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The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*

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Summary

Crocodilians tow their large muscular tail behind them during terrestrial bouts when they high walk (a walking trot). Analysis of ground reaction forces in the American alligator (*Alligator mississippiensis*) revealed the consequences of tail-dragging. Individual limb and tail ground reaction force records show that the hindlimbs of *Alligator* take on a substantial role in body mass support consistent with the more caudal location of its center of mass due to the presence of a particularly heavy tail (representing nearly 28% of total body mass). Furthermore, because the constant drag imposed by the tail is substantial, both fore- and hindlimbs in *Alligator* have a heightened propulsive role as a means of countering the net braking effect of the tail. Ground reaction forces of the whole body were used to assess how well *Alligator* was able to utilize mechanical energy-saving mechanisms (inverse pendulum or mass–spring). A high-walking *Alligator* recovers, on average, about 20% of its mechanical energy by inverse pendulum mechanics. These modest energy recovery levels are likely to be due to a combination of factors that may include low locomotor speed, imprecise coordination of contralateral limbs in the trot, frequent dragging of feet of protracting limbs during swing phase and, possibly, tail dragging.

Key words: locomotion, kinetics, limb function, tail-dragging, ground reaction force, *Alligator mississippiensis*.

Introduction

The role of tails in tetrapod locomotion has been explored in both terrestrial and aquatic habitats. During terrestrial locomotion, the tail may act to counterbalance an elevated trunk of a biped (Snyder, 1962; Alexander, 1985) and to regulate stride frequency (Hamley, 1990). Tail orientation may improve limb muscle function in tetrapods for which hindlimb retractor muscles attach to the tail, e.g. dorsiflexion of the tail in lizards may stretch the caudofemoralis muscle, thereby enhancing the muscle's ability to generate propulsive force (Irschick and Jayne, 1999). Highly derived aquatic animals produce thrust using oscillations of tails that have been modified into wing-like hydrofoils (Lighthill, 1969; Fish, 1996). Many semiaquatic animals have also adapted their tails to provide hydrodynamic thrust when paired with dorsoventral (*Lutra canadensis*) or mediolateral (*Alligator mississipiensis*) body flexion, while others use their tails to facilitate efficient generation of thrust by the hind feet by preventing yaw (*Ondatra zibethicus*; Manter, 1940; Fish, 1996).

A tail may not always be a positive attribute during terrestrial locomotion. Large tails may need to be elevated in order to avoid interfering with hindlimb movements (Irschick and Jayne, 1999) or to reduce rotational inertia when the animal attempts a sharp turn (Carrier et al., 2001). Tails that provide propulsive power during swimming in semiaquatic tetrapods may compromise terrestrial locomotion. The enlarged, muscular tails of crocodilians, for example, are key to their predatory success in aquatic attacks (Manter, 1940) but these same tails presumably apply a constant decelerative impulse to the center of mass during terrestrial locomotion because they are typically not elevated off the ground. Yet, crocodilians spend a substantial amount of time on dry land, periodically trekking long distances between aquatic resources (Tucker et al., 1997), all the while dragging their tails behind them.

Limbs must resist the force of gravity, modulate forward impulsion and maintain lateral stability during terrestrial locomotion. These efforts are energetically costly, but studies in bipedal and quadrupedal tetrapods have shown that some external mechanical energy can be conserved by two energy-saving mechanisms (Cavagna et al., 1977). Inverse pendulum mechanics are employed at slower speeds, when gravitational potential energy and kinetic energy cycle out-of-phase with one another and therefore may be exchanged in a pendulum-like manner. At higher speeds, spring mechanics may be used, where gravitational potential and kinetic energies are exchanged with elastic strain energy through the stretching and

recoiling of spring elements in the limbs (e.g. tendons and ligaments). These models have been documented for a wide array of terrestrial vertebrates, including birds, humans and cursorial mammals (Cavagna et al., 1977). However, the ubiquity of these models across terrestrial tetrapods may be overstated and, furthermore, the effect of an unelevated tail on locomotor mechanics has not been explored.

In the present study, we explore locomotor biodynamics in the American alligator (*Alligator mississippiensis*) during high walking. The high walk is the most common terrestrial locomotor behavior of extant crocodilians; it is a trotting gait with a semi-erect locomotor posture (in which limb orientation is between sprawling and erect grades during terrestrial locomotion; Gatesy, 1991; Reilly and Elias, 1998). Ground reaction forces are examined to address two fundamental questions. First, how does *Alligator* partition the roles of body mass support, braking and propulsive effort, and mediolateral stability among its supporting limbs and tail? And, second, can high-walking, tail-dragging alligators capitalize on the same energy-saving mechanisms found in more sprawling and more erect animals (walking with inverse pendular mechanics or running with spring–mass mechanics)?

Materials and methods

Animals

Locomotor kinetic data were collected from five specimens of American alligator (*Alligator mississippiensis* Daudin 1801). The alligators were obtained from the Department of Wildlife and Fisheries of the Rockefeller Wildlife Refuge (Grand Chenier, LA, USA). Body masses ranged from 2.24 kg to 4.00 kg (mean ± S.E.M. 2.96±0.32 kg) and snout-vent lengths ranged from 41.2 cm to 49.0 cm (44.5±1.29 cm). All procedures were approved by the Ohio University Institutional Animal Care and Use Committee.

The alligators were conditioned for terrestrial locomotion over three months. The animals were removed from their tanks regularly and were encouraged to walk repeatedly along a 5 m trackway as well as to walk freely in the holding room.

Data collection

Ground reaction force data were captured as the alligators moved across a Kistler force platform (plate Type 9281B; Amherst, NY, USA) mounted flush with the surface of a 6.1 m trackway. Force outputs were captured at 500 Hz and resolved into vertical, craniocaudal and mediolateral force components using the Kistler Bioware 2.0 software. Each animal was permitted to choose its own locomotor speed, as attempts to encourage faster trials yielded unacceptable behavior (reversing direction or attacking the encouraging hand). Each trial was recorded at 250 frames s^{-1} using a MotionScope 500 camera (Redlake Corp., San Diego, CA, USA). These recordings enabled the identification of footfall patterns (gait), estimation of mean forward speed (using a reference grid of 10-cm increments along the back wall of the trackway), stride duration (elapsed time between ground strikes of individual feet) and support duration (duration of foot contact with the ground). Duty factor was computed as the quotient of stride duration to support duration. Kinematic gait was determined with the Hildebrand (1976) gait graph by plotting limb phase, or the percent of the stride that the ipsilateral forelimb lands after the reference hindlimb, against duty factor.

