

Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou *Eudromia elegans*

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Whereas humans and certain birds experience an abrupt change in locomotor dynamics when shifting from walks to runs, a smooth walk–run transition characterizes many ground-dwelling birds. This study defines the biomechanical distinction between walks and runs in the Elegant-crested Tinamou *Eudromia elegans* using ground reaction forces. Three birds were filmed at 250 Hz from a lateral view as they moved over a force plate built into a trackway. Centre of mass mechanics and kinematic variables were analysed in 81 steady-speed trials that represented a speed range from 0.66 to 2.78 m/s. *E. elegans* undergoes two speed-related changes in locomotor mechanics. The first is a shift from walking strides that utilize vaulting mechanics to low-speed runs that exhibit bouncing mechanics; this transition occurs at Froude numbers between 0.4 and 0.6. Such low-speed runs exhibit duty factors exceeding 0.5 and, hence, lack an aerial phase between steps. The second transition, from grounded running to aerial running, occurs when duty factors decrease below 0.5. Grounded running in birds may enhance vision by stabilizing visual stimuli over the retina. The eventual incorporation of an aerial phase during running enables increased locomotor speeds primarily through longer stride lengths.

Birds differ from other vertebrates in many aspects of their biology. An unusual feature of the terrestrial locomotion of ground-dwelling birds is the capacity to move at medium to high speeds without including an aerial phase (period of suspension when no limbs are in contact with the ground) between steps. Although some species (e.g. Ostrich *Struthio camelus*, Emu *Dromaius novaehollandiae*, Greater Rhea *Rhea americana*, Brown Kiwi *Apteryx australis*, Wild Turkey *Meleagris gallopavo*, Helmeted Guineafowl *Numida meleagris*, Painted Quail *Coturnix* spp., formerly *Excalfactoria*) eventually incorporate an aerial phase at their highest speeds (Gatesy & Biewener 1991, Gatesy 1999, Abourachid & Renous 2000), others (e.g. Bobwhite *Colinus* spp., Mallard and Indian Runner ducks *Anas platyrhynchos*, Southern Cassowary *Casuarius casuarius*, Japanese Quail *Coturnix japonica*) remain grounded, alternating between periods of single and double limb supports, throughout their

ranges of speed (Gatesy & Biewener 1991, Abourachid & Renous 2000, Abourachid 2000, 2001, Reilly 2000). The ratio of single limb support duration to stride duration is known as duty factor, a footfall-based parameter that has been used to distinguish walks from runs (Hildebrand 1976): walks occur at duty factors greater than or equal to 0.5 whereas runs occur at lower duty factors. In bipeds, an aerial phase occurs when the duty factor falls below 0.5. By this criterion, walking would be considered to be the primary mode of terrestrial locomotion in ground-dwelling birds.

Walking and running dynamics involve much more than footfall patterns. The complex movements of the limbs, torso, neck and head during terrestrial locomotion can be summarized by the movement of the centre of mass (COM). Two basic patterns of COM mechanics have been observed in birds during terrestrial locomotion (Cavagna *et al.* 1977, Heglund *et al.* 1982, Muir *et al.* 1996, Griffin & Kram 2000, Rubenson *et al.* 2004). At slow speeds, limbs function as stiff struts so that the external mechanical energies of the bird's COM fluctuate in a manner that

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resembles an inverted pendulum (vaulting mechanics). Gravitational potential energy (E_p) of the COM cycles out of phase with total kinetic energy ($E_{k,tot}$) so that the COM is at its highest position during midstance when kinetic energy is at a minimum. Such dynamics allow for pendulum-like exchange of external mechanical energy that provides an opportunity to reduce muscular effort and, hence, improve locomotor efficiency. At faster speeds tetrapod limbs are more compliant, such that the COM no longer rises during the first half of stance but rather drops to its lowest position at midstance (spring-mass or bouncing mechanics). The resulting in-phase fluctuations in E_p and $E_{k,tot}$ are inconsistent with pendular mechanisms, yet some recovery of mechanical energy is still possible via the storage and release of elastic strain energy in the musculoskeletal system of the limbs.

There is a theoretical limit to how quickly tetrapods can move and still take advantage of pendular mechanics (Alexander 1976, Usherwood 2005). As the COM moves in an arc over a stiff limb it resembles a mass attached to the end of a string moving in a circle. For the mass to continue moving in a circle a centripetal force (mv^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) must cause an acceleration of the mass towards the centre of the circle. In walking the centripetal force is provided by gravitational force (mg , where g is acceleration due to gravity). The COM will continue to move about the arc as long as the centripetal force required to maintain the movement does not exceed gravitational force. The ratio of the required centripetal force to gravitational force is known as a Froude number ($Fr = v^2/gl$); Fr also reflects the ratio of $E_{k,tot}$ to E_p . Therefore, animals must switch from pendular mechanics to spring-mass mechanics either at or before $Fr = 1$. In reality, animals switch mechanics when moving at much lower Fr because of the prohibitive cost of swinging a limb faster than its natural frequency (Usherwood 2005). Among bipeds, humans transition from a walking gait to a running gait at $Fr \sim 0.4$ – 0.6 (Alexander 1977, Gatesy & Biewener 1991) and, similarly, crows Corvidae transition from a walking gait to a hopping gait at $Fr \sim 0.5$ (Hayes & Alexander 1983). As duty factor is inversely related to Fr (Alexander & Jayes 1983, Hayes & Alexander 1983), gaits used above these critical Fr values typically display aerial phases (duty factor < 0.5).

