Correlation of Symmetrical Gaits and Whole Body Mechanics: Debunking Myths in Locomotor Biodynamics

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ABSTRACT
Independent maturation of gait (Hildebrand) and whole body mechanics (Cavagna et al.) traditions in locomotor analyses has led to conflicting terminology. Re-evaluation of these traditions yields three primary insights. First, walking and running should be recognized by their fundamentally different mechanics. Because duty factor fails to consistently distinguish these mechanics, its use in discriminating walks from runs should be abandoned in preference to parameters that more accurately reflect the movements of the center of mass (COM; phase difference in external mechanical energy or Froude number). Second, “trot” should be reserved as a descriptor of a particular footfall pattern. This and all gait terms lack explicit information about limb compliance and thus COM movements. Third, symmetrical gait definitions should be broadened to reflect the four primary footfall patterns: the lateral-couplet dominated pattern of the pace, the diagonal-couplet dominated pattern of the trot and the more independent sequencing of footfalls of the two singlefoots. Intermediate gaits (perennially confusing and a mouthful to pronounce) are thereby subsumed by these four discrete gaits. Confusion between gait terminologies would be avoided if limb phase were consistently reported. J. Exp. Zool. 305A:923–934, 2006. © 2006 Wiley-Liss, Inc.

How to cite this article: Biknevicius AR, Reilly SM. 2006. Correlation of symmetrical gaits and whole body mechanics: debunking myths in locomotor biodynamics. J. Exp. Zool. 305A:923–934.

Scientific discovery is disseminated through published reports or professional presentations. The common feature of both venues is the reliance on words—words that link the thoughts of the author with the imagination of the audience. While science prides itself in its precision, sometimes the same words are applied to different physical entities. For example, a “navicular bone” is one of the tarsal bones in humans but it is also the distal sesmoid bone in the feet of ungulates (Riegel and Hakola, '99). Adoption of common words to reflect discrete physical entities in science is perhaps even more likely to yield confusion. Hence, reference to a “knee” conjures up the image of the femur–tibia articulation unless, of course, the audience is composed of equine researchers for whom “knee” implies the carpus (Riegel and Hakola, '99). Independent development of terminology can occur because of disciplinary isolation or methodological differences between avenues of research (Reilly and Biknevicius, 2003). One consequence of autonomously maturing research fields is that “walks” and “runs” have been defined using different parameters that signify overlapping, but not equivalent, physical realities.

Walking and running footfall patterns—Hildebrand gait model
The first method to distinguish walks from runs is based exclusively on duty factor (the ratio of support duration to stride duration), a parameter.
that is frequently used as a proxy for locomotor speed (duty factor most commonly scales inversely with speed; Demes et al., '94). As codified by Hildebrand ('65), with inspiration from earlier workers (e.g., Howell, '44), running occurs when duty factor falls below 0.5; conversely, duty factors ≥0.5 are considered to be walks.

Walks and runs are further categorized into gaits (timing of footfalls), a tradition that stems from at least the time of Goiffon and Vincent (1779). About 200 years later, Hildebrand ('65, '76) systematized symmetrical gaits according to limb phase, defined as the phase difference between the touchdowns of ipsilateral hind- and forelimbs as a ratio of stride duration (Fig. 1A). A forelimb lands progressively later in the stride duration relative to its ipsilateral hindlimb as limb phase increases, i.e., ipsilateral fore- and hindlimbs land synchronously at a limb phase of 0 whereas forelimb touchdown is half a stride duration after the ipsilateral hindlimb when limb phase is 0.5. The discrete symmetrical gaits are pace (limb phase = 0), trot (0.5) and the two singlefoots (0.25 and 0.75), allowing approximately ±0.06 limb phase about these values. The remainder of the limb phase range can either be considered to represent intermediate gaits or less synchronized versions of the discrete gaits (e.g., a 0.41 limb phase is either deemed a lateral-sequence diagonal couplets or a 4-beat trot, respectively). [We refer the readers to Reilly and Biknevicius (2003) or Stevens (this volume) for a more detailed explanation of how symmetrical gaits are identified.] The classic Hildebrand symmetrical gait plot (Fig. 1A) charts limb phase (gait) against duty factor (speed); the footprint-shaped area on the plot circumscribes symmetrical gaits in walks and runs (as per Hildebrand, '76). By this method, some gaits are theoretically possible as both walks and runs (trots, singlefoots) whereas other gaits occur primarily as runs (pace) or as walks (all other symmetrical gaits).