Individual limb and tail kinetics

In order to optimize the capture of force records for individual limb strikes, a triangular insert (244.25 cm^2) was firmly affixed to the surface of the force platform (Fig. 1A); the uninstrumented part of the runway covered the remainder of the force platform. Video reviews eliminated trials that lacked clean footfalls, i.e. partial or overlapping. Forward speed was also determined videographically using the 10 cm grid along the back wall of the trackway. Trials in which the animals were clearly accelerating or decelerating were not analyzed. This was assessed by comparing forward velocity estimated immediately over the force platform to the mean velocity determined over a longer distance (70 cm); trials for which the central velocity differed from the mean velocity by greater than 5% were dropped from the analysis.

Ground reaction force records for individual limbs were evaluated for peak forces (maximum displacement of a force record) and impulses (area under a force profile). The vertical component of force was analyzed as the peak vertical force and vertical impulse, measuring the role of the limbs in body mass support. Horizontal forces were distinguished into craniocaudal and mediolateral components. Net craniocaudal impulse reflected the overall role of the limb in controlling forward momentum; negative values reflected overall braking efforts whereas propulsive efforts were positive. The craniocaudal records were further subdivided into the braking (negative) and propulsive (positive) components, and impulses for each were calculated. Net mediolateral impulses were standardized so that negative values reflected an overall lateral push by the limb on the ground (i.e. a medially directed ground reaction force). The units for force and impulses are body weight units (BWU) and BWU·s, respectively, in order to adjust for differences in body size across individuals.

The entire surface of the Kistler force platform (60 cm × 40 cm) was used to obtain ground reaction forces from the tail (Fig. 1B). The tail was dragged behind the animal, so that pure tail records were obtained once the animal completely stepped off the plate. Peak forces were thus obtained for the tail. However, because the hindlimb record overlapped the initial segment of the tail record, precise determination of impulses over the entire support phase of the tail could not be determined. Rather, we estimated tail impulses over the mean step duration of the fore- and hindlimbs (1.54 s).

Vertical impulse (Q_z) was used to estimate the role of each limb and the tail in body mass support. The relative role of the forelimb in body support ($\%Q_{z,fore}$, or relative support impulse) during the high walk was calculated using an equation modified from Jayes and Alexander (1980):

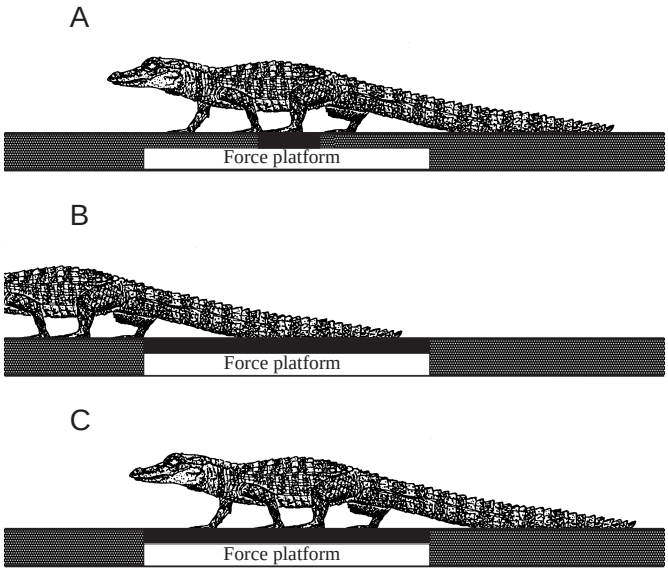


Fig. 1. Configurations of the trackway for capture of ground reaction forces for (A) individual limbs, (B) tail and (C) whole-body mechanics (to which tail data were subsequently added). The black segment represents the instrumented part of the trackway; the remaining (hatched) trackway is isolated from the force platform.

$$\%Q_{z,fore} = [Q_{z,fore} / (Q_{z,fore} + Q_{z,hind} + Q_{z,tail})] \times 100 , \quad (1)$$

where $Q_{z,fore}$, $Q_{z,hind}$ and $Q_{z,tail}$ are the vertical impulses of the forelimb, hindlimb and tail, respectively. The role of hindlimbs and tail in body mass support were similarly computed.

Using the criteria described previously for assessing steady speed, analysis of individual foot function was conducted on 60 trials (12 trials per animal). A repeated-measures analysis of variance (SYSTAT 9) was used to evaluate differences between forelimbs and hindlimbs in speed, support duration, peak forces, impulses, time to peak vertical force, and timing of the shift from braking to propulsion in the craniocaudal force record. Limb pairs were treated as independent factors crossed with the five subjects. No individual effects were found within the timing and kinetic variables for each limb; hence, the data from all individuals were pooled. Sequential Bonferroni corrections were made for multiple comparisons (following Rice, 1989). Additionally, reduced major axis regression evaluated speed effects on support duration, peak vertical force, and craniocaudal and mediolateral impulses (SYSTAT 9).

Whole-body mechanics

The entire surface of the Kistler force platform (60 cm × 40 cm) was also used for the whole-body mechanics study (Fig. 1C). The alligators typically took one full and two partial steps as they crossed the force platform. Analysis focused on a single step (forelimb strike to contralateral forelimb strike). Valid trials for this analysis were identified as those for which craniocaudal velocity, determined by the first integration of the craniocaudal force, was fairly well balanced about mean forward velocity (determined videographically), indicating that the animal was neither strongly decelerating nor accelerating during the step. Only 15 out of nearly 500 trials from four alligators met both criteria and were used in this analysis. Although the platform surface was sufficiently long to obtain a complete step with all limbs over the platform, it could not simultaneously support the entire tail. Therefore, force records produced by the tail alone (see above) were added to those of the limbs at equivalent speeds to obtain whole-body records. This was possible because the force records of the tail were non-oscillating.

Force data for single steps were imported into a LabView (National Instruments, Austin, TX, USA) virtual instrument in order to determine fluctuations of external mechanical energy, following the method described by Blickhan and Full (1992) and Donelan et al. (2002). Because the high walk of alligators has some temporal irregularities in footfalls (i.e. they are somewhat ‘sloppy’ trotters), a step is defined as the time between the touchdown of the first limb in a diagonal couplet to the touchdown of the first limb of the opposite couplet. Accelerations of the center of mass in vertical, craniocaudal and mediolateral directions were obtained by dividing the forces by body mass; body weight was first subtracted from the vertical forces. Velocities of the center of mass for each direction were then estimated by taking the first integration of acceleration. While the integration constant for the craniocaudal direction was set to mean forward velocity (Blickhan and Full, 1992), the constants were estimated as the mean value for the vertical and mediolateral records (Donelan et al., 2002). Velocities (v) were used to calculate kinetic energies ($E_k=\frac{1}{2}Mv^2$, where M is body mass in kg) in the vertical ($E_{k,V}$), craniocaudal ($E_{k,CC}$) and mediolateral ($E_{k,ML}$) directions. Total kinetic energy of the center of mass ($E_{k,tot}$) during the step was then calculated as the sum of all three components ($E_{k,V}+E_{k,CC}+E_{k,ML}$). Finally, changes in the vertical displacement of the center of mass (h) were determined by integrating vertical velocity (integration constant estimated as the mean vertical record). Changes in vertical displacement were used to determine changes in gravitational potential energy ($E_p=M\boldsymbol{g}h$, where $\boldsymbol{g}$ is gravitational acceleration or 9.81 m s^{-2}) during the step.

