

Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase

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It has been argued that minimization of metabolic-energy costs is a primary determinant of gait selection in terrestrial animals. This view is based predominantly on data from humans and horses, which have been shown to choose the most economical gait (walking, running, galloping) for any given speed. It is not certain whether a minimization of metabolic costs is associated with the selection of other prevalent forms of terrestrial gaits, such as grounded running (a widespread gait in birds). Using biomechanical and metabolic measurements of four ostriches moving on a treadmill over a range of speeds from 0.8 to 6.7 m s⁻¹, we reveal here that the selection of walking or grounded running at intermediate speeds also favours a reduction in the metabolic cost of locomotion. This gait transition is characterized by a shift in locomotor kinetics from an inverted-pendulum gait to a bouncing gait that lacks an aerial phase. By contrast, when the ostrich adopts an aerial-running gait at faster speeds, there are no abrupt transitions in mechanical parameters or in the metabolic cost of locomotion. These data suggest a continuum between grounded and aerial running, indicating that they belong to the same locomotor paradigm.

Keywords: gait transition; biomechanics; energetics; locomotion; ostrich

1. INTRODUCTION

Terrestrial animals adopt a wide range of gaits when moving over ground, for example walking to move at slow speeds and running, trotting, galloping and hopping for faster locomotion. This broad spectrum of gaits raises the question of the factors that govern gait selection. Several explanations for gait transitions have been proposed based on kinematic factors (Hreljac 1995), mechanical loading, such as musculoskeletal force (Farley & Taylor 1991) and bone strain (Biewener & Taylor 1986), muscle activation (Prilutsky & Gregor 2001), mechanical restrictions (Alexander 1984) and dynamic-systems theory (Diedrich & Warren 1995; Raynor *et al.* 2002).

Margaria (1938), who investigated the walk-run transition in humans, was among the first to report a metabolic advantage of gait selection by showing that above 2 m s⁻¹, approximately the speed where humans change gait, walking is metabolically more expensive than running, whereas below this speed the converse is true. A similar metabolic advantage has been observed in horses as they select among walking, trotting and galloping gaits (Hoyt & Taylor 1981; Wickler *et al.* 2003). Hopping animals, such as the kangaroo, also seem to select metabolically optimal gaits, the transition in this case being from pentapedal walking to bipedal hopping (Dawson & Taylor 1973). These findings have led to the view that gait selection is a trait that has been selected for in several species to minimize their metabolic costs of locomotion.

The relationship between the metabolic cost of locomotion and gait selection has been explained largely on the basis of the kinetics of locomotion (Cavagna *et al.* 1977; Minetti 2000). During walking, the body behaves as an 'inverted pendulum', with the body's centre of mass (COM) vaulting over a stiff supporting leg. The gravitational potential energy and kinetic energy of the COM fluctuate close to 180° out of phase and, at moderate walking speeds, attain nearly equal magnitude. The inverted-pendulum mechanism thereby results in an energy exchange between gravitational potential energy and kinetic energy and, consequently, saves a substantial amount of the mechanical energy required to move the body's COM (up to 70% in humans; Cavagna *et al.* 1977). However, as walking speed increases, the amount of energy exchange between gravitational potential energy and kinetic energy is reduced and at fast walking speeds considerably more mechanical work is probably done via active muscle contraction, thus contributing to the steep increase in metabolic cost (Kram *et al.* 1997). It is thought that humans and horses avoid this problem by adopting a run, a bouncing gait that takes advantage of a second energy-saving mechanism, namely elastic-energy storage and release. During running, there is little energy saved by pendular-energy conservation because the gravitational potential energy and kinetic energy of the COM fluctuate in phase. Instead, the spring-like properties of muscles and tendons in the stance phase of running result in an exchange between the kinetic energy of the COM and the elastic energy stored in these tissues (Cavagna *et al.* 1964, 1977; Ker *et al.* 1987; Roberts *et al.* 1997). At fast speeds, when the inverted-pendulum

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mechanism of walking is impaired, this bouncing gait provides a highly effective means of reducing the metabolic cost of locomotion.

While inverted-pendulum and bouncing gaits have been observed in mammals, birds, lizards and arthropods (Cavagna *et al.* 1977; Heglund *et al.* 1982; Blickhan & Full 1987; Farley & Ko 1997), the pattern of leg movements (kinematics) at the transition between an inverted-pendulum gait and a bouncing gait is markedly different among these species. In humans and horses, the transition to a bouncing gait is accompanied by a host of abrupt kinematic discontinuities, including the sudden occurrence of an aerial phase. Although some regard the occurrence of an aerial phase as the classic definition of the walk–run transition (Hildebrand 1985), many animals that switch to a bouncing gait do so in the absence of an aerial phase and other marked kinematic transitions. The resulting gait, previously referred to as compliant walking (Alexander & Jayes 1978) or ‘groucho’ running (McMahon 1985), is referred to here as ‘grounded running’. This term is introduced because McMahon’s definition of groucho running (running with bent knees) does not necessarily preclude the occurrence of an aerial phase. Grounded running is a common mode of locomotion shared by birds (Gatesy & Biewener 1991; Muir *et al.* 1996; Gatesy 1999), crabs (Blickhan & Full 1987), elephants (Hutchinson *et al.* 2003) and non-human primates (Kimura 1996; Schmitt 1999), and may also have been present in pre-modern humans (Schmitt 2003). Animals that use a grounded-running gait have been found either never to acquire an aerial phase (e.g. small terrestrial birds, Gatesy & Biewener 1991; elephants, Hutchinson *et al.* 2003) or to acquire an aerial phase only with a further increase in locomotor speed.