The popularity of this footfall-kinematics approach to defining walks and runs (as well as gaits) is its ease of data capture: all that is required is a camera, preferably high-speed. As early as 1976, a rich database already existed on the gaits of at least 143 non-avian tetrapod genera (seven amphibians, four lizards, two crocodilians and 130 mammals) plus 37 dog breeds and 13 horse breeds (Hildebrand, '65, '67, '68, '76). Hildebrand’s work recorded gaits across a wide array of locomotor behaviors, including linear and turning trials as well as steady and non-steady speed. Although subsequent studies largely focused on steady speed and level terrestrial locomotion (e.g., White and Anderson, '94; Parchman et al., 2003), some have branched out to other substrates (e.g., arboreal locomotion: Lammers and Biknevicius, 2004; Stevens, 2006). The underlying importance of understanding footfall gaits is that they are one way to quantify the output of the neuromotor system to move the body in response to environmental demands.

**Walking and running center of mass (COM) mechanics—Cavagna et al. model**

Another method for distinguishing walks from runs involves the movements of the COM of the entire body (Fig. 1B) and is referred to here as the whole body mechanics approach (Cavagna et al., '77). Because slow moving tetrapods travel with limbs that have a high level of stiffness, their COM is at its highest position near midstance when the forward velocity of the COM is low. Consequently, gravitational potential energy ($E_p$) cycles out of phase with total kinetic energy ($E_k$) and the phase difference between minima of $E_p$ and $E_k$ ("phase shift") is near 180°. This pendulum-like exchange of energies provides an opportunity to recover external mechanical energy with every step, thereby reducing muscular effort and the metabolic cost of locomotion at slow speeds. At faster speeds, the limbs of tetrapods function with...
greater compliance so that the COM no longer rises during the first half of stance but rather drops to its lowest position near midstance. The resulting in-phase fluctuations in $E_p$ and $E_k$ are inconsistent with pendulum-like mechanics (phase shift near $0^\circ$) but some recovery of mechanical energy is still, at least theoretically, possible via the storage and release of elastic strain energy (another form of potential energy) in the ligaments, tendons and muscles of the limbs and back. Therefore, from the perspective of whole body mechanics, walks and runs are synonymous with inverted pendulum (vaulting) and spring-mass (bouncing) mechanics, respectively.

There is a limit to how quickly tetrapods can move and still take advantage of inverted pendulum mechanics while retaining constant contact with the ground (Alexander, '76). As the COM moves in an arc over a stiff limb, it resembles a mass attached to the end of a spring moving in a circle. The mass will continue to move about the circle as long as the centripetal force required to maintain the movement of the body mass along the arc ($mu^2/l$ where $m$ is mass, $v$ is forward velocity and $l$ is length of the string or, in the case of walking, hip height at midstance) does not exceed gravitational force ($mg$ where $g$ is the gravitational acceleration or $9.81\,\text{m sec}^{-1}$). The ratio of these forces is known as Froude number ($Fr = v^2/gl$). In theory, animals may continue to move with inverted pendulum mechanics as long as $Fr<1$ but empirical data show that animals typically switch to bouncing mechanics at much slower speeds ($Fr \sim 0.5$ for bipeds, $\sim0.35$ for quadrupeds; Alexander, '77; Alexander and Jayes, '83; Gatesy and Biewener, '91; Griffin et al., 2004), so that the trigger for a vault–bounce transition is determined not by the limits of centripetal force but rather by some metabolic, mechanical and/or perceived exertion factors (Hoyt and Taylor, '81; Farley and Taylor, '91; Raynor et al., 2002; Griffin et al., 2004). Because $Fr$ also reflects the ratio of $E_k$ to $E_p$, this approach is actually an extension of the whole body mechanics approach.

The dataset for whole body mechanics is less extensive than that for gaits. Nearly 30 years later after Cavagna et al.'s ('77) study, whole body mechanics have been recorded for only 18 non-avian genera (one amphibian, three lizards, one crocodilian and 13 mammals; Table 1). The count rises to 29 genera when birds (eight genera) and invertebrates (three) are included, still a far cry from the sampling of gaits in tetrapods. Furthermore, whole body mechanics studies tend to explore a small subset of terrestrial locomotor behavior, namely, steady-speed locomotion on level substrates. When an animal moves in bursts, $E_k$ is lost and the work required for locomotion increases (Alexander, '89).