Phase-shifts between total kinetic energy ($E_{k,tot}$) and gravitational potential energy (E_p) during a step were calculated as the difference between when $E_{k,tot}$ and E_p reached their minimal values relative to the duration of the stride multiplied by 360° (Farley and Ko, 1997). Perfect inverted-pendulum mechanics are characterized by 180° phase shift between $E_{k,tot}$ and E_p so that $E_{k,tot}$ is at its minimum when E_p is maximum (i.e. $E_{k,tot}$ and E_p are out-of-phase). By contrast, $E_{k,tot}$ and E_p are in-phase (phase shift=0°) in spring–mass mechanics because $E_{k,tot}$ and E_p each reach their minimal values simultaneously during the step. These energy patterns have been used to distinguish walks from runs from the whole-body perspective (Cavagna et al., 1977). We specify these as mechanical walks and runs, because movements of the center of mass are determined through force data, as a contrast to the

kinematic walks and runs determined by footfall patterns (gaits) alone.

Recovery of mechanical energy (*%R*) due to pendulum-like exchange between $E_{k,tot}$ and E_p during a step was calculated according to Blickhan and Full (1992):

$$\%R = \frac{(\Delta E_{k,tot} + \Delta E_p) - \Delta E_{m,tot}}{\Delta E_{k,tot} + \Delta E_p} \times 100, \qquad (2)$$

where $E_{m,tot}$ is computed as $E_{k,tot}+E_p$, and $\Delta E_{k,tot}$, ΔE_p and $\Delta E_{m,tot}$ are the sum of the positive increments of the $E_{k,tot}$, E_p and $E_{m,tot}$ profiles, respectively (positive increments are those portions of an energy profile during which there is a net gain of energy during a step). The amount of energy recovered is dependent not only on the phase relationship between $E_{k,tot}$ and E_p but the magnitudes of these energies as well. For all external mechanical energy to be recovered, $E_{k,tot}$ and E_p must be exactly 180° out-of-phase with one another and fluctuate at equal magnitudes. The amount of energy recovered decreases as the phase relationship between $E_{k,tot}$ and E_p deviates from 180° or as discrepancies between the magnitudes of the two types of external mechanical energy increase. Percent recoveries were computed twice: first, with all three components (vertical, craniocaudal and mediolateral) and then without the lateral component in order to assess the significance of rolling in pendulum mechanics (Griffin and Kram, 2000).

Finally, the positive work done against gravity was computed as the sum of the positive increments of (E_p+$E_{k,V}$). Similarly, summing the positive increments of $E_{k,CC}$ and $E_{k,ML}$ provides the positive work done to accelerate the body forward and laterally, respectively.

Center of gravity

At the completion of the study, all alligators were euthanised with an overdose of sodium pentobarbital, and the craniocaudal and dorsoventral positions of their centers of gravity were determined using the reaction board method (Ozkaya and Nordin, 1999). Three conditions were evaluated. First, centers of gravity were determined in intact animals with limbs replicating a midstance semi-erect posture. Second, shifts in the center of gravity were recorded when the diagonal limbs were fully protracted and then fully retracted (replicating limb movements during a trot). Finally, tails were removed at the first caudal vertebra in order to assess the impact of the tail on the craniocaudal positioning of the center of gravity. The craniocaudal position of the center of gravity was determined relative to the distance between the scapular glenoid fossa and the acetabulum, so that 0% and 100% reflect glenoid and acetabular locations of the center of gravity, respectively.

Results

Gaits

The alligators always assumed the semi-erect posture characteristic of high walks (Reilly and Elias, 1998) and consistently used walking trot gaits (Fig. 2A). The duty factors ranged from 0.73 to 0.83 (i.e. never dipping below 0.5), and forelimb touchdown followed hindlimb strike by 46.5±0.10% (mean ± S.E.M.) of the stride cycle (Fig. 2B). No aerial phase was observed in any trial as the alligators always had at least two feet on the platform when high walking (Fig. 2B).

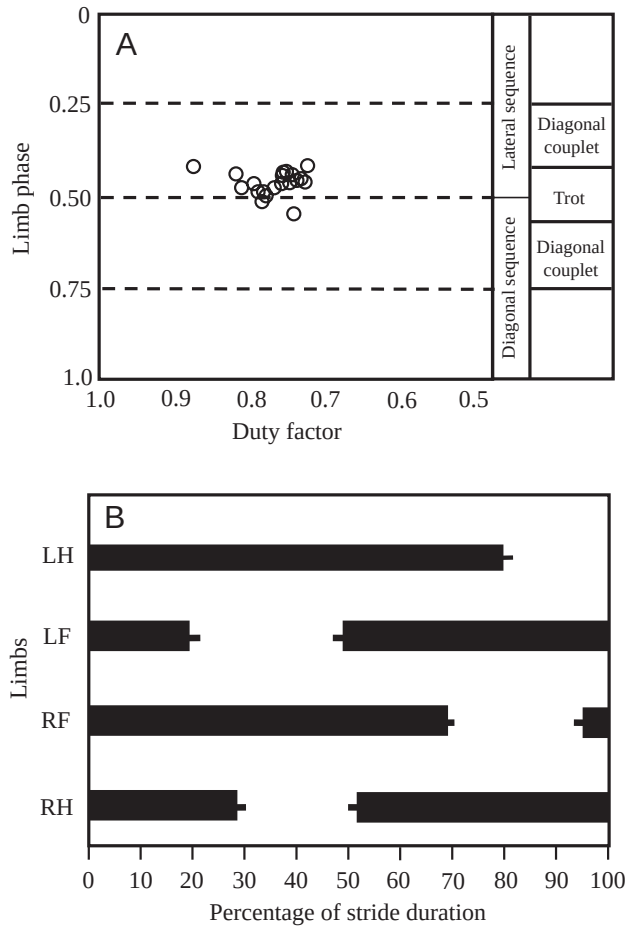


Fig. 2. Kinematic summary of high walking in *Alligator mississippiensis*. (A) The gait graph (based on Hildebrand, 1976) confirms that high walks are walking trots. (B) The gait plot reveals asynchronous footfalls and liftoffs of diagonal couplets. The mean timing of footfalls and their 95% confidence intervals are shown.

Individual limb and tail kinetics

Alligator chose to high walk within a speed range of 0.16±0.01 m s^{-1} (0.07–0.26 m s^{-1}). Support durations were, on average, comparable between forelimbs and hindlimbs (Table 1), and speed-related increases in support duration were observed in both limb pairs (Table 2).

