

LOCOMOTION IN *ALLIGATOR MISSISSIPPIENSIS*: KINEMATIC EFFECTS OF SPEED AND POSTURE AND THEIR RELEVANCE TO THE SPRAWLING-TO-ERECT PARADIGM

STEPHEN M. REILLY* AND JASON A. ELIAS

Department of Biological Sciences, Ohio University, Athens, OH 45701, USA

*e-mail: reilly@ohiou.edu

Accepted 18 June; published on WWW 25 August 1998

Summary

In terms of locomotory posture, amphibians and lizards are considered to be sprawlers, mammals and dinosaurs are considered to be erect, and extant crocodilians are considered to be intermediate because they use the 'high walk', a semi-erect posture where the body is held half-way between the sprawling and erect grades during locomotion. In addition, crocodilians occasionally use a sprawling posture. Extant crocodilians, therefore, provide an interesting model in which to investigate the sprawling-to-erect transition in vertebrate evolution. This study quantifies the sprawl and high walk kinematics of the alligator *Alligator mississippiensis* moving at different speeds on a treadmill and compares them with kinematic data available for other vertebrates. These data allow us to examine the effects of speed on crocodilian postures and to examine how crocodilian locomotion relates to the sprawling-to-erect paradigm in vertebrate locomotion.

Our results show that the crocodilian sprawl is not functionally equivalent to the primitive sprawling behaviors exhibited by salamanders and lizards. In fact,

although the high walks and sprawls of alligators exhibit some kinematic differences, they are actually much more similar than expected and, essentially, the crocodilian sprawl is a lower version of a high walk and could be termed a 'low walk'.

In terms of the sprawling-to-erect transition, the high walk has knee kinematics intermediate between those of birds and non-archosaurian tetrapods, but alligators increase speed in a way completely different from other terrestrial vertebrates (distal rather than proximal limb elements are used to increase speed). These kinematic data viewed in the light of the fossil and phylogenetic evidence that modern crocodilians evolved from erect ancestors suggest that modern crocodilians have secondarily evolved a variable semi-erect posture and that they are problematic as an intermediate model for the evolutionary transition from sprawling to erect postures in archosaurs.

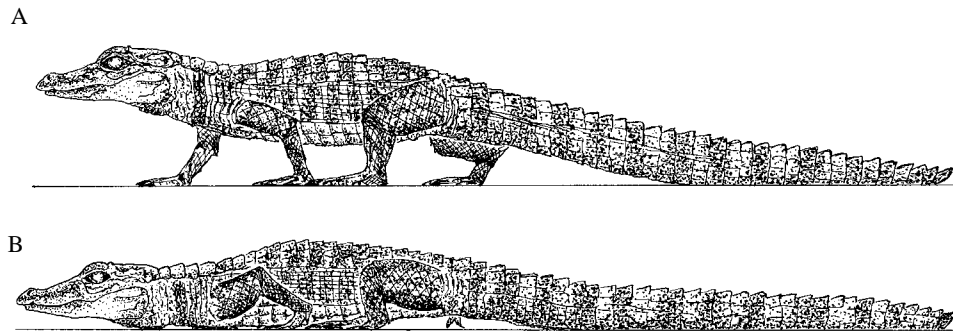
Key words: Crocodylia, kinematics, sprawling, locomotion, high walk, functional morphology, alligator, *Alligator mississippiensis*.