**Integrating walking and running gaits with vaulting and bouncing COM mechanics**

How well do the footfall and whole body mechanics approaches to defining walks and runs coincide? The most simplistic (and optimistic) synthesis (Reilly and Biknevicius, 2003) would map vaulting mechanics (out-of-phase fluctuations of $E_p$ and $E_k$) on the walking side (duty factor $>0.5$) of the Hildebrand gait space and bouncing mechanics (in-phase $E_p$ and $E_k$) on the running side (duty factor $<0.5$; Fig. 1C). Locomotor data on tetrapods that include hindlimb duty factor, whole body mechanics and gait (footfall patterns of all limbs) are surprisingly limited (12 non-hopping quadrupeds: Table 1); nevertheless, a clear pattern has emerged (Fig. 1D). At first, the idealistic synthesis appears to have some support: vaulting mechanics is limited to high duty factors and only bouncing mechanics occurs at low duty factors. But on closer inspection, one finds that the 0.5 duty factor line does not cleanly separate vaulting and bouncing strides because bouncing mechanics repeatedly breaches the 0.5 walk–run duty factor boundary (e.g., trotting opossums, singlefooting horses; Fig. 1D). In fact, the entire mechanical repertoire of some species, such as rats, occurs at duty factors greater than 0.5! The idealistic synthesis is, therefore, soundly rejected, and one is led to the conclusion that the Hildebrand (footfall kinematics) and Cavagna et al. (whole body mechanics) definitions of walks and runs are not interchangeable.

**BRIDGING THE VOCABULARY GAP**

Recognizing that some terminology (walk, run, trot) is used inconsistently within the locomotor biodynamics community is but the first and easiest step in resolving semantic conflicts. Much more difficult is implementing a change in the culture so that these inconsistencies and misunderstandings are minimized. In the subsequent sections, we offer several compromises that are supported by empirical evidence from both the Hildebrand and Cavagna et al. traditions. These are organized as
“Myths”—popular beliefs that are unsupported by facts and that result in distorted truths. The first involves the belief, held by some kinematically oriented biomechanists, that runs necessarily include a flight phase. The second myth explores the assumption, held by some biomechanists of the whole body mechanics tradition, that trots are always runs.

**Myth 1: “Runs contain an aerial phase”**

We propose that walk and run be used to explicitly describe vaulting and bouncing COM mechanics, respectively (a convention that will be used hereafter in this paper). There is no simple equivalence between the Hildebrand (footfall) and Cavagna et al. (whole body mechanics) definitions.
of walks and runs, and in this section we present supportive evidence that duty factor fails to provide consistent and meaningful mechanical distinctions between locomotor behaviors.

At the core of the first myth ("runs contain an aerial phase") is the 0.5 duty factor boundary between walks and runs sensu Hildebrand ('65). The concept that running requires a period of suspension between steps is virtually dogma in common parlance. It is fostered by Muybridge’s (1887) sensational serial snapshot photographs that revealed aerial phases in trotting horses or the fact that human racewalkers fault when an aerial phase is detected (Rogers, 2000). Yet, data from both the Cavagna et al. and Hildebrand traditions have repeatedly shown that a flight phase is not a prerequisite for running.

Bipedal locomotion in striding birds that employ phase complicity to produce similar results (McMahon et al., '87; Bertram et al., 2002). The artificial running gait of humans is instructive. Two key parameters in Groucho running are a high degree of limb compliance ("bent knee running") and prolonged support durations (McMahon et al., '87; Bertram et al., 2002). The sprawled and crouched postures of small tetrapods may provide multiple links along the limb to enhance limb compliance. For example, birds that move with a more crouched posture (kiwi, guinea fowl, quail) rarely demonstrate an aerial phase when running after crossing the vault–bounce Fr boundary, rather they preferentially stay with a grounded run (Gatesy and Biewener, '91; Reilly, 2000). By comparison, the "stretched limb cursorial birds" (tinamous, rhea, ostrich), that presumably have greater limb stiffness, transition to an aerial run following a period of grounded running (Abourichid and Renous, 2000; Abourichid, 2001; Blickhan and Full, '87; Full and Tu, '90, '91). In other words, grounded running is a common feature of terrestrial locomotion at intermediate to fast speeds.