Peak vertical forces were significantly higher for the hindlimbs than for the forelimbs (Fig. 3A,B; Table 1). Hindlimb vertical force records were also distinctive because they usually displayed a brief impact spike and because the peak vertical force of the hindlimbs occurred significantly earlier in the support phase than that of the forelimbs (Fig. 3A; Table 1). Significant speed-related increases in peak vertical force were found for the hindlimb only (Table 2). Vertical

Table 1. *Force and timing parameters for forelimbs, hindlimbs and tail in* Alligator mississippiensis

Variables	Forelimb	Hindlimb	*P*	Tail*
Support duration (s)	1.51±0.09	1.57±0.07	0.814	–
Peak vertical force (BWU)	0.41±0.01	0.53±0.01	<0.0005**	0.08±0.01
Vertical impulse (BWU·s)	0.36±0.02	0.51±0.02	0.005**	0.12±0.01
Net craniocaudal impulse (BWU·s)	–0.01±0.01	0.04±0.01	<0.0005**	–0.03±0.01
Braking impulse (BWU·s)	–0.02±0.01	–0.01±0.01	0.001**	–0.03±0.01
Propulsive impulse (BWU·s)	0.01±0.01	0.05±0.03	0.002**	0
Peak breaking force (BWU)	–0.05±0.02	–0.05±0.02	0.414	–0.02±0.02
Peak propulsive force (BWU)	0.04±0.03	0.07±0.03	0.001**	0
Peak mediolateral force (BWU)	0.07±0.01	0.10±0.04	0.001**	–0.02±0.01
Net mediolateral impulse (BWU·s)	0.07±0.04	0.09±0.04	0.035	–0.01±0.01
Relative time to peak vertical force (% support duration)	68.2±0.9	34.5±0.9	<0.0005**	–
Relative time to braking-propulsion transition (% support duration)	62.0±1.0	15.2±0.7	<0.0005**	–

Values are means ± S.E.M. Sample sizes for limb and tail data are 30 and 17, respectively.
*Tail impulses are estimated over the mean support duration of the limbs (1.54 s).
**Fore- and hindlimbs significantly different at $P<0.006$, established by sequential Bonferroni correction $\alpha/k=0.05/9$.

Table 2. *Reduced major axis regressions of individual limb locomotor parameters against forward speed (m s^{-1})*

	Forelimb			Hindlimb		
Variables	Slope (±95% CI)	r^2	*P*	Slope (±95% CI)	r^2	*P*
Support duration (s)	–12.27±2.26	0.815	<0.0005	–6.29±2.04	0.588	<0.0005
Peak vertical force (BWU)	–0.18±0.29	0.051	0.233	0.23±0.20	0.162	0.028
Net craniocaudal impulse (BWU·s)	0.17±0.09	0.336	0.001	–0.34±0.11	0.598	<0.0005
Braking impulse (BWU·s)	0.21±0.08	0.520	<0.0005	–0.01±0.02	0.044	0.269
Propulsive impulse (BWU·s)	–0.04±0.04	0.108	0.076	–0.34±0.11	0.605	<0.0005
Net mediolateral impulse (BWU·s)	0.54±0.13	0.753	<0.0005	0.40±0.13	0.582	<0.0005

forces applied by the tail were substantial (0.08±0.02 BWU); these forces were, on average, 18.5% and 14.4% of fore- and hindlimb values, respectively.

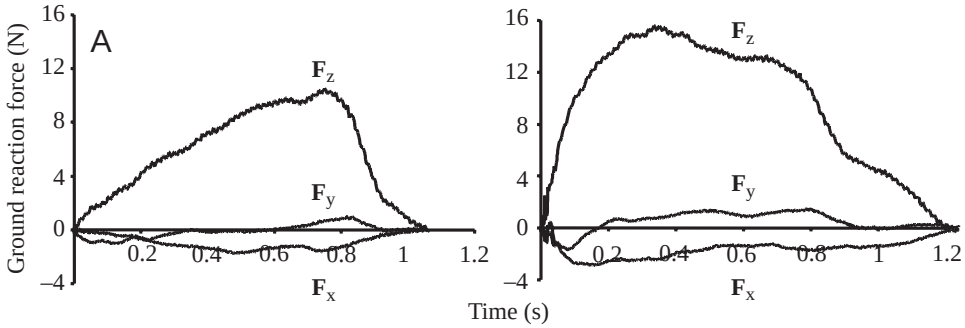
Although both limbs displayed an initial braking effort followed by a propulsive effort (Fig. 3A), braking impulses were significantly greater in the forelimbs whereas greater propulsive impulses were generated by the hindlimbs (Table 1). The high braking impulses of the forelimbs were due to the lengthened braking phase in the forelimb records (68% of support phase compared with only 15% in hindlimbs), whereas the high propulsive impulses in the hindlimb records were reflective of the greater peak propulsive forces (Table 1). Hence, net craniocaudal impulses were negative (braking) in forelimbs but positive (propulsive) in hindlimbs (Fig. 3C). Net craniocaudal impulses for both forelimbs and hindlimbs decreased with speed (Table 2), driven by reductions in braking impulses by the forelimbs and in propulsive impulses by the hindlimbs. The tail's craniocaudal impulse (estimated over the mean support duration of the limbs, or 1.54 s) was –0.02±0.02 BWU·s, reflecting a constant braking impulse.

Both forelimbs and hindlimbs consistently pushed laterally on the ground during the support phase (as shown by the medially directed ground reaction forces; Fig. 3A). Although hindlimb mediolateral impulses tended to be greater than those of the forelimbs, the difference was not significant (Table 1). Peak mediolateral forces were high in *Alligator* (Table 1), averaging 16.1% and 19.1% of peak vertical forces in the fore- and hindlimb, respectively. More striking, however, are the ratios of peak mediolateral force to peak craniocaudal force, which reached 137.5% in the forelimb and 144.3% in the hindlimb. Both fore- and hindlimb mediolateral impulses decreased significantly with speed (Table 2). Negligible mediolateral forces were recorded for the tail.

Body weight support and center of gravity

Using relative vertical impulse (*%Q*) to reflect the role of the limbs and tail in body weight support, it was estimated that the diagonal forelimb and hindlimb in a walking trot support 36.8±1.6% and 51.3±1.5% of body weight, respectively. The remainder, 11.8±0.5%, was supported by the alligator's tail.