Introduction

A general paradigm in vertebrate locomotion is that locomotor postures in tetrapods evolved from a sprawling posture, with the limbs held laterally to the body, to an erect posture, with the limbs held directly under the body (e.g. Gregory, 1912; Bakker, 1971; Charig, 1972; Kardong, 1995). Considerable discussion of scenarios of how mammals and archosaurs made the transition from sprawling to erect postures has led to a three-grade system in which vertebrates are placed in 'sprawling', 'semi-erect' or 'erect' postural categories (Bakker, 1971; Charig, 1972; Edwards, 1977) primarily on the basis of the angle of the femur relative to the body as inferred from anatomical studies (Bakker, 1971; Dodson, 1974; Rewcastle, 1980, 1981; Hildebrand, 1985; Parrish, 1987). Although Gatesy (1991) has argued that it is a continuum, amphibians and lizards are generally considered to be sprawlers, mammals and dinosaurs to be erect and extant crocodilians to be intermediate because they customarily use

the 'high walk' (Fig. 1A), which has been shown to be a semi-erect posture with the body held half-way between the sprawling and erect grades during locomotion (Brinkman, 1980; Gatesy, 1991). If the high walk is an intermediate posture, then studying locomotory kinematics in extant crocodilians would provide important information about changes that may have occurred during the sprawling-to-erect transition. In addition, crocodilians also move using a sprawling posture (Cott, 1961; Brinkman, 1980; Webb and Gans, 1982), which has not been studied (Fig. 1B). If the sprawl of extant crocodilians is similar to the primitive sprawling posture in more basal vertebrates, and the semi-erect high walk is intermediate, then comparisons of the momentary transition between these postures in living individuals may identify key functional transformations critical to understanding the evolutionary transition to more erect postures in archosaurs.

Fig. 1. Representative drawings of the 'high walk' and 'sprawl' postures used by alligators during locomotion. The high walk (A) is the primary posture used for overland travel, and the body is held off the ground. The sprawl (B) is generally a transitional posture (to and from a high walk) or is used to slide the animal short distances across wet substrata.



However, there is a polarity problem. Studies of archosaur limbs and pelvises indicate that the plesiomorphic posture for Crocodylia and its three closest outgroups is an erect posture and that basal crocodylomorphs were highly terrestrial and cursorial, with some forms even using digitigrady (Crush, 1984; Parrish, 1986, 1987; Sennikov, 1989; Gomani, 1997). The living crocodylians, therefore, are secondarily semi-erect and secondarily sprawling, probably in association with the invasion of aquatic habitats (Parrish, 1987). Have the living crocodylians reverted back to the ancestral semi-erect and sprawling postures of more basal vertebrates, are their postures novel intermediate and sprawling postures, or are they basically modified erect postures? These questions are explored here by comparing the kinematics of the sprawl and the high walk in a living crocodylian with kinematic data for other sprawling vertebrates and for erect birds and mammals.

It has also been suggested that the transition from the sprawl to the high walk in crocodylians is related to speed and the degree of terrestriality, with animals using the sprawl at slow speeds and in muddy situations and the high walk at higher speeds and in drier situations, with a transition to a gallop at even higher speeds and on more heterogeneous substrata (Webb and Gans, 1982). Do crocodylians change postures to increase speed? This question can be examined by studying the postures of living crocodylians moving at different speeds.

The goal of this study is to quantify the three-dimensional sprawl and high walk kinematics of a living crocodylian, the alligator *Alligator mississippiensis*, moving at different speeds and to compare them with kinematic data available for other vertebrates. These data will allow us to examine the speed dynamics of crocodylian postures and to determine whether the evolutionary return to semi-erect and sprawling postures in crocodylians involves a reversion to primitive locomotory kinematics, the development of novel limb mechanics or the retention of a modified form of essentially erect limb movement patterns. The results of these comparisons have direct relevance to the utility of extant crocodylians as a model for the transitional form between sprawling and erect postures.

Materials and methods

One-year-old *Alligator mississippiensis* were obtained from the Department of Wildlife and Fisheries of the Rockefeller Wildlife Refuge Grand Chenier, LA, USA. Initially, six