What predisposes some tetrapods to use grounded running? Once again, a comparison with the artificial running gait of humans is instructive. Two key parameters in Groucho running are a high degree of limb compliance ("bent knee running") and prolonged support durations (McMahon et al., '87; Bertram et al., 2002). The sprawled and crouched postures of small tetrapods may provide multiple links along the limb to enhance limb compliance. For example, birds that move with a more crouched posture (kiwi, guinea fowl, quail) rarely demonstrate an aerial phase when running after crossing the vault–bounce Fr boundary, rather they preferentially stay with a grounded run (Gatesy and Biewener, '91; Reilly, 2000). By comparison, the “stretched limb cursorial birds” (tinamous, rhea, ostrich), that presumably have greater limb stiffness, transition to an aerial run following a period of grounded running (Abourichid and Renous, 2000; Abourichid, 2001; Hancock et al., 2004). Foot length may be another factor determining grounded running: the relatively long feet of birds (Gatesy and Biewener, '91) as well as the plantigrade feet of many non-avian tetrapods may predispose these animals to grounded running by incurring relatively high support durations. This may explain why, for example, the desert spiny lizard Sceloporus magister, which has especially long hindfeet and toes, transitions from an aerial trot to a grounded trot with slower speeds (all the while using bouncing mechanisms; A.R.B and S.M.R., pers. obs.).
Gait choice is also a potent factor in determining whether or not a tetrapod uses grounded running. For example, while a crouched posture (and presumably higher limb compliance) may contribute to grounded trots in the short-tailed gray opossum *M. domestica*, a speed-related shift in limb phase may be equally important in explaining its other grounded runs (Fig. 2). *Monodelphis* tends to shift from a trot to a lateral-sequence diagonal couplets (4-beat trot) as speed decreases (Parchman et al., 2003). Support durations of each limb are more evenly distributed over the stride during a 4-beat gait than they are in a trot. Consequently, there is a range of duty factors at which the lateral-sequence diagonal couplets lack periods of suspension whereas the trots at these duty factors are already aerial. Finally, slight shifts in the timing of touchdown or liftoff can result in the inclusion or exclusion of an aerial phase during the stride (illustrated by * in Fig. 2).

Any discussion on grounded running would not be complete without highlighting the observation that some symmetrical gaits virtually never display periods of suspension even at their highest speeds and lowest duty factors. These are the singlefoot gaits, in which feet land sequentially approximately 0.25 limb phase after one another. Animals that use the lateral-sequence singlefoot across a large range of speeds (walking through running) include elephants (Hutchinson et al., 2003) and breeds of gaited horses (Hildebrand, ’65). For example, the tölt, the lateral-sequence singlefoot gait characteristic of Icelandic horses, is used at speeds and duty factors that overlap with fast walking to cantering (albeit leaning towards the lateral-sequence lateral couplets gait space, or 4-beat pace, at higher speeds; Zips et al., 2001). Although töltting Icelandic horses rarely obtain a suspension phase, all töltts for which whole body mechanics were recorded displayed in-phase fluctuations $E_p$ and $E_k$ (Biknevicius et al., 2006), thus töltts are grounded runs. The lack of a period of suspension in lateral-sequence singlefoot gaits in either elephants or gaited horses is related neither to posture nor foot length because these are extremely erect and/or cursorial animals. Rather, an aerial phase in a pure lateral-sequence singlefoot gait is simply impossible unless duty factors $<0.25$, i.e., speeds at which singlefoot gaits have never been recorded.

In summary, the exploration of the first myth draws several conclusions about locomotor biodynamics. First, the myth is soundly debunked: both bouncing mechanics (in-phase $E_p$ and $E_k$) and Hildebrand-defined running gaits (duty factor $<0.5$; singlefoots) have the capacity to occur without a period of suspension. The widespread representation of grounded running at intermediate speeds signifies that grounded running is a common locomotor behavior in terrestrial tetrapods. Therefore, *running does not require an aerial phase*. Second, the Hildebrand definition of walks and runs based solely on hindlimb footfall patterns (duty factors $<0.5$) is inadequate for discriminating the mechanics of the COM. Indeed, an arbitrary designation of any other duty factor would similarly fail to distinguish vaulting and bouncing mechanics across all tetrapods (Fig. 1D).