It is well established that striding birds use pendular mechanics during walking and bouncing mechanics

during aerial running (Cavagna *et al.* 1977, Heglund *et al.* 1982, Muir *et al.* 1996, Griffin & Kram 2000), but what is the mechanical nature of their grounded high-speed locomotion? In this study, we examine whether high-speed grounded locomotion conforms more closely to mechanical expectations for walking (vaulting mechanics) or running (bouncing mechanics). Using kinetic data, Clark and Alexander (1975) found bouncing mechanics in Japanese Quail across a speed range of 0.35–1.4 m/s and, because quail rarely incorporate an aerial phase (Gatesy & Biewener 1991), these are likely to be grounded runs. Kinematic support for grounded running also exists (Gatesy & Biewener 1991). Gatesy (1999) observed changes in limb kinematics during grounded locomotion in Helmeted Guineafowl suggestive of a shift from vaulting to bouncing mechanics prior to incorporation of an aerial phase. Similarly, Rubenson *et al.* (2004) used changes in hip height during stance phase to infer that Ostriches transition from vaulting mechanics to bouncing mechanics before incorporating an aerial phase. However, Ostriches are highly derived cursors that do not have the capacity for flight; hence they may differ from the general avian condition. Indeed, at high Fr values cursorial mammals have lower duty factors than non-cursorial mammals (Alexander & Jayes 1983). The goal of this study was to examine relationships among gait, locomotor mechanics (based on kinetic data), and the presence or absence of an aerial phase in a more generalized basal bird, the Elegant-crested Tinamou *Eudromia elegans* (hereafter Tinamou). These Neotropical ground-dwelling birds are related to the ratites but are capable of taking flight when startled.

METHODS

The kinetics and kinematics of terrestrial locomotion were analysed in three Tinamous (623–865 g). The birds were filmed in lateral view at 250 Hz using an NAC camera (HSV-500, Simi Valley, CA, USA) as they moved over a Kistler force platform (plate type 9281B, Amherst, NY, USA) built into a 4.9-m trackway. The force platform longitudinal length (0.6 m) was adequate to capture between two and five steps during each trial depending on the speed at which the birds moved. The force platform recorded vertical, fore–aft (longitudinal) and mediolateral (transverse) ground reaction forces (GRFs) at 1000 Hz. Video and force data were synchronized using Motus version 7.2.6 (Peak Performance Technologies, Centennial, CO, USA).

Locomotor kinematics

Reflective markers were attached to the tip of the middle toe, synsacrum (between the femoral heads, approximating the acetabulum) and breast (between the furcula and keel). The markers were digitized using Motus version 7.2.6 software (Peak Performance) at touchdown, temporal midstance and liftoff of each foot. The forward speed of the birds was calculated videographically using the travel time of the breast marker across two 30-cm intervals marked on the back wall of the trackway and overlying the force platform. Only trials that differed in velocity by less than 10% between the initial and final intervals (steady speed) were analysed further [$100 * |(v_1/v_t) - (v_2/v_t)|$, where v_1 , v_2 and v_t are the forward velocity of the first half of the trial (30 cm), the second half of the trial (30 cm) and the whole trial (60 cm), respectively]. These trials also displayed balanced braking and propulsive components of their forward velocity profiles estimated from GRFs (see below).

Kinematic variables included duty factor (support duration/stride duration), Froude number ($Fr = v_t^2/gl$, where v_t is forward speed, g is gravitational acceleration, 9.81 m/s^2 , and l is hip height measured as the perpendicular distance from the platform surface to the synsacrum marker at temporal midstance, $\sim 0.17 \text{ m}$; Alexander & Jayes 1983), relative stride length (stride length/ l) and stride frequency (stride duration $^{-1}$).

Centre of mass mechanics

A customized LabView program (National Instruments, Austin, TX, USA) was used to calculate fluctuations in kinetic (E_k) and gravitational potential (E_p) energies of the COM from the GRFs following Cavagna *et al.* (1977) and Willey *et al.* (2004). Vertical (minus body weight), fore–aft and mediolateral GRFs were divided by the body mass to determine acceleration in each direction. Each acceleration was then integrated once to obtain velocities of the COM in the three directions, and vertical velocity was further integrated to obtain vertical displacement of the COM. Average forward speed was used as the integration constant for fore–aft velocity, whereas vertical and mediolateral integration constants were estimated as the mean values for vertical and mediolateral records. Velocities were then used to calculate E_k for each direction as $E_k = 1/2mv^2$, where m is the animal's mass and v is velocity.

Summing vertical, fore–aft and mediolateral E_k yielded total kinetic energy ($E_{k,tot}$). Gravitational potential energy was computed as $E_p = mgh$ where h is the vertical displacement of the COM. Lastly, total external mechanical energy ($E_{m,tot}$) was computed as $E_{k,tot} + E_p$.