alligators were filmed on a speed-controlled treadmill to probe the range of speeds and gaits that the animals use. We found that the alligators did not use single-foot sequence gaits but consistently used a walking trot. A steady trot, however, was used only over a narrow range of speeds from 0 to approximately 0.2 m s^{-1} . Above this speed, the animals stopped, trotted quickly ahead and rode the belt back in a sort of burst-and-glide movement or occasionally, at higher speeds, attempted to gallop for part of a stride before stopping. Initial examination of sprawling (belly dragging) *versus* high walk (body elevated) strides (Fig. 1) revealed that posture was not related to speed. Alligators predominantly use the high walk posture, and the sprawling posture appears to be a transitional behavior in going to, or from, a high walk. Thus, we chose to compare locomotory patterns for the sprawling and high walk postures over a doubling of speeds within the range for which they consistently matched treadmill belt speed (0.074 and 0.146 m s^{-1}). The quantitative analyses and descriptions are based on kinematic data for three alligators (snout-vent lengths, SVL, 202, 220 and 220 mm).

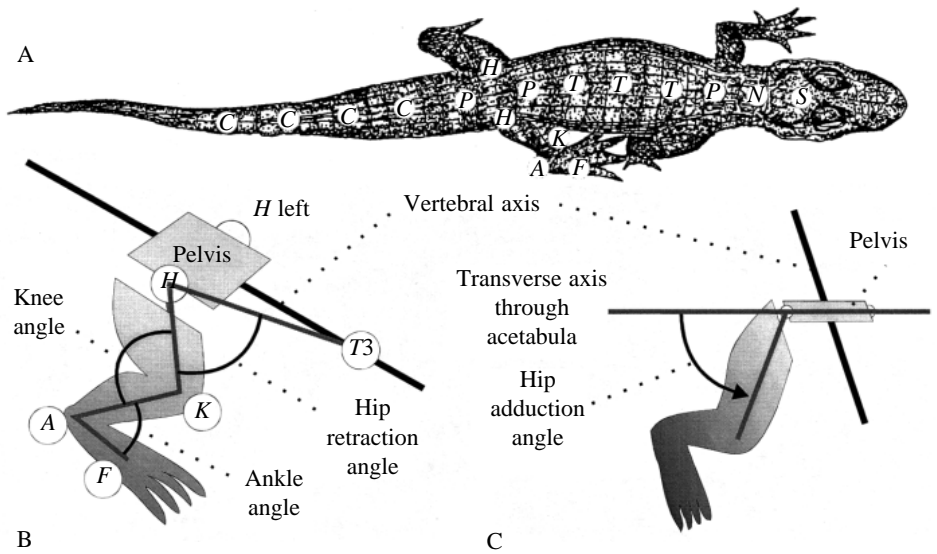
Kinematic analysis

The alligators were filmed under strobe lights at $200 \text{ fields s}^{-1}$ using a NAC HSV-400 high-speed video system. Elapsed time in milliseconds was recorded on each video frame during filming. Lateral and dorsal views of the alligators during locomotion were filmed (using mirrors) on a 70 cm long canvas treadmill. Locomotion was elicited by pinching the tail when the treadmill was turned on; the alligators trotted, matching the treadmill speed for dozens of strides. The cloacal body temperature of the alligators before and after the runs was $22\text{--}25^\circ\text{C}$. Reflective landmarks (2 mm diameter paint dots) were painted on the skin of the alligators (Fig. 2) to mark positions along the vertebral column, the position of the hip joints (directly over the acetabula) and three landmarks on the right hindlimb: the knee joint (on the anterolateral point of the knee when flexed), the ankle joint (posterolateral point of the ankle when flexed) and the foot (lateral aspect of the metatarsal-tarsal articulation). The skin of the alligator is tightly attached to the underlying tissues and does not move during the step cycle. Thus, the skin landmarks closely correspond to the underlying skeletal landmarks. The landmarks were visible in both the lateral and dorsal views. A series of axial landmarks (Fig. 2) was used to visualize axial bending patterns in two dimensions.