What still remains to be established is whether animals that select between an inverted-pendulum walking gait and a grounded run minimize their metabolic cost of locomotion, as is observed in human and equine gait selection, and whether a similar minimization also occurs with a selection between grounded and aerial running. These are important issues given that grounded running may be present in a substantial proportion of terrestrial locomotors and probably most bipedal species. To address these questions, we chose to focus on avian bipedalism as grounded running is a common gait in birds. Moreover, because the metabolic cost of locomotion is most conveniently assessed indirectly by measuring oxygen consumption, it was necessary to choose an animal species that can walk and run aerobically to avoid an underestimation of the metabolic cost resulting from anaerobic contributions. As small species exhibit a transition to aerial running at speeds approaching their maximum running speed (Gatesy & Biewener 1991), we chose to explore the mechanics and energetics of gait transition in the largest avian biped, the ostrich, as their transition to aerial running occurs at a speed far below their maximum speed. Our first goal was to determine whether grounded running is one of the gaits adopted by the ostrich. Our second and most important objective was to determine whether gait selection between inverted-pendulum walking, grounded running and aerial running over a range of speeds optimizes locomotor economy.

2. MATERIAL AND METHODS

(a) *Animals*

Four ostriches that were obtained from a local breeder (Perth, Western Australia), two males and two females (68.5 ± 5.5 kg; mean \pm s.e.), were housed in a 300 m² climate-controlled indoor pen (24 °C) with unlimited access to food and water. Each bird was trained to walk and run on a motorized treadmill for 20 min per day, 4 days per week, over a period of four months prior to testing. All experiments were performed in accordance with the guidelines of the Animal Ethics Committee of the University of Western Australia.

(b) *Kinematic and kinetic calculations*

High-speed video recordings (200 fields s⁻¹, PEAK Performance, USA) were obtained in lateral view of the birds moving over a range of speeds from 0.8 to 6.7 m s⁻¹. The treadmill speed was calibrated by digitizing a painted mark on the tread belt as it travelled along the length of the treadmill. Stride frequency was determined directly from the video recordings, and stride length was obtained by dividing the forward velocity (v) by the corresponding stride frequency. From the duration of the contact phase of each foot (t_c) and the swing time (t_s), the duty factor (fraction of the stride in which each foot is in contact with the ground) was calculated. The step length (L_c), defined as the horizontal distance travelled by the body COM during foot contact, was estimated by multiplying the forward velocity of the bird by t_c .

The mechanical-energy fluctuation of the COM was calculated directly from the motion of the body obtained from our video recordings. Owing to the importance of accurately locating the COM from kinematic data, we developed an anatomical model of the ostrich trunk similar to that of Fedak *et al.* (1982), which allowed us to identify the COM from the location of key anatomical landmarks. The carcass of an ostrich, different from the animals used in the treadmill experiments but of similar mass (67.2 kg) and stature, was disarticulated and frozen. The COM was located as described in Fedak *et al.* (1982) and expressed relative to the cranial aspect of the ilium where it meets the sixth thoracic vertebra (point A) and the caudal end of the prominent ridge on the midline of the dorsal aspect of the ilium (post-acetabular; point B). These points were chosen because they could most easily be located on the living animal with the least amount of variability. The COM was located by drawing an orthogonal to the vector BA (ventral direction), the length of which was 85% of vector BA with its origin located 73% along this vector. The location of the two landmarks on the living animal was made possible by positioning a wand fitted with two in-line retro-reflective markers over each landmark. By digitizing the wand markers, the anatomical landmarks could be located by projecting a known distance from the bottom (lower wand) marker along the axis created by the upper and lower wand markers. Although the approach used here to track the COM does not take into account the effect of independent limb movement on the position of the overall body COM (a problem that can be overcome by using force-plate measurements; Blickhan & Full 1992), it provides an accurate assessment of the movement of the body COM. This is because the movement of the limbs generally has a small effect on the position of the overall body COM compared with trunk movement, owing to their proportionately small mass relative to body mass (less than 20% as measured in this study) and because force-plate and kinematic analyses have been shown to be in close agreement (Belli *et al.* 1993).

The displacement of the body COM was smoothed using a fourth-order zero-lag Butterworth low-pass filter and normalized to one complete stride using a cubic spline interpolation to 100 points. The cutoff frequency was determined separately for each trial using a residual analysis of the difference between filtered and unfiltered data (Winter 1990). The instantaneous velocities of the body COM in the x and y directions were calculated from the derivative of the displacement of the body COM with respect to time. Using the displacement and velocity of the COM, the horizontal and vertical kinetic energies of the COM (E_{kh} and E_{kv} , respectively), the potential energy of the COM (E_p) and the total energy of the body COM (E_{tot}) were calculated, where E_{tot} is simply the instantaneous sum of E_p , E_{kh} and E_{kv} . Traditionally, the mechanical work of moving the body COM (W_{ext}) has been associated with elevating and accelerating the body COM (Cavagna *et al.* 1976, 1977). As such, W_{ext} was calculated as the sum of the positive increments of E_{tot} over one complete stride.