The phase shift between E_p and $E_{k,tot}$ was calculated by dividing the time difference between the minimum values of E_p and $E_{k,tot}$ by the duration of the stride and then multiplying that value by 360° (Cavagna *et al.* 1977). Two external mechanical energy patterns were identified based on the phase shift between E_p and $E_{k,tot}$ minima: vaulting mechanics (E_p and $E_{k,tot}$ fluctuate out of phase; phase shifts $> 90^\circ$) and bouncing mechanics (E_p and $E_{k,tot}$ fluctuate in phase; phase shifts $< 90^\circ$). Trials with bouncing mechanics were further subdivided into grounded runs (duty factors ≥ 0.5) and aerial runs (< 0.5).

The amount of external mechanical energy recovered via pendular mechanics was calculated following Blickhan & Full (1992):

$$\%R = 100 * [(\Delta E_p + \Delta E_{k,tot}) - \Delta E_{m,tot}] / (\Delta E_p + \Delta E_{k,tot})$$

where ΔE_p , $\Delta E_{k,tot}$ and $\Delta E_{m,tot}$ are the sums of the positive increments of the E_p , $E_{k,tot}$ and $E_{m,tot}$ profiles, respectively.

A repeated-measures ANOVA was performed using SYSTAT (version 11) software to evaluate differences in locomotion between the individual birds. The independent variable was bird identity and the dependent variables were speed, Froude number, duty factor, phase shift, energy recovery, relative stride length, stride frequency and peak vertical force. Because some significant differences were found a *post-hoc* analysis was performed to determine which individuals were different.

To illustrate trends in the data on the graphs both linear ($y = ax + b$) and non-linear ($y = ax^b$) regressions were executed using SYSTAT (version 11) software for phase shift, per cent recovery, duty factor, peak vertical force, relative stride length, and stride frequency vs. Froude number and phase shift vs. duty factor. For each variable pair, the adjusted R^2 from the linear regression was compared to with mean-corrected R^2 from the non-linear regression to determine the best fit curve. The majority of trends were non-linear, except the linear trend of peak vertical force vs. Froude number for which the adjusted R^2 for the linear regression was greater than the mean-corrected R^2 for the non-linear regression.

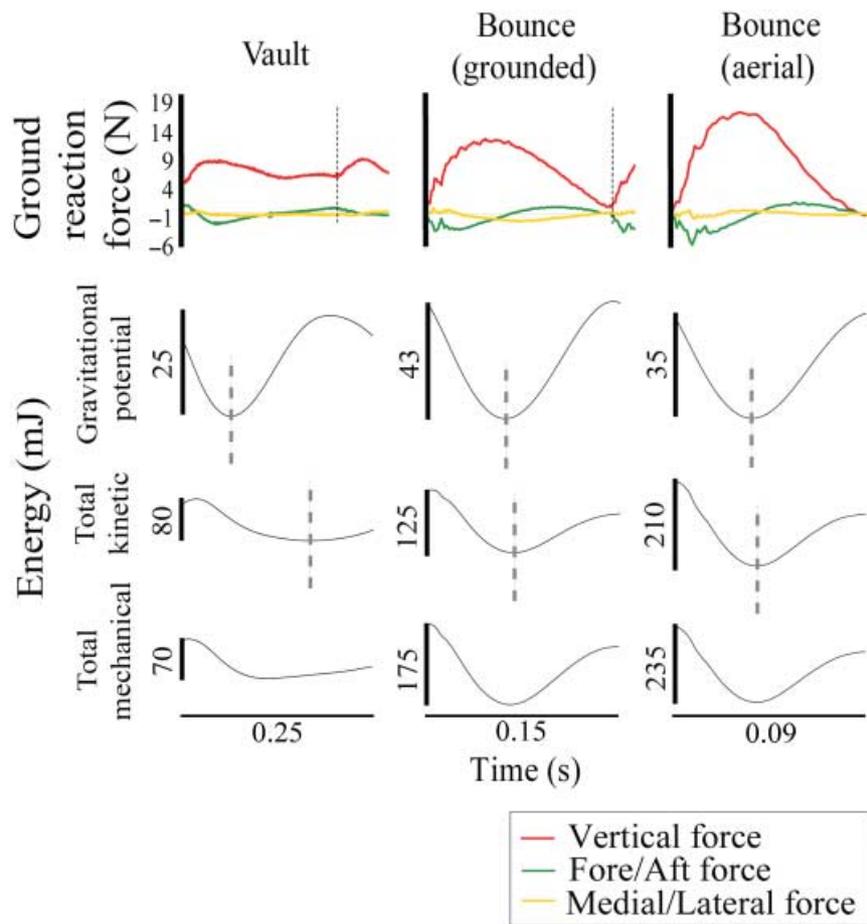


Figure 1. External mechanical energy profiles for representative trials exhibiting vaulting mechanics (forward velocity, $v_t = 0.64$; duty factor, $d = 0.69$; Froude number, $Fr = 0.25$), grounded bouncing mechanics ($v_t = 1.56$; $d = 0.56$; $Fr = 1.57$) and aerial bouncing mechanics ($v_t = 2.78$; $d = 0.39$; $Fr = 4.48$). Illustrated are (top to bottom) ground reaction forces, gravitational potential energy, total kinetic energy and total external mechanical energy during a single step. The vertical dotted lines in the ground reaction force profiles indicate the touchdown of the contralateral foot; the vertical dashed lines in the energy profiles indicate the minima of the gravitational potential and total kinetic energy profiles.