The center of gravity of alligator carcasses with limbs approximating standing posture was found to be located at 70.0±0.1% of the gleno-acetabular distance, i.e. closer to the hip joint than the shoulder joint. Simultaneous protraction of diagonal limbs (i.e. replicating touchdown of fore- and hindlimbs in a trot) shifted the center of gravity cranially by only 0.3±0.1%. By contrast, removal of the tail (which represented 27.8±0.1% of total body mass) relocated the center



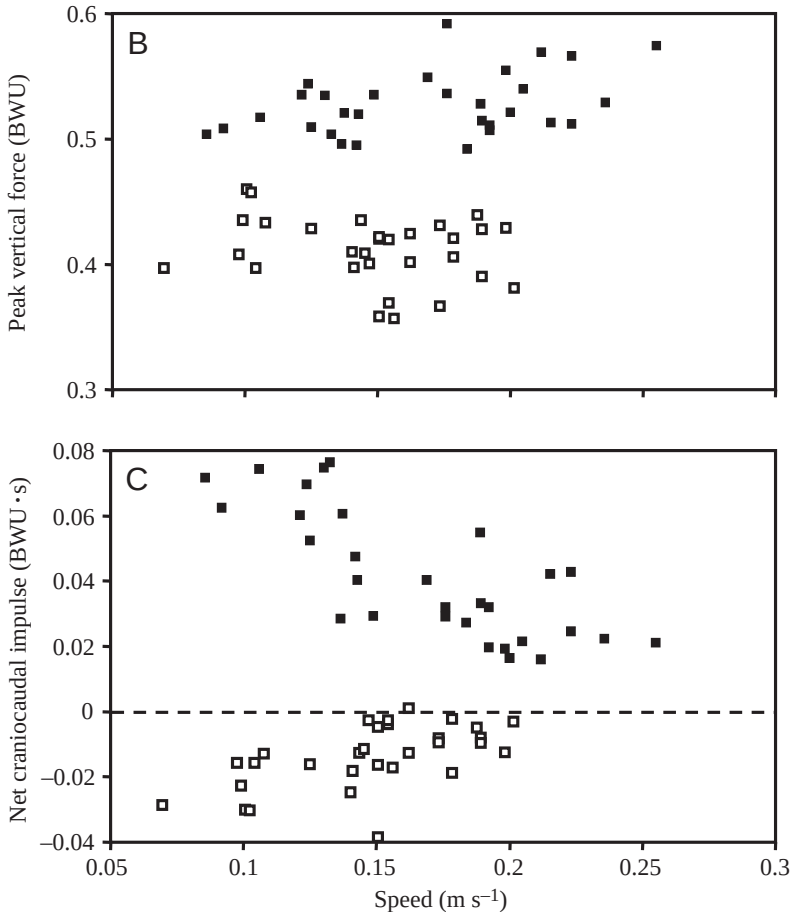


Fig. 3. (A) Representative forelimb (left) and hindlimb (right) ground reaction forces in *A. mississippiensis* (trials 2C26 and 2C29; 0.202 m s^{-1} and 0.198 m s^{-1}, respectively). Negative and positive values in the craniocaudal forces are reflective of braking and propulsive efforts, respectively. Positive mediolateral forces reflect lateral pushes by the limbs. Data are unfiltered in order to preserve the impact spike on the hindlimb record. Abbreviations: $\mathbf{F}_x$, mediolateral forces; $\mathbf{F}_y$, craniocaudal forces; $\mathbf{F}_z$, vertical forces. Plots of (B) peak vertical force and (C) net craniocaudal impulse against speed. Symbols: open square, forelimb; filled square, hindlimb.

of gravity cranially to a position 28.2±0.1% of the gleno-acetabular distance.

The dorsoventral position of the center of gravity of alligators with limbs approximating a standing posture was located 3.70±0.20 cm inferior to the dorsal surface of the animals. Maximal protraction of a fore- and hindlimb pair shifted the center of gravity by 1.1 cm dorsally, on average.

Whole-body ground reaction forces

Steady speed high walks in the whole-body mechanics study ranged from 0.10 m s^{-1} to 0.20 m s^{-1} (mean 0.16 m s^{-1}). Whole-body vertical ground reaction forces fluctuated around body weight (Fig. 4). A large vertical spike (in excess of 1 BWU), developed early in the step, represented the touchdown of the step-initiating limb superimposed over the terminal portion of the stance phase of the previous step's diagonal limbs. The ground reaction force records of the diagonal limbs were superimposed because only 0.05±0.01 s separated each footstrike (equivalent to 5.58±1.14% of step duration; see Fig. 2B).

Both horizontal ground reaction forces were much smaller in magnitude than the vertical forces in alligators (Fig. 4A). Whole-body craniocaudal forces changed sense (braking *versus* propulsion) several times during the stance phase because steps overlapped temporally. An early cranially directed ground reaction force represented the greater propulsive effort of the previous step's diagonal limbs. Soon thereafter, however, a braking effort of the step of interest dominated as the limbs of the previous step prepared for and completed lift-off. During the remainder of the step, the animal's center of mass accelerated forward. In contrast to the consistently high mediolateral forces of individual limbs, mediolateral ground reaction forces of the whole body were small in magnitude and fluctuated around zero with no consistent pattern.

Fluctuations in the velocity and vertical displacement of the center of mass

Velocity fluctuations were comparable in magnitude in all three directions (Fig. 4A). Initial negative values in vertical velocity reflect a brief downward movement of the center of mass. Subsequently, vertical velocity followed a bell-shaped curve: increasing as the center of mass moved upwards, then decreasing with the falling of the center of mass. In all trials, the center of mass was lowest at the beginning and end of the step, reaching its greatest height at midstep. The fluctuation in vertical displacement of the center of mass during a walking trot was 1.0±0.1 cm. Craniocaudal velocity fluctuated about the mean forward velocity. The high forward velocity at the