Fig. 2. Kinematic landmarks (reflective paint dots) and angles used to describe limb and axial movements in alligators during locomotion. (A) Two-dimensional

movements of the vertebral column were quantified by digitizing the following two-dimensional landmark points along the midline from head to tail: (S) the middle of the skull behind the eyes, (N) the neck, (P) the pectoral girdle (midline between the arms), three equally spaced trunk landmarks (T), the anterior and posterior aspects of the pelvis (P) and four equally spaced caudal landmarks (C). Pelvic angle was calculated as the two-dimensional angle between line T3–C1 and the direction of travel [indicating pelvic rotation to the left (negative) and right (positive) angles]. Three-dimensional coordinates were digitized for the third trunk landmark (T3)

and landmarks for the hip joint (H: on both sides, H left, H right), the knee (K), the ankle (A) and the foot (F: on the skin on the lateral aspect of the metatarsal–tarsal articulation). (B) Three-dimensional angles were calculated for hip (femoral) retraction angle (the angle between landmarks T3, H and right-K indicating primarily femoral retraction/protraction movements), knee angle (angle H–K–A indicating knee flexion and extension) and ankle angle (angle K–A–F indicating foot flexion and extension). (C) Hip (femoral) adduction angle (angle H–left–H–right–K) was calculated to quantify the degree of hip adduction relative to a transverse line through the acetabula.



From the numerous strides recorded for each speed and posture, we selected five strides for each of the three individuals during which the alligators moved parallel to the treadmill and matched the treadmill speed. Thus, 60 strides were used in the analysis. For every eighth video field for each stride (40 ms sampling), the three-dimensional coordinates of each landmark were digitized using stereo Measurement TV (the sMTV; Updegraff, 1990). Landmarks were digitized in both video views and the software provided the three-dimensional coordinates for that point (the sMTV algorithm is described in the Appendix). The coordinate data were then used to calculate three-dimensional angles for each video field to quantify movements of the pelvis, hip, knee and ankle through the stride as illustrated in Fig. 2B,C. Angle measurement accuracy was $\pm 1^\circ$.

Kinematic variables

Stride characteristics

The durations of the stance phase, swing phase and entire stride were measured from footfall patterns for each stride. From these, the duty factor (percentage of the stride that the foot is on the ground) was calculated. In addition, we calculated stride length (stance duration \times speed) and stride width (the lateral distance from the midline of the pelvis to the foot coordinate at foot down) for each stride.

Limb and pelvic movements

To assess quantitatively the effects of speed and posture on hindlimb kinematics, a series of angular and timing variables were taken from each stride to describe and compare statistically movements of the pelvis (in two-dimensional

space) and hindlimb joints (in three-dimensional space). The variables were chosen to capture the minimum and maximum excursion angles (and associated timing) of the pelvis and each of the three major joints of the hindlimb (the hip, knee and ankle) as described in Fig. 2. Hip movements were quantified using two variables: hip retraction (indicating retraction/protraction movements relative to the longitudinal axis of the pelvis) and hip adduction (indicating adduction/abduction movements relative to the mediolateral axis of the pelvis). The femoral retraction angle was measured relative to a line from the acetabulum and the third trunk landmark, and it therefore overestimates the angle relative to a sagittal plane by approximately 15° . For the femoral adduction angle, 0° indicates no femoral adduction (the femur held straight out laterally from the acetabulum) and 90° is parallel to the sagittal plane. This angular configuration was chosen to follow the convention of the sprawling-to-erect paradigm, which categorizes sprawling femoral angles as 0° and erect ones as 90° (Bakker, 1971; Charig, 1972; Parrish, 1986, 1987).

The angular variables were as follows. The angles of each limb joint were measured at the time of right foot down. These angles indicate the positions of the three joints and the pelvis at the beginning of the stance phase. The remaining angular variables quantified the minima and maxima of each joint movement and excursions between them. For hip movements, the femoral retraction maximum (near the end of the stance phase), minimum (near the end of the swing phase) and excursion (from minimum to maximum retraction) plus the femoral adduction maximum (in early swing phase), minimum (in late swing phase) and excursion (during the swing phase)

were measured. For knee movements, the minimum (in early swing phase), maximum (near the end of the swing phase) and excursion (during the swing phase) were measured. For ankle movements, the maximum, minimum and excursion during the stance phase and the minimum and maximum during the swing phase were measured. Pelvic movements were quantified in terms of maximum rotation to the right (the side of ground contact) and the total excursion of the pelvis from right to left.