RESULTS

Eighty-one steady-speed trials were captured with speeds ranging from 0.66 to 2.78 m/s; the Tinamous refused to move at lower or higher speeds in the laboratory. Similar locomotor patterns were observed between individuals in relation to speed, Froude number, duty factor, relative stride length and peak vertical force. However, individual differences were observed in phase shift ($P = 0.014$), stride frequency ($P < 0.001$) and energy recovery ($P = 0.006$). *Post-hoc* analyses revealed that Tinamou A differed from Tinamous B and C, but Tinamous B and C were similar. These differences could be a result of Tinamou A preferentially moving at slow speeds (0.76–1.53 m/s),

whereas Tinamous B and C moved at greater ranges of speed (0.64–2.78 and 0.66–1.83 m/s, respectively). Accordingly, because Tinamou A generally moved more slowly, its phase shift and energy recovery values were generally higher and its stride frequency values were generally lower than Tinamous B and C.

Figure 1 illustrates the vertical, fore–aft and mediolateral GRFs and their associated $E_{k,tot}$, E_p and $E_{m,tot}$ profiles for representative trials with vaulting and bouncing (grounded and aerial) mechanics. Vaulting mechanics were observed only at the slowest speeds, whereas Tinamous were capable of utilizing bouncing mechanics throughout the speed range observed (Fig. 2a). Bouncing mechanics (phase shift $< 90^\circ$) were used in the majority of the trials

