214 For $\hat{I} > 1$, double-stance induces an upward force on the vaulting limb. The vaulting limb therefore
215 responds by *reducing* its applied force, maintaining its length (figure 2d). At some large \hat{I} , this strategy will
216 fail; the vertical joint reaction force induced on the vaulting limb exceeds its upward ground reaction force
217 ($\sim 0.5mg$). This constraint does not seem to govern the transition to two-beat walking, however. $\hat{I} = 1.5$
218 and $U' = 0.3$ is at the border between four-beat and two-beat walking (figure 2a), yet the vaulting limb only
219 reduces its applied force by $0.2 mg$ (figure 2d).

220 Two-beat walking forms a wedge in the upper-left corner of figure 2a (example sequence in figure 2e),
221 and the transition to four-beat running occurs at lower speeds as the Murphy number increases. The four-
222 beat “running” solution at $U' = 0.5$, $\hat{I} = 10$ demonstrates why (figure 2f; see also supplemental video 2).
223 The solution is to perform a single-limb vault over forelimbs, then hindlimbs, and repeat this pattern. This
224 solution is feasible because the Murphy number is so extreme that the body barely pitches during single
225 stance, even though it is supported only at one end.

226 As we increase Murphy number, we approach the limit where any pitching can be effectively ignored. In
227 this limit, we expect all gaits to be four-beat; it is analogous to a point mass biped with half the stride length.
228 At slow speeds, a point mass biped should use a vaulting walk to minimize work [38]. With an extra set of
229 legs, it can reduce contact losses by taking twice as many steps per stride (similar to the solution observed in
230 figure 2f). At intermediate speeds, a point-mass biped should use a hybrid gait: a pendular run with single-
231 leg contacts [38]; again, adding two legs means we simply halve the stride length. The simulation discovers a
232 similar hybrid gait (figure 2g)–reminiscent of the slow tölt [11]. The same logic applies to impulsive running,
233 the minimal-work high-speed gait for a point-mass biped, resulting in a familiar fast tölt (figure 2h). The
234 extreme case of $\hat{I} = 10$ has sufficient pitching energies that a two-beat walking gait is optimal at slow speeds
235 (figure 2e); as we further increase \hat{I} , we expect the four-beat transition speed to decrease.

236 4 Summary and Conclusions

237 Contact forces axial to the a quadruped’s legs pitch its body, unless compensated by a counter torque.
238 The Murphy number parameterizes the tendency of these contacts to pitch the body *vs* accelerate the
239 center of mass. Large Murphy numbers result in less energy going into pitching *versus* translation by single
240 limb contact. As a result, four-beat gaits are favoured, which reduce the collisional cost of changing COM
241 momentum. At lower Murphy numbers, the opposite is true, and more oscillation of the COM is worth the

242 price for avoiding costly pitching. The transition point between two-beat and four-beat running occurs close
243 to $\hat{I} = 1$, matching an analysis by Usherwood [14].

244 However, Murphy number has the opposite effect on walking energetics, due to the geometric constraints
245 of four-beat walking and the ability of the vaulting limb to counteract some of the effects felt by transfer of
246 support at the opposite pair of limbs. Altogether, the work-based model correctly predicts the walking and
247 slow running gaits selected by dogs, non-gaited horses, elephants, and a quadrupedal robot. It also correctly
248 predicts that giraffes should use a slow four-beat gait and avoid trotting at high speeds. It does not (nor
249 can it) predict a canter as the slow-running gait of choice for giraffes, and predicts that giraffes should use
250 a two-beat walking gait at intermediate to fast walking speeds (for which there is currently no data).

251 Point-mass collisional dynamics predict that all quadrupedal gaits should be four-beat with alternating
252 single stance contact. It is only by considering pitching dynamics that other gaits emerge as energetically
253 optimal solutions. Except for some specialized gaits—trotting, cantering, and possibly transverse galloping
254 [7]—, the net torque about the COM is appreciable and energetically costly. Furthermore, these non-pitching
255 gaits may be commonly used *precisely because* pitching would otherwise be extremely costly. Pitching may
256 be so important energetically, that the optimal solution is often to render it absent.

257

258 **Data Availability**

259 The dataset supporting this article has been uploaded as part of the supplementary material (Table 1), and
260 on Zenodo at <https://doi.org/10.5281/zenodo.3765877>.