Therefore, we propose that Hildebrand’s walk–run definitions be abandoned and that the
terms **walk and run explicitly imply whole body mechanics** (vaulting and bouncing mechanics, respectively).

This proposal creates some practical difficulties because few labs are equipped to verify whole body mechanics, it is difficult to apply in field situations and, thus far, it is only applicable to steady-state locomotion. How then can students of locomotion infer vaulting and bouncing mechanics when whole body mechanics data are impractical to capture? Fortunately, Froude number ($Fr$) may provide an acceptable and accessible alternative. The same equipment that is used to determine forward velocity and midstance hip height required for calculating $Fr$. Currently, “walk–run” boundaries determined empirically for bipeds and quadrupeds using $Fr$ (Alexander and Jayes, '83) are better indicators of vault–bounce boundaries than of transitions between walking and running sensu Hildebrand based on the few studies that report both $Fr$ and COM mechanics (e.g., Farley and Ko, '97; Rubenson et al., 2004). Unfortunately, the ability of $Fr$ to serve as a truly robust measure for distinguishing vaulting (walking) and bouncing (running) mechanics across tetrapods awaits a broader survey of tetrapods.

**Myth 2: “A trot is always a run”**

Cavagna et al.’s ('77) seminal study figured the external mechanical energy fluctuations of “run = hop = trot” trials separately from “walk” trials. Although “run” clearly refers to the bouncing mechanics of the striding bipeds (humans, birds) in their study, its equivalency to the hop of ricochetal mammals or trot of quadrupedal mammals was set in the minds of many comparative biomechanists. The labeling shorthand has led to the assumptions that all trots are necessarily runs (bouncing mechanics) and that trotting gait and vaulting mechanics are mutually exclusive.

At first glance, these assumptions appear reasonable. There is a historical bias toward studying a subset of trotters: large, primarily cursorial and often domesticated, mammals. These models cross the walk–run transition by switching between discrete gaits, from a non-trotting walking gait to a trot for running. Although the precise walking gaits of the quadrupeds were not identified by Cavagna et al. ('77), inferences are possible by surveying studies that explicitly recorded footfall patterns in these or similar animals. Among the many walking gaits reported for the domestic dog *Canis familiaris* (including lateral-sequence lateral couplets, singlefoot and diagonal couplets represented on the high duty factor half of the Hildebrand, '68 gait plot), they choose the lateral-sequence lateral couplets (4-beat pace) gait when walking at steady speed (Griffin et al., 2004). Because steady speed is a requirement for whole body mechanics studies, it is likely that the Cavagna et al.’s dogs similarly moved in this gait. Gait data for the ram *Ovis musimon* are less accessible but can be expected to parallel bovids and equids that walk using one of two lateral-sequence gaits (singlefoot or lateral-couplet; Hildebrand, '76). Finally, both lateral-sequence singlefoots and diagonal-sequence diagonal couplets have been reported for walking adult macaques (Hildebrand, '67). In other words, the quadrupedal mammals in Cavagna et al. ('77) typically use non-trotting gaits to walk using vaulting mechanics.

However, for many terrestrial tetrapods, a trot represents a viable gait for walking (vaulting mechanics) and running (bouncing mechanics). Indeed, many tetrapods use trots and 4-beat trots across large range of speeds and duty factors (from less than 0.2 to greater than 0.8; Fig. 1A; Hildebrand, '76). While it is likely that trots occurring with duty factors <0.5 are all runs (bouncing mechanics), and it is conceivable that at least some the trots with duty factors of 0.5–0.6 are also operating under bouncing mechanics (grounded runs), under which whole body mechanics model do the remaining trots operate? Slow trots have been reported in frogs, turtles, lizards and crocodilians as well as in an array of mammals as different as hedgehogs and hippopotamus (Hildebrand, '76; White and Anderson, '94; Ahn et al., 2004; McElroy et al., 2004; Willey et al., 2004), but data on whole body mechanics of slow trots are limited to a few amphibians and reptiles (Fig. 1D; Farley and Ko, '97; Ahn et al., 2004; McElroy et al., 2004; Willey et al., 2004). In these trials, phase shifts between minima of $E_k$ and $E_p$ hover closer to 180° than 0°, so that these slow trots are inverted pendulum (walking) gaits. Thus, vaulting mechanics can and does occur with a trotting footfall pattern.