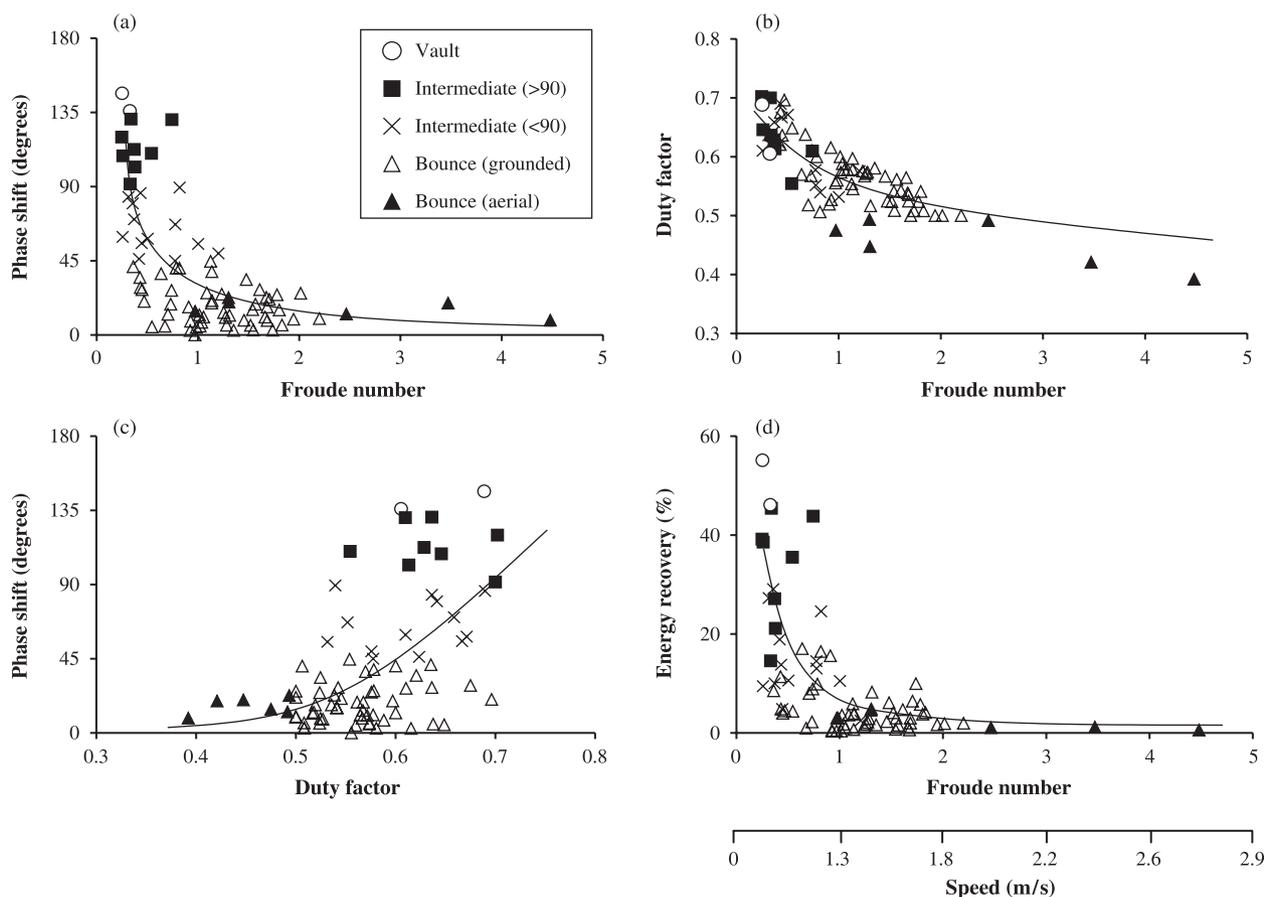


Figure 2. (a) Phase shift vs. Froude number (non-linear regression line: $a = 25.2$, $b = -1.11$; mean corrected $R^2 = 0.577$). With increasing Fr , Tinamous generally shift from moving with vaulting mechanics (phase shift $> 135^\circ$) through intermediate mechanics (vaulting-like mechanics $135\text{--}90^\circ$; bouncing-like mechanics $90\text{--}45^\circ$) to bouncing mechanics ($< 45^\circ$). (b) Duty factor vs. Fr (non-linear regression line: $a = 0.56$, $b = -0.14$; mean corrected $R^2 = 0.689$). (c) Phase shift vs. duty factor (non-linear regression line: $a = 530$, $b = 4.95$; adjusted $R^2 = 0.295$). (d) Percentage energy recovery vs. Fr (non-linear regression line: $a = 5.68$, $b = -1.34$; mean corrected $R^2 = 0.517$).

(87.6%). Because phase shifts deviating substantially from perfect vaulting (180°) or bouncing (0°) mechanics were commonly present, we represent these trials as displaying intermediate mechanics in Figures 2 and 4 ($45\text{--}135^\circ$, following Ahn *et al.* 2004).

Tinamous exhibited duty factors ranging between 0.39 and 0.70 (Fig. 2b, Table 1). Aerial phases (duty factor < 0.5) were observed in only 7.4% of trials, all of which followed phase shift expectations for bouncing mechanics. Only two of the three birds ran with aerial phases; aerial trials in these birds occurred at distinct Fr values (Tinamou A displayed aerial trials at $Fr \sim 1$, whereas Tinamou B exhibited aerial phases at $Fr > 2$, see Fig. 2b). Grounded trials (duty factors ≥ 0.5 , Fig. 3) constituted the remainder of the sample, including all strides with vaulting

mechanics as well as 92% of trials for which bouncing mechanics were observed. As such, duty factor cannot be regarded as a clear predictor of mechanics for this sample: although vaulting seems invariably associated with relatively high duty factors (≥ 0.5), only 8% of the trials exhibiting bouncing mechanics were accounted for by low (< 0.5) duty factors. Furthermore, there was broad overlap between duty factor values for walking (vaulting) and grounded running trials (Fig. 2c).

Froude numbers (Fr) in this study ranged from 0.25 to 4.48 (Table 1). Tinamous using vaulting mechanics tended to move with Fr at or below the 0.4–0.6 mechanical transition zone determined empirically for terrestrial tetrapods (Alexander 1977, Alexander & Jayes 1983, Gatesy & Biewener 1991); only one

Table 1. Centre of mass mechanics and footfall parameters in Elegant-crested Tinamou.

Mechanics	Phase shift	n	Duty factor	Froude number	% Recovery
Vaulting	$> 90^\circ$	10	0.64 ± 0.05 (0.55–0.70)	0.38 ± 0.15 (0.25–0.74)	36.7 ± 12.4 (14.6–55.1)
Bouncing (grounded)	$< 90^\circ$	65	0.57 ± 0.05 (0.50–0.70)	1.08 ± 0.50 (0.26–2.20)	6.41 ± 6.53 (0.32–29.1)
Bouncing (aerial)	$< 45^\circ$	6	0.45 ± 0.04 (0.39–0.49)	2.33 ± 1.41 (0.97–4.48)	2.54 ± 1.87 (0.57–4.83)

Values are means \pm se (min. – max. range).

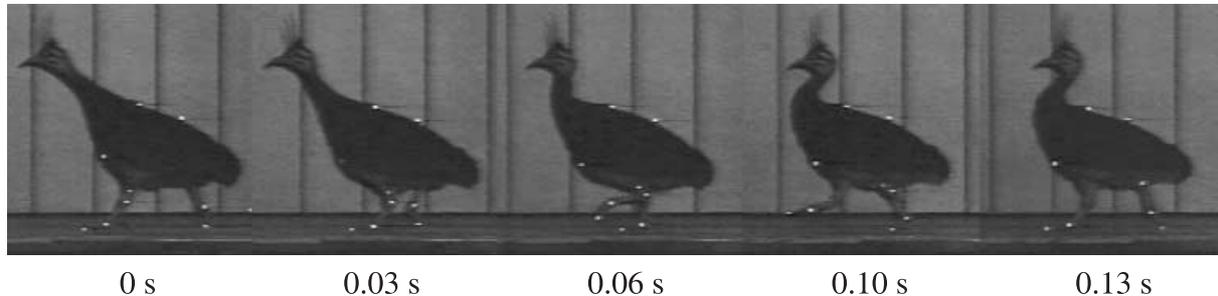


Figure 3. Video images of a Tinamou utilizing grounded running locomotion ($v = 1.58$ m/s, $Fr = 1.46$, $d = 0.57$). The first image (0 s) is touchdown, the second (0.03 s) approximates the time of peak vertical force and the last (0.13 s) is liftoff of the left limb. Reflective markers represent the base of the neck, breast and synsacrum (approximating the hip joint) on the torso, the mid-tibiotarsus and ankle joint on the left limb and the tarsometatarsal–phalangeal joint and the tip of the middle toe on the left and right limbs.

vault-like trial exhibited a higher Fr (0.74). In comparison, bouncing mechanics (grounded or aerial) virtually always occurred at or above the 0.4–0.6 transition zone; no aerial runs and only 6% of bouncing trials fell below 0.4 Fr .