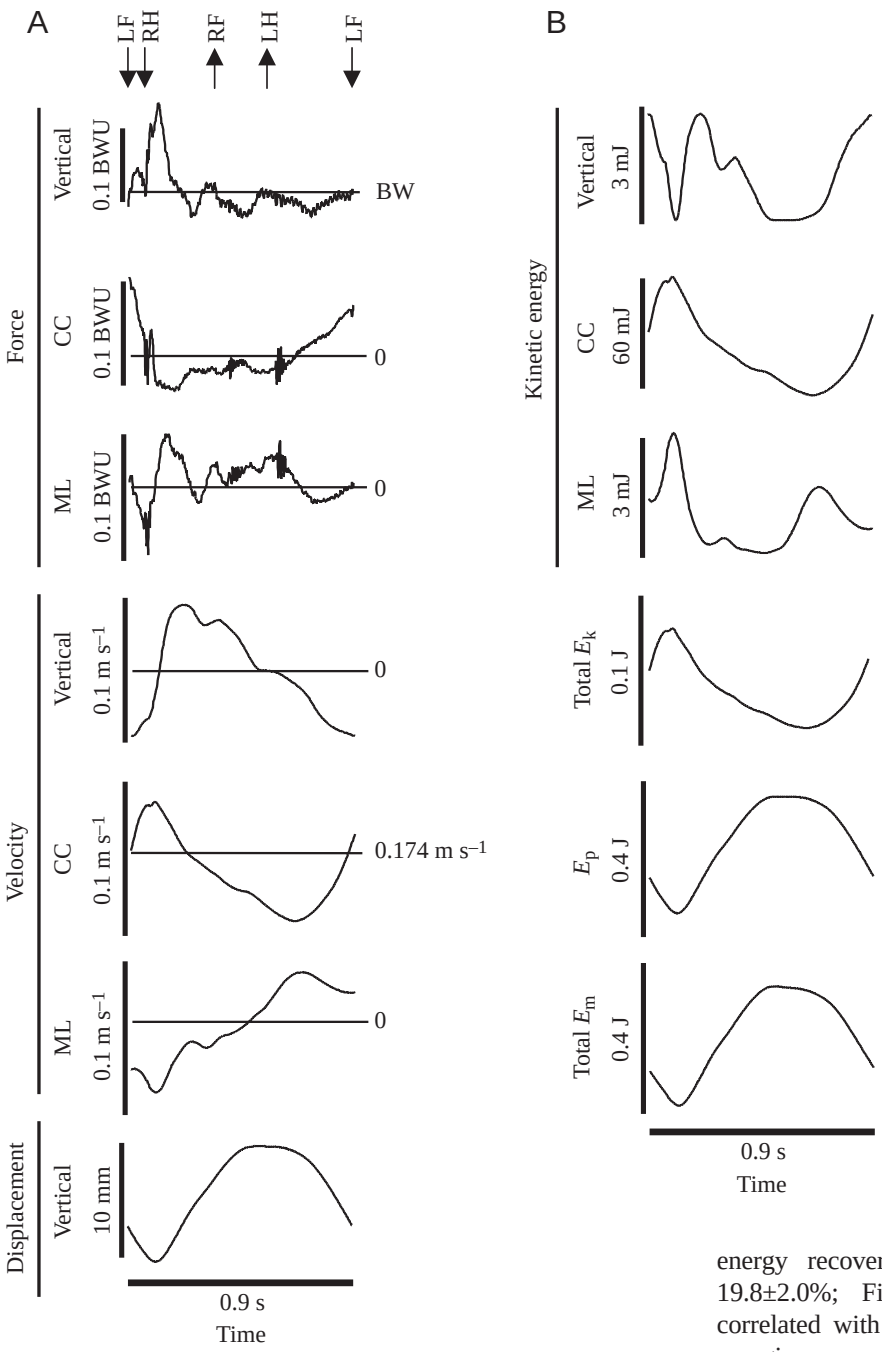


Fig. 4. Whole-body mechanics in *A. mississippiensis* during a single step of a walking trot (trial GC13; 0.174 m s^{-1}). (A) Representative plots of whole-body ground reaction force, velocity of the center of mass and vertical displacement of the center of mass *versus* time. Footfalls (↓) and liftoffs (↑) are indicated for individual feet during the step (F, forelimb; H, hindlimb; L, left; R, right). (B) Representative profiles of kinetic (E_k), gravitational potential (E_p) and total mechanical energies (E_m) of the center of mass *versus* time.

onset of the step represented the end of the propulsive effort of the previous step's diagonal limbs. This was consistently followed by a sinusoidal decrease (braking) and then increase (propulsion) in forward velocity. The profiles for the mediolateral velocities were somewhat more variable, although all patterns fluctuated about zero; the most common pattern displayed a single change in direction at midstep.

Fluctuations in the mechanical energy of the center of mass

Kinetic energy curves in the three orthogonal directions reached their minimum values at approximately midstep (Fig. 4B). The magnitude of the fluctuations in craniocaudal kinetic energy was greater than for the vertical and mediolateral directions. The profiles of total kinetic energy were U-shaped, with minimum values at midstep. By contrast, the profiles of the gravitational potential energy were consistently bell-shaped, so that gravitational potential energy was lowest at the beginning and the end of the step and reached its maximal values at midstep (Fig. 4B). In general, the magnitude of gravitational potential energy fluctuations was much greater than that of total kinetic energy.

Only one pattern of external mechanical energy fluctuations was found for *Alligator*. Total kinetic and gravitational potential energies were consistently out-of-phase: total kinetic energy was near its minimal values at midstep as gravitational potential energy was approaching its maximum (Fig. 4B). The relative phase relationship for the minima of gravitational potential and kinetic energy curves was 177.9±11.9° (Fig. 5A).

Alligator did recover some external mechanical energy by pendulum-like mechanisms across each step, with percent energy recoveries ranging from ~7.6% to 32.4% (mean 19.8±2.0%; Fig. 5B). Energy recovery was significantly correlated with speed (r=0.657, P=0.04). When total kinetic energies were recomputed without the lateral component, mean percent recovery dropped by 6.9±2.0% (Fig. 5B).

Vertical work in high walking significantly exceeded work in the craniocaudal and mediolateral directions (Table 3). Significant speed effects were only observed in vertical work, which was found to decrease with speed.

Discussion

The limbs of terrestrial tetrapods function to support body weight and to regulate forward impulsion. They also have an important role in enabling energy-saving mechanisms to reduce muscular effort during terrestrial locomotion. Locomotor mechanics in *Alligator mississippiensis* allude to

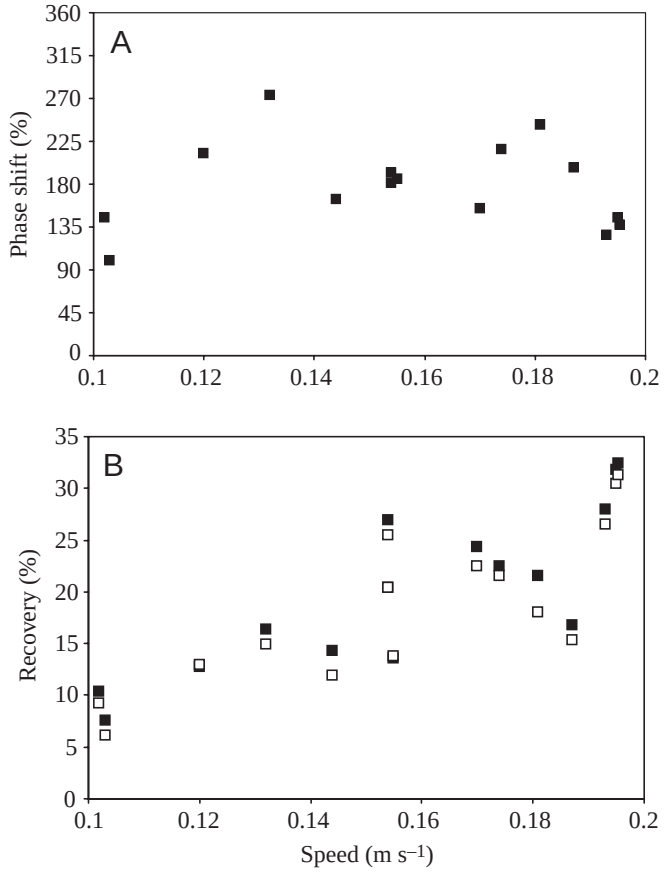


Fig. 5. (A) Phase shift between the fluctuations in gravitational potential and total kinetic energies for high walks in *Alligator mississippiensis*. (B) Percent recovery of mechanical energy by pendular mechanics for high walks in *A. mississippiensis*. Symbols: open squares, energy recoveries computed without the mediolateral component; closed squares, energy recoveries computed with all three components.