To distinguish between inverted-pendulum mechanics and spring-like mechanics of locomotion it is important to quantify the percentage of pendular-energy recovery. This was determined as described by Cavagna *et al.* (1976):

$$\% \text{ recovery} = \frac{W_v + W_h - W_{ext}}{W_v + W_h} \times 100, \quad (2.1)$$

where W_v , the vertical work per stride, is the sum of the positive increments of ($E_p + E_{kv}$), and W_h , the horizontal work per stride, is the sum of the positive increments of E_{kh} . The percentage recovery of mechanical energy is dependent not only on the magnitudes of W_v and W_h but also on the phase between the traces of E_{kh} and $E_p + E_{kv}$, a key feature discriminating pendular and bouncing modes of locomotion. In perfect inverted-pendulum mechanics, E_{kh} and $E_p + E_{kv}$ are 180° out of phase, whereas in a bouncing gait they are 0° out of phase (in phase). We determined the phase difference between the traces of E_{kh} and $E_p + E_{kv}$ over one stride by running a standard unbiased cross-correlation between E_{kh} and $E_p + E_{kv}$ and computing the lag between the traces. Because one complete stride represents two periods, the computed lag can be converted to degrees by multiplying by 720 and dividing by the number of frames in each stride.

(c) Metabolic measurements

Metabolic rates were measured at rest and at seven speeds ranging between 1.0 and 4.0 m s^{-1} using an open-flow metabolic system similar to those described previously by Withers (1977). The rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were measured continuously during each trial, and only steady-state values were used for analysis. Trials were repeated several times, on separate days, and an average net $\dot{V}O_2$ for each speed was calculated by subtracting the resting metabolic rate (measured from birds lying quietly) from the gross values. Although faster running speeds were achieved during our testing, they could not be maintained at a steady pace for long enough for adequate metabolic measurements. The birds ran with their head and neck inside a canopy constructed from clear PVC plastic while environmental air was drawn through the chamber at metered rates via a small opening at the base of the canopy. Water vapour pressure was measured downstream of the canopy using a digital hygrometre (Vaisala HMP41/45, Finland). A continuous sample of the air exiting the pump was dried (Drierite, Hammond Co.) and passed through oxygen (Servomex 500A, UK) and carbon dioxide (Datex CD-102-21-02, Finland) analysers. $\dot{V}O_2$ and $\dot{V}CO_2$ were calculated

as described previously (Withers 1977). The O_2 and CO_2 analysers were calibrated using two calibration-gas mixtures (BOC, Australia): room air and nitrogen gas. The entire system was calibrated before and after testing by bleeding a known flow rate of nitrogen gas into the metabolic chamber and comparing the measured $\dot{V}O_2$ with the theoretical value obtained from the nitrogen dilution (Fedak *et al.* 1981). This was repeated over the range of flow rates used to determine the linearity of our flow meter. The net energy cost of locomotion ($\text{J kg}^{-1} \text{m}^{-1}$) was determined by converting the net oxygen consumption to an energy expenditure using the measured respiratory exchange ratio ($\dot{V}CO_2/\dot{V}O_2$) and the appropriate energy equivalent, and by dividing this latter value by the walking or running speed. To assess whether the animals were relying on aerobic metabolism, blood was sampled after 5 min of exercise at each speed from a catheter placed in the radial vein of the animal. The blood was centrifuged and the plasma was removed, immediately frozen in liquid nitrogen and later analysed for lactate concentration using standard biochemical techniques (Bergmeyer 1984).

(d) Statistical analysis

Data from at least five strides per bird per speed were used to calculate each stride variable, and data from at least three trials per bird per speed were used to calculate metabolic rates. To identify transitions in locomotor variables we fitted regression lines to the data and varied the breakpoints to minimize the least-squares error between the regression equations and the experimental data. A continuous linear or curvilinear relationship was adopted to describe the results if it fitted the entire data range with a higher r^2 value than that obtained with a combination of two regression lines. Moreover, where two linear regressions were not statistically different (i.e. no difference in slopes), a single r^2 value was calculated from the entire dataset.

3. RESULTS

(a) Kinematics

Over the range of speeds examined in this study, the stride length increased linearly (figure 1*a*). Stride frequency, however, showed a curvilinear relationship with speed, increasing less rapidly at faster speeds (figure 1*b*). The ground contact time (t_c) decreased hyperbolically from 0.98 s at 1.1 m s^{-1} to 0.19 s at 6.7 m s^{-1} (figure 1*c*). The duration of the swing phase (t_s) decreased only moderately with speed and can be said to remain much more constant across speed than does t_c (figure 1*d*). Overall, stride frequency was, therefore, determined primarily by changes in t_c . Step length (L_c) also increased in a curvilinear manner with speed (figure 1*e*). The duty factor fell in a smooth manner with no inflection points across the entire speed range tested (figure 1*f*) but decreased more rapidly over slow and intermediate speeds than over faster speeds. The duty factor reached 0.5 at a speed of 3.05 m s^{-1} , indicating the transition to an aerial phase.

(b) Mechanical-energy fluctuations and recovery

At slow speeds, a phase difference of close to 180° was present between the fluctuations of E_{kh} and $E_p + E_{kv}$ (figure 2*a*). The maximum percentage pendular-energy recovery of 55% was observed at 1.1 m s^{-1} (figure 2*b*). At speeds above and below 1.1 m s^{-1} , the phase between E_{kh} and $E_p + E_{kv}$ dropped, as did pendular-energy recovery, resulting in inverted 'U' shapes in the relationships