Trials with vaulting mechanics recovered the greatest amount of external mechanical energy via pendulum-like exchange of E_p and $E_{k,tot}$ (Fig. 2d, Table 1). The maximum energy recovered (55.1%) was found in the slowest walk (0.64 m/s). Because the Tinamous were unwilling to walk more slowly, we did not obtain the expected bell-shaped distribution of energy recovery (low at slow and fast walking speeds and high at intermediate walking speeds) and therefore we cannot verify whether this value is the absolute maximum amount of energy that Tinamous are capable of recovering. Much lower energy recoveries were obtained for trials exhibiting bouncing mechanics (maximum 29.1 and 4.8% for grounded and aerial runs, respectively).

Peak vertical force increased linearly with Fr and similarly across all gaits, whereas relative stride length and stride frequency followed a more curvilinear pattern (Fig. 4). No discrete change in peak vertical

force was observed between vaulting trials, grounded runs and aerial runs. Trials with aerial runs exhibited longer relative stride lengths but less frequent strides compared with grounded runs of similar speed and Froude number. Thus, neither the peak vertical force nor the limb stride kinematics predictably distinguished the vaulting (walking) vs. grounded running trials, although stride kinematics do discriminate grounded vs. aerial runs.

DISCUSSION

Gait transitions are traditionally identified by changes in limb kinematic parameters such as phase relationships between footfalls or the absence or presence of an aerial phase between steps (Hildebrand 1965). This study suggests that striding birds switch gaits (as measured by COM mechanics) long before they begin to use aerial running (duty factor < 0.5) and the presence of grounded runs obfuscates these mechanical gait transitions. Some birds, such as the Black-billed Magpie *Pica pica*, show changes in kinematic parameters as they switch from a striding walk to a hop (Verstappen & Aerts 2000), but many

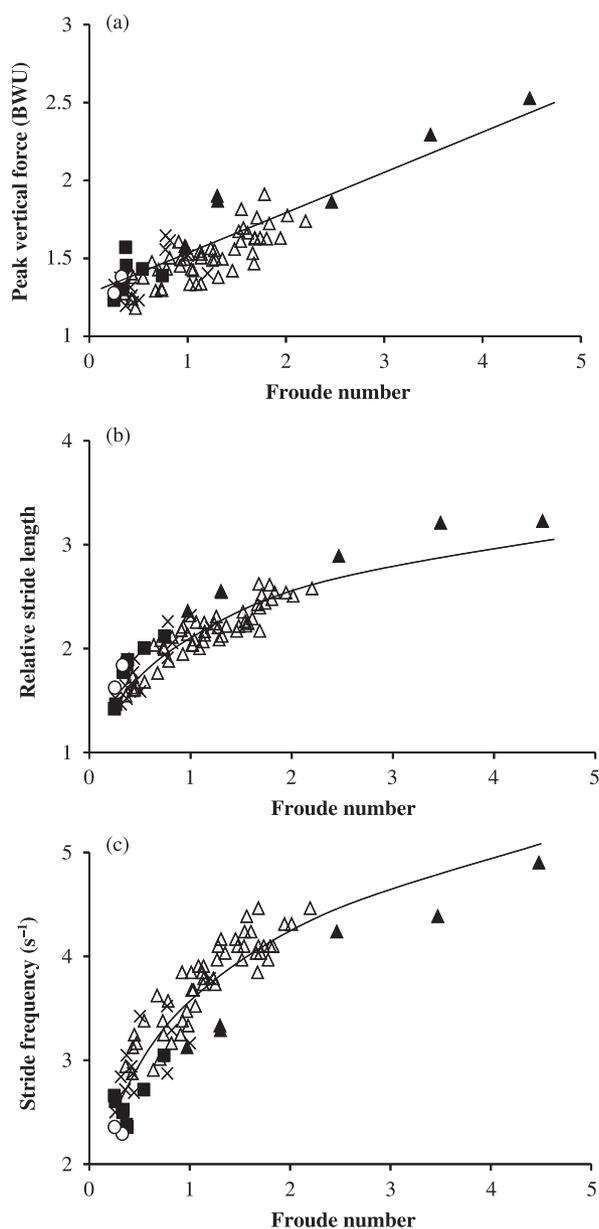


Figure 4. Kinetic and kinematic parameters plotted against Froude number. (a) Peak vertical force (linear regression line: $a = 0.28$, $b = 1.21$; adjusted $R^2 = 0.748$); (b) relative stride length (non-linear regression line: $a = 2.14$, $b = 0.26$; mean corrected $R^2 = 0.863$); and (c) stride frequency (non-linear regression line: $a = 3.56$, $b = 0.25$; mean corrected $R^2 = 0.842$). Symbols follow Figure 2.

birds move solely by striding and do not show discrete changes of kinematic parameters over most of their speed range (Gatesy & Biewener 1991, Gatesy 1999, Abourachid & Renous 2000, Abourachid 2000, Fujita 2004). Even among striding birds, however, kinematic

signals exist that suggest changes in COM mechanics with speed (Gatesy & Biewener 1991, Gatesy 1999, Fujita 2004). For example, discontinuities in the relationship of stride frequency, swing phase duration and maximum knee joint angle with speed occur before the onset of aerial phases in Helmeted Guineafowl (discontinuities at $0.5 Fr$ vs. aerial phase at $2.3 Fr$, Gatesy 1999).