That a walking trot exists (and functions as an inverted pendulum gait) should not be particularly surprising. Indeed, the walk of humans is akin to a bipedal trot, with contralateral upper and lower limbs swinging in unison. Both bipedal and quadrupedal trots are dynamically stable gaits in spite of their small base of support. However,
while walking bipeds can maximally recover ~70–80% of their external mechanical energy through pendulum-like exchange of $E_p$ and $E_k$ (Cavagna et al., '77; Griffin and Kram, 2000), the maximum energy recoveries of walking trots range lower, from 51% in the western skink *Eumeces skiltonianus* (Farley and Ko, '97) to a mere 32% in the American alligator *Alligator mississippiensis* (Willey et al., 2004). Possible detrimental factors limiting the pendulum-like exchange of $E_k$ and $E_p$ in primitive tetrapods may include their lumbering locomotor behavior paired with a more sprawling posture, a high degree of asynchrony in the footfalls of the diagonal limbs, the use of non-optimal speeds and interference due to tail dragging via its effect on limb retraction dynamics (Willey et al., 2004; Reilly et al., 2005; Reilly et al., 2006).

In summary, a trot is a footfall pattern observed in quadrupedal tetrapods in which diagonal-couplet limbs land more-or-less synchronously. “Trot” alone does not specify a movement pattern of the COM because trotting may occur with bouncing or vaulting mechanics. Confusion arising from equating trots with runs would dissolve if “trot” were reserved for describing a diagonal-couplet gait, as per its original sense for hundreds of years (Reilly and Biknevicius, 2003), without presumption of how the COM is moving. Thus, we propose that “trot” be reserved as a designation for a gait (a footfall pattern) with no a priori expectation of whole body mechanics patterns.

**REVISITING HILDEBRAND’S SYMMETRICAL GAIT DEFINITIONS**

Hildebrand’s symmetrical gait definitions, based on limb phase, remain credible descriptors of footfall patterns over the range of observed speeds (reflected by duty factor). Even more modern gait syntheses use limb phase as their foundation (e.g., Abourichid, 2003). Hildebrand envisioned symmetrical gaits as a continuum of limb phases along the ordinate of the symmetrical gait plot but he somewhat arbitrarily organized the named gaits around the octiles of limb phases (Fig. 1A). Designation of the four primary symmetrical gaits is largely uncontested, and the pace, lateral-sequence singlefoot, trot and diagonal-sequence singlefoot are easily distinguished as the four fast gaits represented by the “fingers” on the symmetrical gait space. By contrast, the slow symmetrical gaits represent a progressive desynchronization in the touchdowns of the forelimb relative to its ipsilateral hindlimb that lacks instantly recognizable boundaries. Thus, following Hildebrand’s (’65) terminology, increasing limb phase shifts gaits seamlessly from the lateral-sequence lateral couplets through the lateral-sequence singlefoot to the lateral-sequence diagonal couplets to the trot and finally to the diagonal-sequence diagonal couplets (Fig. 1A). Clearly, some of the slow gaits are the same as those listed as fast (running) gaits (trot, lateral-sequence singlefoot). The remaining gaits represent the intermediate footfall patterns: lateral-sequence lateral couplets, lateral-sequence diagonal couplets, diagonal-sequence diagonal couplet. Just how “real” are these intermediate gaits?

To answer this question, it helps to begin by examining the discrete gaits, beginning with the trot. How synchronously must contralateral limbs land for a gait to still qualify as a trot? Simultaneous footfalls of diagonal couplets are rare even among the premier trotters (e.g., dogs; Bertram et al., ’97). Hildebrand (’76) allowed for some variation in footfall timing when he defined the trot as the middle octile on his plot, so that 0.5 limb phase ±6% (range: 0.44–0.56) are the traditional boundaries for the true trot. Flanking the traditional trot boundaries lay what Hildebrand described as non-trot walks (lateral-sequence diagonal couplets and diagonal-sequence diagonal couplets). These are often termed the 4-beat trot, trot-like walk or even “dirty” trot (Zips et al., 2001; Reilly and Biknevicius, 2003; Lammers and Biknevicius, 2004). These alternative labels include reference to the trot because the contralateral fore- and hindlimbs are landing more in sync than are the ipsilateral limbs, i.e., these gaits are essentially diagonal-couplet dominated as their formal Hildebrand titles indicate (Fig. 1D). Similarly, the lateral-sequence lateral couplets can be regarded as poorly synchronized version of the pace (4-beat pace, pace-like walk). Complete incorporation of the intermediate gaits into the trot and pace demonstrates a bias away from the, admittedly less common but still legitimate, singlefoot gaits. For example, the lateral-sequence lateral couplets and lateral-sequence diagonal couplets intermediate gaits could also be considered to represent poorly coordinated variants of the lateral-sequence singlefoot; a similar linkage may be drawn for the diagonal-sequence diagonal couplets and diagonal-sequence singlefoot.