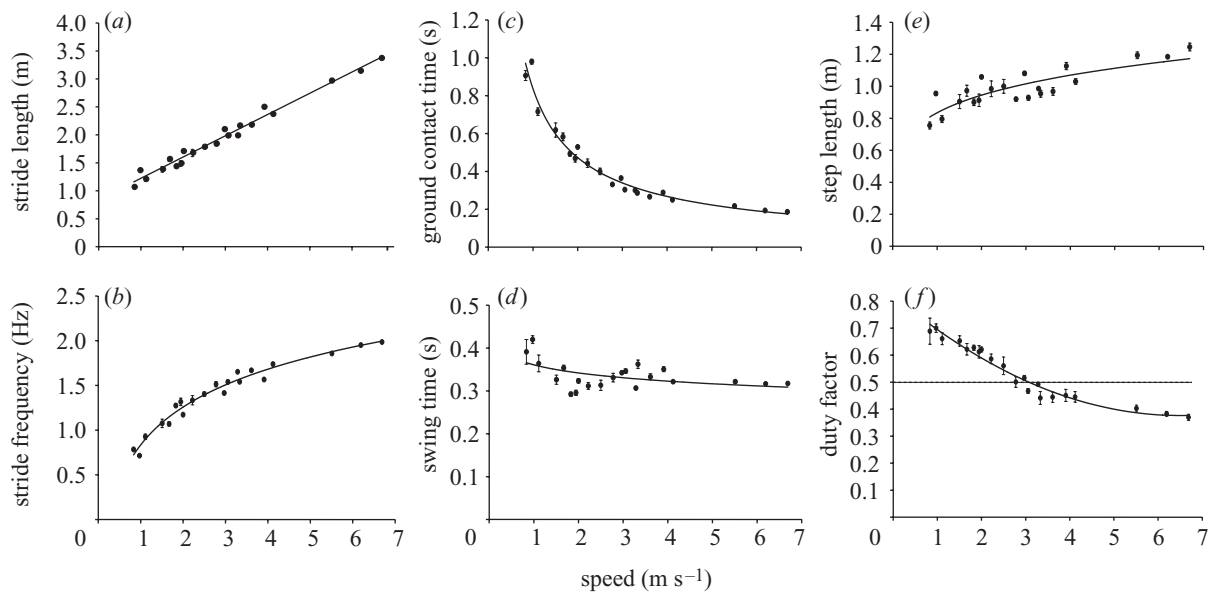


Figure 1. Kinematic variables as functions of locomotor speed (\pm s.e.m.): (a) stride length ($y = 0.38x + 0.84$; $r^2 = 0.98$), (b) stride frequency ($y = 0.611 \ln(x) + 0.8347$; $r^2 = 0.97$), (c) ground contact time ($y = 0.83x^{-0.82}$; $r^2 = 0.98$), (d) swing time ($y = -0.0274 \ln(x) + 0.361$; $r^2 = 0.261$), (e) step length ($y = 0.8341x^{0.18}$; $r^2 = 0.69$), (f) duty factor ($y = 0.0105x^2 - 0.137x + 0.8211$; $r^2 = 0.97$; the dashed line represents the onset of an aerial phase).

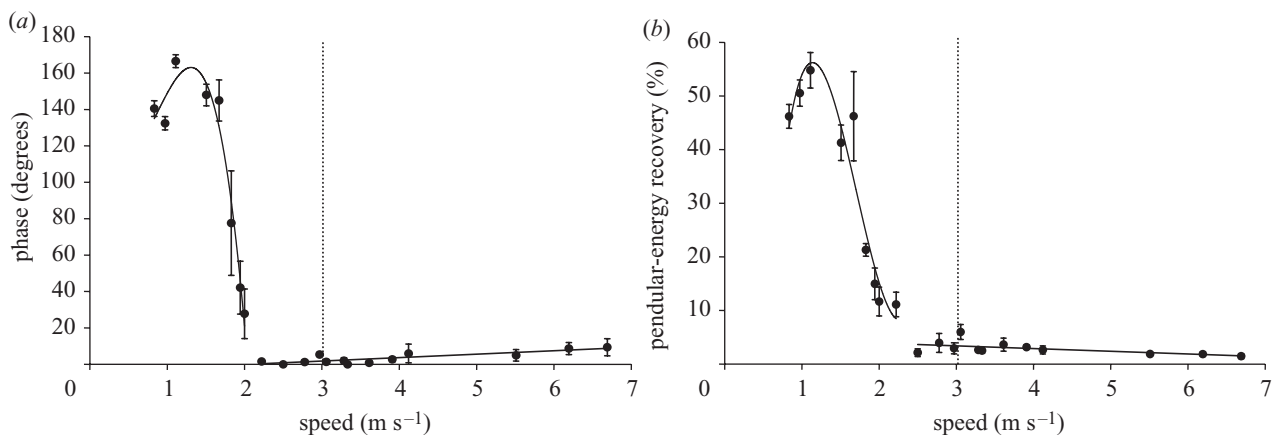


Figure 2. (a) The phase in degrees between E_{kh} and $E_p + E_{kv}$ and (b) the percentage of pendular-mechanical-energy recovery as functions of locomotor speed (\pm s.e.m.). At a phase of 180° the maximum E_{kh} occurs simultaneously with the minimum $E_p + E_{kv}$, whereas at a phase of 0° the minimum and maximum E_{kh} and $E_p + E_{kv}$ occur concurrently. A high percentage of pendular-energy recovery indicates an inverted pendulum gait while a low percentage of pendular-energy recovery indicates bouncing gait. The phase data (a) are fitted with a third-order polynomial between the speeds of 0.8 and 2.0 $m s^{-1}$ ($y = -146x^3 + 381.2x^2 - 243.9x + 158.5$; $r^2 = 0.96$) and a linear regression over faster speeds ($y = 1.89x - 3.91$; $r^2 = 0.71$). The pendular-energy recovery data (b) are fitted with a third-order polynomial between the speeds of 0.8 and 2.2 $m s^{-1}$ ($y = 65.5x^3 - 334.9x^2 + 508.0x - 184.6$; $r^2 = 0.92$) and a linear regression over faster speeds ($y = -0.50x + 4.91$; $r^2 = 0.33$). The dotted lines represent the onset of aerial running.