Timing variables were taken to describe the timing of the minima and maxima of the joint movements (the times to the various joint angles described above) and the durations of the joint excursions described above. All timing variables were taken relative to time zero at right foot down. For comparisons across speeds and postures, all timing variables (including swing-phase features) were scaled to the stance duration for each stride (variables are expressed as a percentage of stance duration with swing features having values over 100%). This was done so that the timing of kinematic events was compared relative to the stance phase during which locomotory forces were conveyed to the substratum and were not confounded by the dynamics of possible changes in the stance and swing phases (Reilly and DeLancey, 1997a).

Axial movements

Axial bending patterns were illustrated by superimposing stick figures of head-to-tail landmark coordinates for each frame for all the frames in a complete stride. The amplitudes of the pectoral and pelvic nodes were quantified by measuring the range of movement of the nodes in the mediolateral direction.

Statistical analyses

To describe the gaits used by the alligators, the timing of footfalls was measured for each foot for each stride (for a complete cycle for each of the four feet), and an overall mean gait diagram for one individual was plotted using mean footfall timing values for five strides for each of the speeds and postures. To illustrate graphically and compare movement patterns of the hindlimb joints and pelvis for each speed and posture, mean kinematic profiles were generated for one individual. Mean angles (± 1 S.E.M.) for five strides from each behavior were plotted with strides aligned by treating the time of right foot down as time zero, with mean profiles scaled to stride duration.

To compare kinematic variables statistically, we used a three-way analysis of variance (ANOVA) with speed (testing the effects of doubling the speed) and posture (testing differences between sprawling and high walk strides) treated as independent factors crossed with the three subjects as the individual effect. Because all individuals serve in all four speed-by-posture treatment combinations, this analysis employs a pure within-subjects (repeated-measures) design (Zolman, 1993, p. 59). This repeated-measures design (performed using Systat version 6.0) has the advantage of testing differences in the main effects after variation among individuals, within individuals within behaviors, and residual

errors have been extracted. The *a priori* choice to use the same individuals in all the treatment combinations was made to control for the problem of interindividual variation and because the within-subjects design provides more conservative tests for significance than standard analysis of variance tests since the *F*-ratios for the main effects and their interaction are calculated by dividing the mean square for these effects by the appropriate interaction mean square rather than the error mean square. Given the more conservative design, we were confident that an alpha level of 0.05 was sufficient to indicate statistical significance even with multiple univariate comparisons within limb joints.

Results

Representative video frames portraying a single stride of the right hindlimb during a high walk are shown in Fig. 3, and stride timing data are presented in Table 1. Mean kinematic profiles for the angular movements of the hindlimb joints and pelvic rotation of one individual are presented in Fig. 4. Mean angular and scaled timing variables pooled across individuals are presented in Tables 2 and 3, respectively, and ANOVA results comparing speeds and postures for these variables are presented in Table 4.

Stride and gait characteristics

The alligators used the sprawl and high walk at all speeds, and the change in posture was not a result of increasing speed. The duration of stance phase and swing phase and total stride duration decrease significantly with increased speed and when changing to the high walk posture. The mean percentage of the stride that the right foot is on the substratum (duty factor) averaged between 69 and 74% (Table 1) and did not differ significantly among the four treatments (see Table 4). Stride length increased significantly with speed (by approximately 20% of SVL) but decreased significantly (by approximately 10% of SVL) when going from the sprawl to the high walk at either speed (Table 1). Stride width (from pelvis to foot laterally) at foot down did not change among the four treatments, remaining at 2.1 cm or 10% of SVL (Table 1). During the high walks analyzed, the height of the belly above the treadmill averaged 2.17 ± 0.2 cm anterior to the pelvis and 2.60 ± 0.28 cm at the pectoral girdle (mean \pm S.E.M., $N=15$).