Table 3. *Positive work in locomotion*

	W_V	W_{CC}	W_{ML}
N	15	15	15
Work (J)	0.29±0.03	0.04±0.01*	0.01±0.01*
b (*P*)	–1.752 (0.002)	0.269 (0.769)	–0.001 (0.290)
r^2	0.277	0.170	0.001

Values are means ± S.E.M.

*Significantly different from W_V (P<0.001).

W_V, work against gravity; W_{CC}, work to accelerate the body forward; W_{ML}, work to maintain mediolateral stability. Reduced major axis regression slopes (*b*) and r^2.

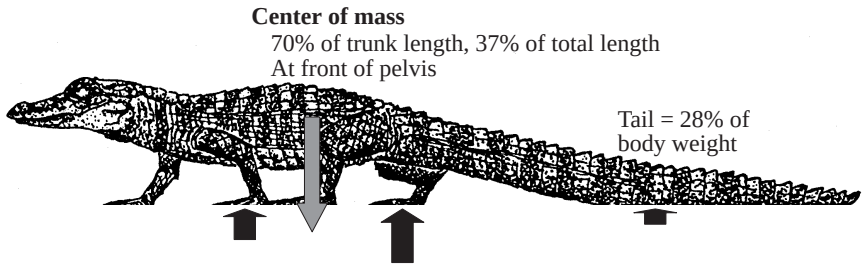
the compromise that towing a large tail across terrestrial terrains has for this semiaquatic animal. Because a long and heavy tail is the basal condition for tetrapods, this study provides insight into terrestrial locomotion in early tetrapods.

Effects of tails on body weight support and forward impulsion

The most potent factor that explains the crocodilian pattern of hindlimb dominance in body weight support is likely to be the alligator's massive tail, which accounts for a substantial percentage of body weight (nearly 28%; Fig. 6). That the tail effectively draws the center of mass caudally towards the hindlimbs in *Alligator* is supported by the cranial shift in center of mass with postmortem removal of its tail. Removal of the tail repositioned the center of mass from 70% of the gleno-acetabular distance to 28%, realigning it closer to the 30–40% position noted for most mammals (Kimura and Endo, 1972; Demes et al., 1994). Relatively high hindlimb vertical forces have also been reported in the lizard *Varanus* (Christian, 1995), which also sports a large tail. The torso and hindlimbs support a substantial portion of the proximal tail in high-walking alligators since vertical impulses of the tail represent only 12% of total vertical impulses even though the tail represents 28% of the total body mass. Finally, Gray (1968) concluded that hindlimbs should support an increased percentage of weight when a quadruped is working against a drag. Hence, the constant braking impulse of the tail may further contribute to hindlimb vertical forces and impulses.

High vertical forces and relative support impulses in the hindlimbs are also characteristics of higher primates (Demes et al., 1994; Schmitt, 1994). Unlike alligators, mass distribution cannot explain the primate condition because cadaveric specimens of primates and other mammals alike tend to have cranially displaced centers of gravity (closer to the forelimbs than the hindlimbs; Vilensky, 1979). Rather, it appears that the activity of hindlimb retractor muscles in primates effectively draws the center of mass caudally, thereby reducing the compressive load on the forelimbs (Vilensky, 1979). This characteristic of primate kinetics has been associated with the more upright trunk (orthograde posture) of higher primates and has been suggested as a prerequisite for the evolution of bipedality (e.g. Kimura et al., 1979). Because basal crocodilians have been reconstructed as cursorial bipeds (Sennikov, 1989; Parrish, 1987, 1988; Gomani, 1997), it may be tempting to ascribe the hindlimb dominance in vertical force generation in extant alligators to historical baggage. But *Caluromys philander* (the highly arboreal wooly opossum) was recently found to replicate the vertical force patterns of primates, strongly indicating that the hindlimb dominance in body mass support in primates primarily reflects arboreal ancestry more so than orthograde posture (Schmitt and Lemelin, 2002). To date, no one has credibly suggested that arboreality plays a role in crocodilian evolution and, so, a caudally positioned center of mass remains the most convincing factor determining limb function in body mass support in alligators.

Vertical force is not the only aspect of individual limb function that is affected by the tail in alligators. While both braking and propulsive impulses are exerted by limbs in walking tetrapods, one function typically dominates: forelimbs tend to be net braking and hindlimbs are net propulsive (Demes et al., 1994). Furthermore, quadrupeds moving at near-constant forward velocity should have balanced propulsive and braking



	FL		HL	Tail
HL-dominated body support				
Peak vertical force	0.411	<	0.528	0.076
Vertical impulse	0.364	<	0.507	0.117
HL-dominated forward impulsion				
Net craniocaudal impulse	–0.014 Braking	≪	0.041 Propulsive	–0.023 Braking
Subequal role in mediolateral stability				
Net mediolateral impulse	0.069	~	0.094	–0.001

Fig. 6. Summary of the differential roles of limbs and tail in high walking in *A. mississippiensis* (see Discussion).

impulses across their four limbs. In *Alligator*, the craniocaudal records of the limbs are strongly unbalanced because of the exceptionally propulsive hindlimbs (Fig. 6). The ratio of propulsive impulse to braking impulse for the hindlimbs of mammals usually falls below 5 (see fig. 11 in Demes et al., 1994) whereas alligators have an extraordinarily high value of 9.4. This great forward propulsive effort by hindlimbs appears to be necessary for counteracting the constant braking effect of the tail.

Sprawling and semi-erect tetrapods have large mediolateral ground reaction forces that have a distinct polarity indicative of a net lateral push by the limbs. By contrast, mediolateral forces of individual limbs in cursorial mammals are sufficiently small and irregular that they are commonly ignored in locomotion studies (e.g. comprising only about 6% of vertical force and 40% of braking force in walking and trotting dogs; Budsberg et al., 1987; Rumph et al., 1994). Mediolateral forces represent ≥20% of vertical force values in the fore- and hindlimbs of *Alligator*, *Iguana* and *Varanus* (Christian, 1995; Blob and Biewener, 2001). More striking is the magnitude of mediolateral force relative to craniocaudal force, with ratios of mediolateral force to craniocaudal force of ~100% for the hindlimb of *Iguana* (Blob and Biewener, 2001) and reaching 140% in the fore- and hindlimbs of *Alligator*. This indicates that the limbs of sprawling and semi-erect tetrapods apply as much, if not greater, effort in pushing laterally than they do craniocaudally with each step. The tail's mediolateral forces are trivially small so that the large lateral push by each limb is unlikely to be a response to the tail. That lateral bending of the axial skeleton alone is an inadequate explanation is borne out by turtles, which are clearly incapable of laterally bending the thoracic and lumbar spine yet show subequal craniocaudal and mediolateral force magnitudes (Jayes and Alexander, 1980; Moon, 1999). Consequently, high mediolateral forces in non-erect tetrapods are probably due to a combination of factors, including sprawling posture, nonparasagittal limb movements and proximal limb bone rotation as well as possibly lateral bending (Gatesy, 1991; Reilly and Elias, 1998; Blob and Biewener, 2001).