261

262 **Competing Interests**

263 The author declares no competing financial interests.

264

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271 References

- 272 [1] Barrey E. Methods, Applications and Limitations of Gait Analysis in Horses. *The Veterinary Journal*.
273 1999 Jan;157(1):7–22.
- 274 [2] Jayes A, Alexander R. Mechanics of Locomotion of Dogs (*Canis Familiaris*) and Sheep (*Ovis Aries*).
275 *J Zool*. 1978;185(3):289–308.
- 276 [3] Leach D, Cymbaluk NF. Relationships between Stride Length, Stride Frequency, Velocity, and Mor-
277 phometrics of Foals. *Am J Vet Res*. 1986 Sep;47(9):2090–2097.
- 278 [4] Pennycuick CJ. On the Running of the Gnu (*Connochaetes Taurinus*) and Other Animals. *J Exp Biol*.
279 1975;63(3):775–799.
- 280 [5] Dagg AI. The Locomotion of the Camel (*Camelus Dromedarius*). *J Zool*. 1974;174(1):67–78.
- 281 [6] Dagg A, Vos A. Fast Gaits of Pecoran Species. *J Zool Lond*. 1968;155(4):499–506.
- 282 [7] Ruina A, Bertram JEA, Srinivasan M. A Collisional Model of the Energetic Cost of Support Work Qual-
283 itatively Explains Leg Sequencing in Walking and Galloping, Pseudo-Elastic Leg Behavior in Running
284 and the Walk-to-Run Transition. *J Theor Biol*. 2005 Nov;237(2):170–192.
- 285 [8] Kuo AD. Energetics of Actively Powered Locomotion Using the Simplest Walking Model. *JBiomechEng*.
286 2002;124(1):113–120.
- 287 [9] Bertram JE, Ruina A, Cannon CE, Chang YH, Coleman MJ. A Point-Mass Model of Gibbon Locomo-
288 tion. *J Exp Biol*. 1999;202(19):2609–2617.
- 289 [10] Polet DT, Schroeder RT, Bertram JEA. Reducing Gravity Takes the Bounce out of Running. *J Exp*
290 *Biol*. 2018 Feb;221(3):jeb162024.
- 291 [11] Biknevicius AR, Mullineaux DR, Clayton HM. Ground Reaction Forces and Limb Function in Töltting
292 Icelandic Horses. *Equine Vet J*. 2004;36(8):743–747.
- 293 [12] Hildebrand M. Symmetrical Gaits of Horses. *Science*. 1965 Nov;150(3697):701–708.
- 294 [13] Andersson LS, Larhammar M, Memic F, Wootz H, Schwochow D, Rubin CJ, et al. Mutations in DMRT3
295 Affect Locomotion in Horses and Spinal Circuit Function in Mice. *Nature*. 2012 Aug;488(7413):642–646.
- 296 [14] Usherwood JR. An Extension of the Collisional Model of the Energetic Cost of Support Qualitatively
297 Explains Trotting and the Trot-Canter Transition. *J Exp Zool Part Ecol Integr Physiol*. 2020;p. 9–19.