Tinamous move with grounded locomotion over all but the highest speeds observed. The slower grounded trials conform to pendular mechanics and are rightly considered to be walks, as has been found in ratites (Greater Rheas, Ostriches) and galliform birds (Wild Turkeys, Chickens *Gallus gallus*; Cavagna *et al.* 1977, Muir *et al.* 1996, Rubenson *et al.* 2004). Although high-speed grounded locomotion has been reported in other striding birds (Gatesy & Biewener 1991, Reilly 2000), the mechanical nature of this locomotor behaviour has been established only in Ostriches (Rubenson *et al.* 2004) and now Tinamous. High-speed grounded locomotion is invariably governed by bouncing mechanics, yet these species differ in the degree to which they utilize grounded running. Tinamous prefer to run without an aerial phase over ~50% of their running Fr range (and one Tinamou did not ever incorporate an aerial phase), whereas Ostriches limit grounded running to the slowest 20% of their running Fr range. Furthermore, Tinamous begin to employ aerial running at higher Froude numbers (0.97) than Ostriches (0.68). Similarly, non-cursorial mammals exhibit larger duty factors than cursorial mammals at similar Fr values as they increase speed (Alexander & Jayes 1983). Although two of the Tinamous eventually incorporated an aerial phase with increasing speed, their long reliance on grounded running is reminiscent of the resistance to aerial running observed in other small ground-dwelling birds (Gatesy & Biewener 1991).

Across vertebrates, grounded locomotion is most commonly associated with walking. Vaulting mechanics used during walking are believed to reduce muscular effort through a pendulum-like exchange of gravitational potential energy and kinetic energy (Cavagna *et al.* 1977). The theoretical limit for when terrestrial animals must switch out of vaulting mechanics occurs at $Fr = 1$, because at this speed gravitational force becomes inadequate for providing the centripetal force necessary to continue moving the COM along a curved path (Alexander 1976). However, changes in COM mechanics reflective of a walk – grounded run transition occur at a range of

0.4–0.7 *Fr* in Tinamous and 0.54 *Fr* in Ostriches, paralleling gait transitions based on limb kinematics in birds (~0.5 *Fr*, Gatesy 1999) and footfall changes in quadrupedal tetrapods (0.4–0.6 *Fr*, Alexander 1977, Alexander & Jayes 1983, Hayes & Alexander 1983). The Tinamous' limit for vaulting mechanics is consistent with predictions of a collisional model of energy costs during bipedal terrestrial locomotion (0.7 *Fr*, Ruina *et al.* 2005).

Why don't animals continue to move with vaulting mechanics at higher speeds? As walking speed increases, animals reach a maximum step length at which vaulting mechanics can occur (Usherwood 2005). In order to increase speeds further, animals can either increase step frequency or choose to switch from vaulting mechanics to bouncing mechanics. It is now appreciated that the swing phase of locomotion is energetically costly: a substantial fraction (about 26%) of a Helmeted Guineafowl's total energy is consumed during this phase of locomotion (Marsh *et al.* 2004), so energetic factors may act to limit step frequencies. Thus, animals are eventually forced to abandon pendular mechanics when step frequencies become unattainable (Usherwood 2005). Gait transitions at lower *Fr* values may reflect a strategy to reduce metabolic costs of locomotion (Hoyt & Taylor 1981, Kram *et al.* 1997, Griffin *et al.* 2004). Indeed, the capacity of birds to recover external mechanical energy through pendular mechanics peaks at intermediate walking speeds and then falls precipitously at higher speeds (Cavagna *et al.* 1977, Rubenson *et al.* 2004); unfortunately, Tinamous in this study did not move at slow enough speeds to display this pattern. Thus, birds may switch from vaulting mechanics to bouncing mechanics at speeds at which pendulum mechanics no longer provide an energetic benefit. For example, Ostriches display a drop in net metabolic work when transitioning from vaulting to bouncing mechanics, whereas at higher speeds Ostriches incorporate an aerial phase with no decrease in net metabolic work (Rubenson *et al.* 2004). By switching to bouncing mechanics, some of the gravitational potential energy and kinetic energy absorbed by the limbs during the first half of the stance phase is recovered as elastic strain energy in the second half of stance as a result of the stretch and recoil of elastic elements within the limb (e.g. tendons, Cavagna *et al.* 1977). Passive elastic mechanisms thereby reduce the work that muscles must accomplish during running. Muscle–tendon springs within the gastrocnemius muscle of Wild Turkeys have been identified as important energy-saving devices

(Roberts *et al.* 1997), although the effectiveness of passive elastic mechanisms during running in smaller vertebrates, such as Tinamous, is debated (Biewener & Blickhan 1988, Bullimore & Burn 2005).