We recommend a more generous interpretation of the four primary gaits. We suggest that the limb
phase axis of the symmetrical gait plot be subdivided into quartiles (rather than octiles; Fig. 1E), thereby subsuming the intermediate gaits into the four primary gaits. The effect of this consolidation of gait terms is two fold. First, it emphasizes that trotting (diagonal-couplet dominated behavior) is the most common gait among tetrapods and that most of what we know about whole body mechanics (both vaulting and bouncing) actually involves trots. Secondly, it draws our attention to the lateral-sequence singlefoot as a viable alternative to the trot for walking slowly. It becomes the gait of choice for domestic dogs moving at steady speed (0.15 limb phase) when optimizing pendulum-like recovery of external mechanical energy (Griffin et al., 2004). It is also the gait of choice when stability needs, and not energy economy, are to be maximized. Of the creeping gaits that retain at least three feet on the ground at all times, the most stable is the lateral-sequence singlefoot (McGhee and Frank, ’68). Not surprisingly, therefore, studies of postnatal gait development in placental carnivorans (cats Felis catus, Peters, ’83; Howland et al., ’95; dogs Canis domesticus, Hildebrand, ’68), rodents (jird Meriones tristrami and dormouse Eliomys meanurus; Elam, ’97) and even primates (baboon Papio cynocephalus and macaque Macaca mulatta; Shapiro and Raichlen, 2005) have reported lateral-sequence walking gaits in the youngest animals. Finally, confusion in describing symmetrical gaits (using either Hildebrand’s seven gaits or our proposed four gaits) can be avoided if workers specify limb phase rather than simply using previous gait terms.

In summary, there is much to be gained by integrating the Hildebrand and Cavagna et al. perspectives on locomotion. First, walking and running should be recognized by their fundamentally different mechanics. Because duty factor fails to consistently distinguish these mechanics, its use in discriminating walks from runs should be abandoned in preference to phase difference in external mechanical energy or Froude number. Duty factor remains useful as a measure of the relative time allotted for reaccelerating and redirecting the COM (when the foot is in contact with the substrate). Furthermore, the yielding of limbs necessary for bouncing mechanics can occur with or without an aerial phase. Second, trots (and all other gait terms) should be reserved as descriptors of footfall patterns. Generalizing findings on cursorial mammals to all tetrapods has led to the misconception that trots are only used with bouncing mechanics. Gait terms lack explicit information about limb compliance and thus COM movements. Finally, symmetrical gait definitions should be broadened to reflect the four primary footfall patterns: the lateral-couplet dominated pattern of the pace, the diagonal-couplet dominated pattern of the trot and the more independent sequencing of footfalls of the two singlefoots. Tetrapods consciously or subconsciously employ gaits that balance the stability demands of the terrain with acceptable levels of energy expenditure. Neuromuscular control determines both gait (footfall patterns interacting with the substrate) and limb compliance (capacity for pendulum-like or spring-like recovery of energy). Knowledge of only gait or only limb compliance inadequately summarizes locomotor effort. Decisions to employ a particular gait or whole body mechanics may reflect other needs than simply energy conservation (e.g., intermittent locomotion associated with foraging for food; Reilly and Biknevicius, in press).

ACKNOWLEDGMENTS

We thank the International Society of Vertebrate Morphology for hosting the symposium “Integrating approaches to the study of terrestrial locomotion” at its Seventh Congress and symposium co-organizer Nancy Stevens. Special thanks go to Beth Brainerd (ICVM Program Officer and associated editor for this issue) and the Journal of Experimental Zoology for publishing the symposium. Eric McElroy kindly shared his lizard and salamander data for Fig. 1; Ohio University undergraduate thesis researchers Amy Back and Kristin Hickey collected the Rattus and Sceloporus data. Jennifer Hancock, Eric McElroy, Nancy Stevens and two anonymous reviewers provided valuable feedback.

LITERATURE CITED