- 298 [15] Murphy KN. Trotting and Bounding in a Simple Planar Model. Carnegie-Mellon University. Pittsburgh,
299 PA; 1984.
- 300 [16] Lee DV, Meek SG. Directionally Compliant Legs Influence the Intrinsic Pitch Behaviour of a Trotting
301 Quadruped. *Proceedings of the Royal Society B: Biological Sciences*. 2005 Mar;272(1563):567–572.
- 302 [17] Ren L, Hutchinson JR. The Three-Dimensional Locomotor Dynamics of African (*Loxodonta Africana*)
303 and Asian (*Elephas Maximus*) Elephants Reveal a Smooth Gait Transition at Moderate Speed. *J R Soc*
304 *Interface*. 2008 Feb;5(19):195–211.
- 305 [18] Schmitt D, Cartmill M, Griffin TM, Hanna JB, Lemelin P. Adaptive Value of Ambling Gaits in Primates
306 and Other Mammals. *J Exp Biol*. 2006 Jun;209(11):2042–2049.
- 307 [19] O’Neill MC. Gait-Specific Metabolic Costs and Preferred Speeds in Ring-Tailed Lemurs (*Lemur Catta*),
308 with Implications for the Scaling of Locomotor Costs. *Am J Phys Anthropol*. 2012 Nov;149(3):356–364.
- 309 [20] Griffin TM, Main RP, Farley CT. Biomechanics of Quadrupedal Walking: How Do Four-Legged Animals
310 Achieve Inverted Pendulum-like Movements? *J Exp Biol*. 2004;2072(20):3545–3558.
- 311 [21] Loscher DM. Kinematische Anpassungen zur Kollisionsreduktion im Schritt vierfüßiger Lauftiere [Dr.
312 rer. Nat.]. Freie Universität Berlin. Berlin, Germany; 2015. Title Variation: “Kinematic adaptations to
313 collision reduction in the walking gait of cursorial quadrupeds”.
- 314 [22] Usherwood JR, Williams SB, Wilson AM. Mechanics of Dog Walking Compared with a Passive, Stiff-
315 Limbed, 4-Bar Linkage Model, and Their Collisional Implications. *J Exp Biol*. 2007 Feb;210(3):533–540.
- 316 [23] Basu C, Wilson AM, Hutchinson JR. The Locomotor Kinematics and Ground Reaction Forces of
317 Walking Giraffes. *J Exp Biol*. 2019 Jan;222(2):jeb159277.
- 318 [24] Young JW, Patel BA, Stevens NJ. Body Mass Distribution and Gait Mechanics in Fat-Tailed Dwarf
319 Lemurs (*Cheirogaleus Medius*) and Patas Monkeys (*Erythrocebus Patas*). *Journal of Human Evolution*.
320 2007 Jul;53(1):26–40.
- 321 [25] Polet DT, Bertram JEA. A Simple Model of a Quadruped Discovers Single-Foot Walking and Trotting
322 as Energy Optimal Strategies. *bioRxiv*. 2019;.
- 323 [26] Alexander RM, Jayes AS. A Dynamic Similarity Hypothesis for the Gaits of Quadrupedal Mammals.
324 *J Zool*. 1983;201(1):135–152.
- 325 [27] Bertram JEA, Hasaneini SJ. Neglected Losses and Key Costs: Tracking the Energetics of Walking and
326 Running. *J Exp Biol*. 2013 Mar;216(6):933–938.

- 327 [28] Usherwood JR, Szymanek KL, Daley MA. Compass Gait Mechanics Account for Top Walking Speeds
328 in Ducks and Humans. *J Exp Biol*. 2008 Dec;211(23):3744–3749.
- 329 [29] Alexander RM. Optimum Walking Techniques for Quadrupeds and Biped. *J Zool*. 1980;192(1):97–117.
- 330 [30] Buchner HHF, Savelberg HHCM, Schamhardt HC, Barneveld A. Inertial Properties of Dutch Warm-
331 blood Horses. *Journal of Biomechanics*. 1997 Jun;30(6):653–658.
- 332 [31] Ren L, Butler M, Miller C, Paxton H, Schwerda D, Fischer MS, et al. The Movements of Limb Segments
333 and Joints during Locomotion in African and Asian Elephants. *J Exp Biol*. 2008 Sep;211(17):2735–2751.
- 334 [32] Henderson DM, Naish D. Predicting the Buoyancy, Equilibrium and Potential Swimming Ability of
335 Giraffes by Computational Analysis. *Journal of Theoretical Biology*. 2010 Jul;265(2):151–159.
- 336 [33] Xi W, Yesilevskiy Y, Remy CD. Selecting Gaits for Economical Locomotion of Legged Robots. *Int J*
337 *Robot Res*. 2016 Aug;35(9):1140–1154.
- 338 [34] Innis AC. The Behaviour of the Giraffe, *Giraffa Camelopardalis*, in the Eastern Transvaal. *Proceedings*
339 *of the Zoological Society of London*. 1958 Sep;131(2):245–278.
- 340 [35] Basu CK, Deacon F, Hutchinson JR, Wilson AM. The Running Kinematics of Free-Roaming Giraffes,
341 Measured Using a Low Cost Unmanned Aerial Vehicle (UAV). *PeerJ*. 2019 Feb;7:e6312.
- 342 [36] Dagg AI. Gaits of the Giraffe and Okapi. *J Mammal*. 1960;41(2):282–282.
- 343 [37] Christian A, Müller RHG, Christian G, Preuschoft H. Limb Swinging in Elephants and Giraffes and
344 Implications for the Reconstruction of Limb Movements and Speed Estimates in Large Dinosaurs. *Fossil*
345 *Record*. 1999 Jan;2(1):81–90.
- 346 [38] Srinivasan M, Ruina A. Computer Optimization of a Minimal Biped Model Discovers Walking and
347 Running. *Nature*. 2006;439(7072):72–75.