Mean gait patterns for both postures and speeds are illustrated in Fig. 5. At both speeds and in both postures, *Alligator mississippiensis* moved using coordinated footfalls of diagonal limb couplets (i.e. a trot). On the basis of these mean data, the gait at both speeds and postures is categorized as a moderate walking trot according to the terminology of Hildebrand (1985).

Axial bending patterns

The basic pattern of axial bending observed in all four treatments is illustrated in Fig. 6 for an alligator high walking at 0.146 m s^{-1} . All strides exhibited an approximate standing wave, with nodes appearing just posterior to the pectoral girdle and just anterior to the pelvis. The amplitudes of the

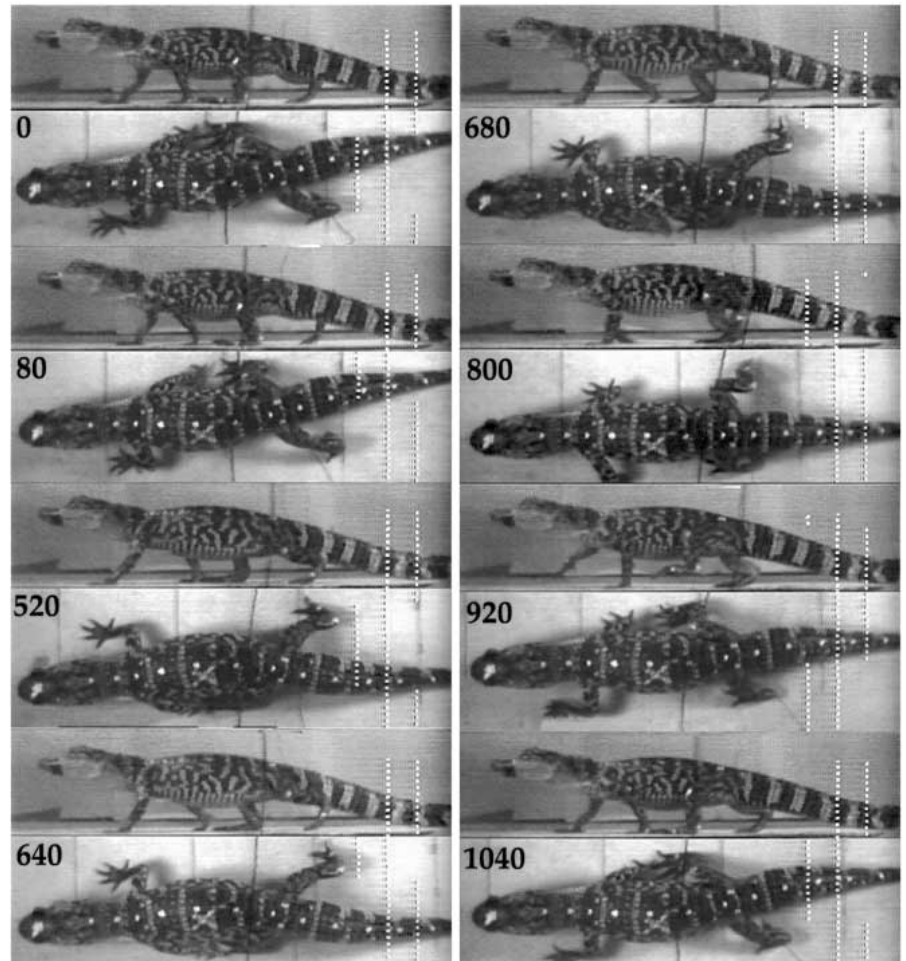


Fig. 3. Lateral and dorsal images from high-speed video recordings illustrating one high walk stride of *Alligator mississippiensis* moving at 0.146 m s^{-1} using a moderate walking trot. Time is indicated on the dorsal frame of each pair of images in milliseconds from foot down (time zero) to the subsequent foot down (1040 ms); foot up is at 800 ms. White dots on images are synchronization pulses.

mediolateral movements at the pectoral and pelvic nodes averaged between 1.2 and 1.15 cm, respectively, and were not significantly different across speeds (all $P > 0.307$) or postures (all $P > 0.120$) for either girdle. Speed and posture do not appear to affect axial bending patterns.