Another factor that may affect gait choice is locomotor force magnitude. Because increased speed is related to higher locomotor forces (GRFs), animals may switch gaits in order to limit overloading their bones or overexerting their muscles (Farley & Taylor 1991, Fewster & Smith 1996). The findings of this study suggest that force magnitudes may not represent a potent stimulus for the walk–run transition in striding birds, as no discrete difference was found in peak vertical GRFs between walks and grounded runs (Fig. 4a). Indeed, the compliant limbs with which striding birds move may serve to dampen peak force magnitudes across the walk–run transition in a manner similar to bent-knee (Groucho) running in humans (McMahon *et al.* 1987).

Although Tinamous can run at intermediate speeds either with grounded runs of relatively short strides and high stride frequency or aerial runs of longer strides and lower frequency (Fig. 4b & 4c), they rely exclusively on aerial runs at speeds greater than 2.2 *Fr*. Smaller ground-dwelling birds increase speed primarily by increasing stride length (Gatesy & Biewener 1991, Abourachid & Renous 2000). Although their crouched posture provides great effective limb length, birds eventually reach the extension limit of their hindlimbs (with or without femoral involvement) and must 'go aerial' in order to continue to increase speed. Therefore, aerial runs have a greater potential for speed than do grounded runs. Furthermore, both external and internal kinetic energy fluctuations may be reduced with the inclusion of an aerial phase at high speeds, which would moderate muscular effort in running (Clark & Alexander 1975).

What possible advantage does grounded running provide over aerial running in birds? At slower running speeds, double limb support phases may help counteract the tendency of the body to pitch when the line of action of the GRF does not pass through the COM at the end of stance phase (Clark & Alexander 1975). In addition, grounded running may provide a visual benefit to striding birds (Gatesy & Biewener 1991). The transmission of impact spikes from the foot to the head is greatly reduced when humans run with bent knees compared with aerial running (McMahon *et al.* 1987). If a compliant hindlimb in birds similarly serves to dampen jarring impact forces then the visual signal will be less

perturbed with each step. This may be especially important to birds (like Tinamous) that bob their heads during terrestrial locomotion. During the hold phase of head-bobbing, the head is held steady relative to the environment (Dunlap & Mowrer 1930), a mechanism believed to function in stabilizing visual stimuli on the retina (Friedman 1975). Head-bobbing and locomotion are well synchronized at slow speeds, with a bob occurring at every step (Davies & Green 1988, Fujita 2002, Fujita 2003), but are poorly synchronized at intermediate speeds (J.A. Hancock unpubl. data), speeds at which Tinamous move in grounded runs. Absence of an aerial phase, in combination with the flexed limb system, during grounded walks and runs in birds may help stabilize vertical movements of the COM during the hold phase of head-bobbing. Therefore, locomotor mechanics, in conjunction with head-and-neck mechanics, may enable a steadier retina and visual signal in birds.

Although the avian visual apparatus may benefit from grounded running, it is not necessarily true that grounded running evolved in conjunction with a need to stabilize visual images on the retina. Whereas Groucho running is a contrived gait in humans, grounded running is a natural part of the locomotor repertoire of many tetrapods. It has been observed in lizards (McElroy *et al.* 2004), frogs (Ahn *et al.* 2004), opossums (Parchman *et al.* 2003) and rats (A.R. Biknevicius unpubl. data) and has been inferred in primates (Schmitt 1999). The sprawled and crouched postures of these quadrupeds may provide a degree of limb compliancy permitting habitual grounded running as a solution to a variety of mechanical challenges unrelated to vision. The use of grounded running in such a broad range of terrestrial tetrapods suggests that striding birds may simply be exploiting a relatively common capacity for grounded running as a means of enhancing visual stimuli.

In conclusion, Elegant-crested Tinamous undergo two speed-related gait changes. The first is a shift from vaulting mechanics (walking) to bouncing mechanics (grounded running) occurring at a $Fr \sim 0.5$. This shift from vaulting mechanics to bouncing mechanics represents a change in energy-saving strategies from a pendulum-like exchange of external mechanical energies during walking to a greater reliance on elastic energy storage and recovery during grounded running. Because the birds continue to move with duty factors > 0.5 , this shift is not readily obvious without performing COM-based studies. The second shift, from grounded running to aerial

running, is easily observed as it occurs when duty factors fall below 0.5 and an aerial phase is incorporated between each step; this represents a strategy to further increase locomotor speed through longer stride lengths while holding down stride frequencies. In addition, grounded running in birds may enhance vision by permitting smoother strides that allow for the vertical stabilization of visual stimuli upon the retina.

We thank Kay Earls for her assistance in data collection and LabVIEW programming, Josh Hill, Emily Bevis and Ozan Sauer who also assisted in data collection and analysis, and the Ohio University Evolutionary Morphology Group, especially Steve Reilly, Eric McElroy and Andy Lammers (now at Cleveland State University), for discussions and support. Financial support was provided by National Science Foundation (IBN 0080158 to S.M. Reilly and A.R.B.).

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Received 30 March 2006;
revision accepted 11 January 2007.