between these variables and speed over slow and intermediate walking speeds. As speed increased above 1.7 $m s^{-1}$, the phase between E_{kh} and $E_p + E_{kv}$ fell dramatically, with the phase between E_{kh} and $E_p + E_{kv}$ approaching a value of 0° at 2.2 $m s^{-1}$ (figure 2a). The reduction in phase between E_{kh} and $E_p + E_{kv}$ was accompanied by a concomitant drop in pendular recovery of mechanical energy (figure 2b). Typical patterns of the fluctuations in the mechanical energy of the COM for walking and grounded running are presented in figure 3a and b, respectively. For comparison, figure 3c shows the typical fluctuations in mechanical energies during running with an aerial phase.

(c) Mechanical and metabolic work

The W_{ext} required to move 1 kg of body mass 1 m increased throughout slow and intermediate walking speeds until a speed of 2.2 $m s^{-1}$ was reached (figure 4, lower curve). At a speed of *ca.* 2.5 $m s^{-1}$, the W_{ext} increased dramatically, but remained nearly constant thereafter with further increases in speed (figure 4, lower curve). The metabolic cost of locomotion increased throughout walking speeds below 2.0 $m s^{-1}$. An almost horizontal slope of the metabolic cost of locomotion versus speed occurred at speeds above 2.5 $m s^{-1}$ (figure 4, upper curve). However, no metabolic transition was observed as the ostrich engaged an aerial phase at

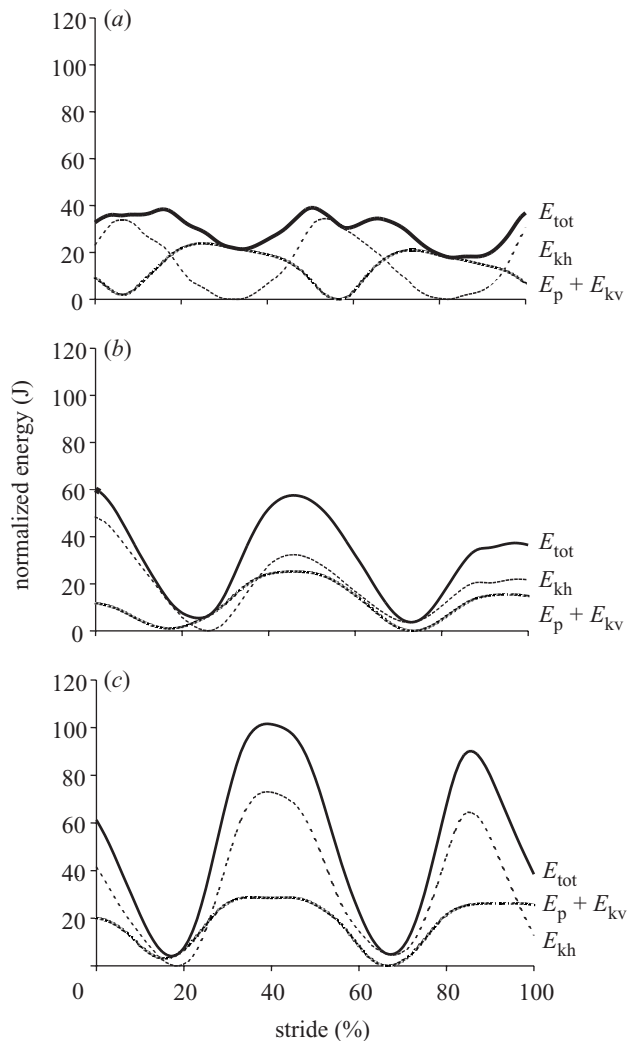


Figure 3. The traces of E_{kh} , $E_p + E_{kv}$ and E_{tot} during (a) walking, (b) grounded running and (c) aerial running. The out-of-phase fluctuations in E_{kh} and $E_p + E_{kv}$ in (a) indicate an inverted-pendulum gait whereas the in-phase fluctuations seen in (b) and (c) indicate a bouncing gait.

3.05 m s^{-1} . The plasma lactate concentration remained below 2 mM at all speeds for which metabolic data were collected, indicating that the animals were relying on aerobic metabolism.

4. DISCUSSION

It has been argued that minimization of metabolic-energy costs is a primary determinant of gait selection in terrestrial animals (Alexander 1989). It has never been investigated, however, whether animals that select between walking, grounded-running and aerial-running gaits also minimize their metabolic cost of locomotion. This is an important question considering that grounded running is a common mode of locomotion, particularly in birds. Using the ostrich as our experimental model, we show that grounded running is the preferred mode of locomotion of the ostrich at intermediate speeds, and that the selection of grounded running over walking results in a minimization of the metabolic cost of locomotion. However, no reduction in the metabolic cost of locomotion is observed at the transition from grounded running to aerial

running, a finding consistent with the absence of discontinuity in mechanical parameters between these two modes of running.