General hindlimb kinematic patterns

In general, the gross patterns of hindlimb and pelvic movements were similar across both speeds and postures in the

alligator. In the following paragraph, the basic similarities of hindlimb kinematics across all four treatments are described relative to the overall limb movements and footfall patterns based on the mean kinematic profiles for one individual (Fig. 4) and the mean angular and timing data pooled for all individuals (Tables 2, 3). Statistically significant differences indicating speed and posture effects (Table 4) are described in the subsequent sections.

Pelvic movement patterns were essentially identical at both

Table 1. Stride characteristics in alligators locomoting in sprawling and high walk postures at two speeds

Variable	Sprawl		High walk	
	0.074 m s^{-1}	0.146 m s^{-1}	0.074 m s^{-1}	0.146 m s^{-1}
Stance duration (ms)	1371 ± 33	858 ± 21	1094 ± 18	779 ± 13
Swing duration (ms)	495 ± 30	389 ± 19	437 ± 24	331 ± 8
Stride duration (ms)	1866 ± 28	1248 ± 21	1538 ± 18	1111 ± 17
Duty factor (stance duration/stride duration)	0.74 ± 0.02	0.69 ± 0.01	0.71 ± 0.01	0.70 ± 0.01
Stride length (cm)	13.9 ± 0.3	17.9 ± 0.4	11.6 ± 0.1	16.1 ± 0.3
Stride length (% snout-vent length)	66 ± 2	87 ± 2	55 ± 1	78 ± 1
Stride width (cm, midline to foot marker)	2.12 ± 0.06	2.14 ± 0.04	2.10 ± 0.03	2.07 ± 0.02

Values are means \pm s.e.m. pooled for three individuals ($N=5$ strides each, total $N=15$).

See Table 4 for results of ANOVA.