Thus, the hindlimbs of alligators assume a large role in body mass support and forward impulsion because these animals drag long and muscular tails. While this may be viewed as an unavoidable consequence of powering aquatic locomotion with the tail, and therefore comparable to other morphological and energetic compromises found in semiaquatic animals (Fish et al., 2001; Williams et al., 2002), it is important to recall that dragging a long and heavy tail behind the body is also the ancestral condition of tetrapods. Hence, the differential limb function noted for alligators may replicate the basal condition for terrestrial quadrupeds.

Effect of tails on pendular mechanics

What determines the efficacy of pendulum-like recovery during terrestrial walking is the phase relationship between total kinetic energy and gravitational potential energy as well as the magnitudes of the fluctuations in the energy profiles (Cavagna et al., 1977). With phase relationships averaging nearly 178°, *Alligator* fulfills the first criterion for efficient energy recovery; that is, the minimum kinetic energy and the maximum gravitational potential energy occur nearly synchronously. However, kinetic energy and gravitational potential energy profiles, although out-of-phase with one another, are not mirror images of each other in *Alligator* as the kinetic energy profiles are demonstrably flatter than those of potential energy. As a result, high walks are not particularly efficient mechanical walks because, on average, 80% of the mechanical energy of each walking step must be supplied by the muscles (compared with less than 65%, on average, in birds and mammals; Cavagna et al., 1977). Modest energy recoveries were also found in *Coleonyx variegatus* (western banded gecko) and *Eumeces skiltonianus* (western skink; Farley and Ko, 1997), tetrapods that similarly drag their tails when walking. While large-mass tails that remain in contact with the ground and limited energy recovery appear to be coupled, other features of alligator locomotor behavior, such as lateral forces, locomotor posture, footfall patterns and locomotor speed, may also contribute to reductions in energy recovery.

Should one assume that large mediolateral limb forces in non-erect tetrapods necessarily equate to locomotor inefficiency? The answer, provided by whole-body mechanics, is a resounding "no". In *Alligator*, the large laterally directed applied forces of contralateral limbs during high walks (walking trots) largely counteract each other, so that moderate mediolateral movements of the center of mass result. Rather

than degrading energy recovery by pendulum mechanics, these residual mediolateral movements actually improve energy recovery in high walking *Alligator* (by nearly 7%, on average). This is consistent with results found for the penguin: although they move with substantial side-to-side waddling, penguins are capable of recovering up to 80% of mechanical energy by pendular mechanics and this recovery is actually aided by waddling (Griffin and Kram, 2000).

Locomotor efficiency does appear to be associated with locomotor posture when walking. Bipeds tend to exceed quadrupeds in maximum mechanical energy recovery (maximum values at ~70% *versus* 50%, respectively; Cavagna et al., 1977), probably because two limbs are less likely to impede pendular mechanics than are four. Furthermore, there is a tendency for animals with erect postures (birds, cursorial mammals) to recover, on average, more mechanical energy by inverse-pendulum mechanisms than do more sprawling animals (Cavagna et al., 1977; Farley and Ko, 1997; Griffin et al., 1999; Muir et al., 1996; Tesio et al., 1998). Although a semi-erect posture clearly does not provide alligators with the energy savings typical of more erect tetrapods, this posture probably serves to lower the overall cost of terrestrial locomotion by increasing effective limb length (hip to substrate length). Again, the contrast with penguins illuminates this point: the high cost of locomotion in penguins has been ascribed to their short legs not to their waddling gait (Griffin and Kram, 2000).

Footfall patterns may also affect the efficiency of inverse-pendulum mechanisms. While the expectation that the footfalls of a diagonal couplet are well synchronized in trots was confirmed in dogs (Bertram et al., 1997), no such precision of footfalls was found in *Alligator* even though high walks are walking trots (diagonal couplet walks with ≥50% duty factor and 50±10% limb phase; Farley and Ko, 1997). In alligators, the forelimbs usually landed before the contralateral hindlimb (by as much as 9% of support duration); in a minority of the steps, hindlimb footfalls slightly preceded the forelimb. High-walking alligators also failed to consistently elevate the feet off the ground during the swing phase, with the toes of a protracting foot dragging forward more frequently in hindlimbs than forelimbs.

Finally, the efficiency of a pendulum-like exchange of gravitational potential energy and kinetic energy is well-known to be speed dependent. In animals as diverse as rheas and rams, the greatest energy recovery occurs at a narrow range of speeds, with lower recoveries at slower or faster speeds (Cavagna et al., 1977). The inverted-pendulum model applies best to intermediate walking speeds when the positive work to increase forward speed of the center of mass (W_f) is most similar to that used to lift the center of mass (W_v). At low speeds, energy recovery is reduced because W_v increasingly exceeds W_f (Cavagna et al., 1977). It is, therefore, not surprising that inverted-pendulum mechanics fails to provide great energy recovery in *Alligator* given that its positive work against gravity is almost an order of magnitude greater than that for forward propulsion. Energy recovery in *Alligator* was seen to increase with speed (Fig. 5B), so it is possible that captured speeds simply fell short of that required for peak energy recovery. The alligators in the present study chose to walk steadily at 0.102–0.195 m s^{-1}, speeds comparable with those obtained by Gatesy (1997) and Reilly and Elias (1998). Our top speed was nearly half that achieved by Blob and Biewener (1999; 0.37 m s^{-1}), suggesting that higher speeds may be possible. However, neither our animals nor those used by Gatesy (1997) could maintain a steady gait at higher speeds.

Therefore, relatively low locomotor speeds together with a semi-erect quadrupedal posture and an irregular trotting gait appear to degrade the ability of alligators to capitalize on pendular mechanics as a means of reducing locomotor costs for terrestrial locomotion. The effect of tail-dragging on pendular mechanics, however, remains questionable. The tail posture in other gaits and in lizards suggests that dragging heavy tails terrestrially may reduce locomotor efficiency. For example, while crocodilians typically walk with tail in tow, *Crocodylus* elevates its tail during quick galloping bouts (Renous et al., 2002), presumably to improve its running mechanics (e.g. by offsetting the tail's decelerative effect for the duration of this high-speed locomotor event).

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