(a) Gait selection

The present study shows that ostriches use an inverted-pendulum walking gait at slow speeds, below 2.2 m s^{-1} . This is indicated by the out-of-phase pattern in the fluctuations of E_{kh} and $E_p + E_{kv}$ (figures 2a and 3a) and the high percentage of pendular-energy recovery at these slow speeds (figure 2b), both of which are typical of walking in bipedal species (Cavagna *et al.* 1976, 1977; Heglund *et al.* 1982; Muir *et al.* 1996). The inverted 'U' shaped relationships between walking speed and both phase and percentage recovery are also characteristic of walking in humans (Cavagna *et al.* 1976) and suggest that a mechanically optimal walking speed exists between 1.0 and 1.5 m s^{-1} in ostriches. A maximum percentage energy recovery of 55% is observed at 1.1 m s^{-1} , but this is somewhat lower than the maximum recovery observed for humans and other avian bipeds (Cavagna *et al.* 1976, 1977; Heglund *et al.* 1982; Muir *et al.* 1996). It is unclear whether this difference is caused by differences in the methods adopted here (kinematic) and in these studies (force-plate approach) to determine mechanical energies or by a true mechanical difference. It is noteworthy that, unlike humans and horses, ostriches show no clear minimum in the mechanical cost of walking ($\text{J kg}^{-1} \text{ m}^{-1}$) over the range of speeds examined here (figure 4), despite what appears to be a mechanically optimal walking speed between 1.0 and 1.5 m s^{-1} . Interestingly, the absence of a minimum in the mechanical cost of walking is consistent with the lack of minima in both the net and gross metabolic costs of walking over these same speeds. It is possible, nonetheless, that at very slow speeds the mechanical and gross metabolic costs of locomotion increase above those seen at 1.0 m s^{-1} , thus resulting in more traditional 'U' shaped relationships in these parameters. Unfortunately, the ostriches examined in this study were uncooperative at such slow speeds and did not walk at a steady pace for long enough to obtain suitable measurements.

At intermediate speeds between 2.5 and 3.05 m s^{-1} , ostriches adopt a grounded-running gait, where the body bounces while maintaining continuous contact with the ground. The transition between the inverted-pendulum walking gait and this bouncing gait occurs between 1.8 and 2.5 m s^{-1} and is characterized by a marked reduction in the phase difference between E_{kh} and $E_p + E_{kv}$ and a marked fall in the percentage energy recovery (figure 2a,b). The transitions in the energy phase and recovery in going from an inverted-pendulum gait to a bouncing gait are abrupt in the ostrich and are comparable with those observed in other birds (Cavagna *et al.* 1977; Heglund *et al.* 1982). Interestingly, our analysis indicates that, over the entire speed range tested, including this transition, ostriches do not exhibit any other speed-dependent kinematic discontinuities (at least in those parameters examined in this study). This is at odds with the studies of Gatesy & Biewener (1991) and Gatesy (1999), who defined gait transition based on inflections of a number of kinematic variables. The reason for this discrepancy may lie in the treatment of kinematic data. For instance, by fitting two linear regressions to our data we can identify

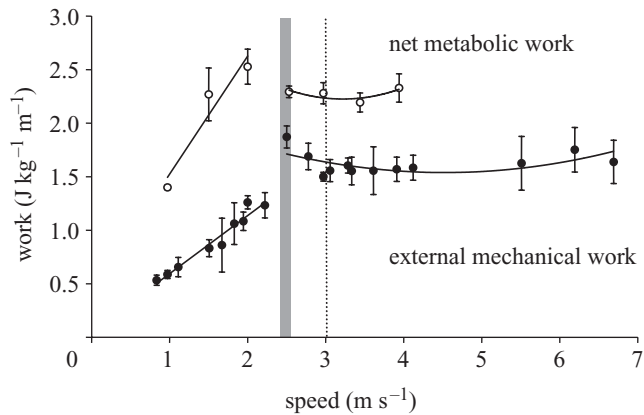


Figure 4. The net metabolic cost of locomotion (open symbols) and the mechanical work of moving the COM (W_{ext} ; filled symbols) as functions of locomotor speed (\pm s.e.m.). Both the metabolic cost of locomotion and W_{ext} increase linearly up to the transition to grounded running ($y = 1.10x + 0.42$; $r^2 = 0.92$ and $y = 0.54x + 0.05$; $r^2 = 0.95$, respectively). After the onset of grounded running, the metabolic cost of locomotion drops significantly ($p < 0.005$) and remains nearly constant with further increases in speed ($y = 0.17x^2 - 1.12x + 4.04$; $r^2 = 0.60$); W_{ext} increases significantly ($p < 0.001$) at the onset of grounded running and likewise remains nearly constant with further increases in speed ($y = 0.04x^2 - 0.38x + 2.40$; $r^2 = 0.35$). The transition to an aerial phase is not associated with any breakpoint in either metabolic cost or W_{ext} . The shaded line and dashed line represent the onset of grounded running and aerial running, respectively.

significant ($p < 0.001$) reductions in the slopes of both stride frequency and swing time versus speed at 2.2 and 2.0 m s⁻¹, respectively. These apparent discontinuities are consistent with those previously used by Gatesy & Biewener (1991) and Gatesy (1999) to define the walk–run transition. However, our data are a better fit (as indicated by a higher r^2 value) to continuous curvilinear functions, and the differences in the linear regressions are probably artefacts of replacing smooth curvilinear data with linear segments. It is possible that a similar artefact may also have been present in previous studies of avian terrestrial locomotion.

It is noteworthy that the transition from an inverted-pendulum walking gait to grounded running occurs at a dynamically similar speed to that of the walk–run transition in humans and many other animals. Dynamic similarity is defined by the Froude number (Alexander 1989), a dimensionless speed equal to v^2/gl , where v is the forward velocity of the animal, g is the gravitational-acceleration constant and l is the length of the pendulum (leg length from hip to ground). From an impressive number of studies of animals spanning a large size range, it is apparent that, as a general rule, legged animals including humans change from a walk to a run at a Froude number of ca. 0.5 (Alexander 1989; Kram *et al.* 1997). Ostriches adopt a grounded-running gait over a range of Froude numbers between 0.54 and 0.68.

At speeds above 3.05 m s⁻¹ ostriches adopt an aerial-running gait, as indicated by a duty factor of less than 0.5. The occurrence of an aerial phase is the kinematic characteristic that has most commonly been used to distinguish walking from running (Hildebrand 1985). It is

generally believed that duty factor decreases in a gradual manner with increasing speed in avian bipeds, thus resulting in a smooth transition to an aerial phase (Gatesy & Biewener 1991), although more abrupt transitions in duty factor have been observed in walking and running magpies (Verstappen & Aerts 2000). For this reason, among others, using the occurrence of an aerial phase as an appropriate means of discriminating different gaits has been debated (McMahon 1985; Blickhan & Full 1987; Gatesy & Biewener 1991). In this study, the transition to aerial running was characterized by a gradual fall in duty factor with speed (figure 1*f*). Moreover, the occurrence of aerial running is not associated with any other abrupt kinematic transitions (figure 1*a–e*), neither does aerial running present a distinct pattern of energy fluctuations of the COM (highlighted in figure 3*b,c*). In line with Alexander (1989), who defined gait transition as a discontinuous change in the pattern of one or more speed-dependent locomotor characteristics, it should therefore be concluded that grounded and aerial running belong to the same locomotor paradigm (bouncing gait) and our results strengthen the claim that duty factor alone should not be used to identify distinct gaits.

(b) *A metabolic explanation for gait selection in ostriches?*

Ideally, to determine that an animal's gait selection minimizes its metabolic cost of locomotion it must be shown that the metabolic cost of using its preferred gait is less than that of using its non-preferred gait. This is the approach that has been used in humans and horses to establish that gait selection over most of their speed ranges minimizes the metabolic cost of locomotion. However, when it is difficult to train an animal to use different gaits at the same speed, the association between gait selection and metabolic energetics is based on the existence of a breakpoint favouring a lower cost of locomotion when an animal reaches its natural gait-transition speed (as observed in humans and horses).

A sharp transition favouring a lower metabolic cost of locomotion is present at the transition from an inverted-pendulum walk to a grounded run in ostriches (figure 4, upper curve). This finding supports the view that gait selection between an inverted-pendulum gait and a bouncing gait is a general mechanism by which the metabolic costs of locomotion are minimized (Alexander 1989). Fedak & Seeherman (1979) also showed a transition in the speed dependency of the rate of oxygen consumption in a single ostrich, but did not provide any information regarding the mechanics of locomotion at this transition. It is interesting to note that the graphs of both the metabolic cost of locomotion (or metabolic work) and external mechanical work versus speed in ostriches (figure 4) resemble remarkably those of humans and horses undergoing a transition between walking and running (trotting) gaits (Minetti 2000). The simultaneous break in metabolic work and mechanical work is consistent with the hypothesis that a shift in the mechanisms responsible for generating the work of locomotion (pendular during walking and elastic recoil during running) is responsible for the observed reduction in the metabolic cost of locomotion at the transition to grounded running. This finding also further strengthens the hypothesis of Kram *et al.*

(1997) that a gait transition at a Froude number of 0.5 may, in general, be representative of speeds at which the mechanical-energy conservation from an inverted-pendulum mechanism becomes inadequate for maintaining economical locomotion compared with the elastic mechanism of running. Our data support this hypothesis given that the transition between these two mechanisms at a Froude number close to 0.5 results in a reduction in the metabolic cost of locomotion. With respect to the above arguments it is important to note that the increase in W_{ext} at the transition to a bouncing gait is only 'apparent' work and does not accurately reflect the mechanical work done by the muscles (Minetti *et al.* 1999) because the energy returned from the elastic energy stored in the limb is not accounted for and, thus, W_{ext} greatly overestimates muscle work. It should also be pointed out that the percentage recovery and W_{ext} are themselves subject to error owing to the simultaneous positive and negative work done by the individual limbs during double support (Donelan *et al.* 2002). Therefore, while traditional inverted-pendulum measurements are useful for revealing general gait mechanisms, care must be used when associating them with mechanical or muscle work and efficiency measures.

Although selecting between an inverted-pendulum gait and a grounded-running gait minimizes the metabolic cost of locomotion in ostriches, it does not follow that it is the metabolic cost of locomotion *per se* that drives this gait transition, a notion that has come to be known as the 'metabolic trigger' hypothesis. The metabolic-trigger hypothesis has been argued against (Farley & Taylor 1991; Hreljac 1993; Minetti *et al.* 1994; Brisswalter & Mottet 1996) on the basis that self-selected gait transition can occur at non-energetically-optimal speeds, despite the obvious optimization at slower and faster speeds. More recently, horses have been found to switch repeatedly between trotting and galloping over a narrow range of speeds where galloping is metabolically optimal (Wickler *et al.* 2003). From this, it was concluded that conflicting signals, other than metabolic cost, are probably responsible for the trot-gallop transition. Ostriches would have to be trained both to walk and run below and above their gait-transition speed to establish whether or not the walk-grounded-run transition adheres to the metabolic-trigger hypothesis. Nevertheless, while metabolic-energy consumption *per se* may not be the primary stimulus for eliciting gait transitions, this does not exclude the possibility that the speeds and associated gaits favourable to lowering the metabolic cost of locomotion have probably been selected for through evolution to make better use of the limited energy sources available. In this respect, it has been shown that humans and other animals will avoid those speeds that result in unnecessarily high costs of locomotion (Hoyt & Taylor 1981; Minetti *et al.* 2003).

While gait selection favouring inverse-pendulum walking and grounded running at low and intermediate speeds, respectively, in ostriches can be explained on the basis of minimizing the metabolic cost of locomotion, this is unlikely to explain the adoption of aerial running at faster speeds (figure 4). The absence of a discontinuity in the energy cost of locomotion over the range of speeds that cross the transition between grounded running and aerial running is consistent with the absence of a discontinuity

in the mechanical work of locomotion at the onset of aerial running. The adoption of an aerial run at higher speeds might be the result of a mechanical factor. Alexander (1984) proposed that the Froude number, which expresses the ratio of the centripetal force to the gravitational force during walking, may play an important role in determining the speed at which an animal becomes airborne, with a Froude number of 1 representing the upper limit to the speed at which an animal adopting an inverted-pendulum mechanism can remain in contact with the ground. Based on this theory the predicted speed limit above which aerial running becomes a necessity in ostriches is 3.0 m s^{-1} , remarkably close to the actual aerial transition speed of 3.05 m s^{-1} . Here, however, the birds undergo their transition to aerial running from grounded running and not from walking; therefore, much of the energy that will determine whether ostriches maintain contact with the ground is not centrifugal, as is the case in the transition from an inverted-pendulum gait, but is the elastic energy provided by the limb spring. This is simply because ostriches during grounded running are already behaving as springs prior to the occurrence of the aerial phase, and it follows that the close agreement between the Froude number and the actual aerial transition speed may be coincidental. The extent to which the transition from grounded running to aerial running in the ostrich can be explained by the elastic potential energy of the limb spring remains to be established.

(c) *Ostriches compared with humans*

Perhaps one of the most intriguing questions that arises from our findings is why the transition to a bouncing gait is associated with an aerial phase in humans but not in ostriches or in most terrestrial bird species studied so far. For a bouncing gait to be effective, the spring in the leg must undergo sufficient strain, which in turn requires a sufficient muscle-tendon force. As such, the adoption of grounded running in ostriches is likely to be favoured by their compliant tendons. The primary springs in the legs of the ostriches are the gastrocnemius tendon and the tendons of the digital flexors. Most of these tendons are extraordinarily long (nearly 80 cm) and thin. As a result, they are much more compliant than the corresponding tendons in humans and offer a greater scope for elastic-energy storage (Alexander *et al.* 1979). Consequently, ostriches do not need to generate as large a muscle-tendon force to stretch their tendons as do humans. This may explain why ostriches can adopt a bouncing gait in the absence of an aerial phase. If ostriches were to possess adequate muscle-tendon force to store the elastic strain energy required to produce the mechanical work of locomotion during grounded running, then the additional muscle-tendon force that would probably result from a sudden transition to an aerial phase would be superfluous and undesirable with respect to the economy of locomotion (Kram & Taylor 1990).

In humans, the primary leg springs are the tendon crossing the ankle joint and the spring in the arch of the foot (Ker *et al.* 1987). When humans run, the presence of an aerial phase greatly increases the peak ground reaction force, which subsequently increases the force in these tendons and allows for a substantial storage of elastic strain energy. However, when humans voluntarily switch to a

grounded run rather than a normal run, the peak ground reaction force is only a fraction of that during normal running owing to a longer foot contact time (McMahon *et al.* 1987). The strain in the tendon springs during grounded running may therefore be significantly reduced (depending on their effective mechanical advantage the ratio of the extensor-muscle moment arm to the ground-reaction-force moment arm about a joint; Biewener 1989) compared with normal running, and, even though grounded running in humans is characteristic of a bouncing gait (McMahon *et al.* 1987), it is possible that much of the bounce may be caused more by the lengthening and shortening of the limb muscles than by the tendons. Furthermore, grounded running in humans involves considerably larger knee flexion, which requires much greater extensor-muscle force (McMahon 1985). Both of these factors may explain why grounded running in humans is nearly 50% more expensive than normal running at the same speed (McMahon *et al.* 1987), which in turn offers a very reasonable explanation as to why humans avoid this mode of locomotion. It is important to note, however, that there are certain circumstances in which grounded running in humans is, in fact, their preferred gait. McMahon (1985) demonstrated that humans running on a very compliant surface prefer to run without an aerial phase. Whether humans chose to run without an aerial phase because it is energetically optimal is still not known. However, an insightful study by Kerdok *et al.* (2002) reported that as humans run on more compliant surfaces they significantly reduce their metabolic cost of locomotion, which they postulated was the result of the energy provided by the rebound of the running surface.

In conclusion, by demonstrating that the selection between an inverted-pendulum walking gait and grounded running in ostriches results in a minimization of the metabolic-energy costs of locomotion this study significantly strengthens the argument that a minimization of metabolic-energy costs is an important determinant of gait selection in terrestrial animals. However, this may not apply to the transition between grounded running and aerial running. The lack of both metabolic and mechanical breakpoints at this latter transition supports the notion that aerial running and grounded running are not distinct gaits. More investigation into the mechanics and energetics of legged locomotion will, nevertheless, be required to determine whether a minimization of the metabolic cost of locomotion best explains the adoption of grounded running by so many animal species over the range of speeds where both inverted-pendulum walking and aerial running are possible.

The authors thank S. K. Maloney for his help in data collection, P. C. Withers for his help in obtaining metabolic measurements, and two anonymous reviewers for their valuable suggestions and criticisms. This project was funded by an Australian Research Council grant to P.A.F. and D.G.L.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.