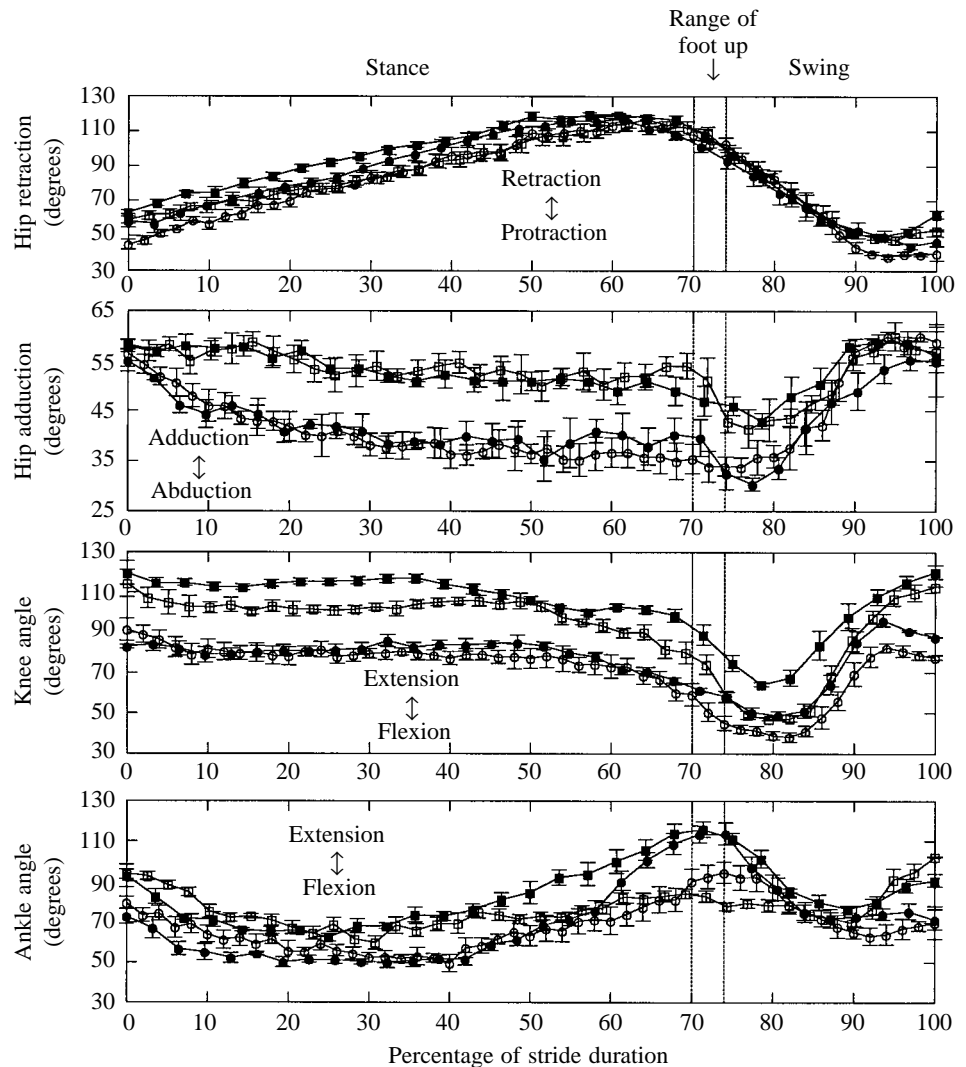


Fig. 4. Mean profiles for right hindlimb joint kinematics (in degrees) for *Alligator mississippiensis* using sprawls (circles) and high walks (squares) at two speeds (open symbols, 0.074 m s⁻¹; filled symbols, 0.146 m s⁻¹). Three-dimensional angular means \pm S.E.M. are shown for five strides from one individual. The x axis indicates time as a percentage of stride duration beginning at right foot down (time zero). For femoral retraction, the hip is protracted at lower values and retracted at higher values; for femoral adduction, the femur is adducted at higher values and abducted at lower values; a femoral adduction angle of 0° means that the limb is oriented straight out from the acetabulum laterally. The knee and ankle are flexed at lower values and extended at higher values. The vertical lines on each plot indicate the range of mean times for the end of the stance phase (foot up). Significant differences between postures and speeds based on analysis of variance results are given in Table 4.

speeds and postures, with maximum pelvic rotation to the left occurring at foot down and maximum pelvic rotation to the right occurring at approximately 73% of the stance phase. The total excursion of pelvic rotation about the direction of travel was approximately 26°. Femoral retraction movements were similar across treatments as well. Maximum protraction of the femur occurred just before foot down (at approximately 95% of stride duration) and maximum femoral retraction of approximately 126° occurred at approximately 86% of stance duration (just over 60% of stride duration; Fig. 4). Femoral adduction angle was relatively constant (at 40° in sprawls and 55° in high walks) for the last three-quarters of the stance phase (Fig. 4). During the swing phase, the femur was abducted slightly at approximately 77% of stride duration, then adducted to its maximum of approximately 59° just before foot down, before abducting to 51° at foot down. Knee movements were similar in pattern except at the end of the swing phase. Knee angle decreased slightly following foot down (from 120 to 110°), then remained essentially constant during the middle stance phase. It then began to decrease late in the stance phase (to 65° in sprawls and to 90° in the high walk) before exhibiting

continued flexion then extension during the swing phase. The minimum knee flexion during the swing phase was consistently at approximately 80% of stride duration. The ankle had a consistent pattern of flexion then extension during the stance phase followed by another cycle of flexion then extension during the swing phase. During the stance phase, the minimum ankle flexion of 45–62° was reached at approximately 38% of stance phase, and maximum ankle extension coincided with the timing of foot up. Consequently, the duration of ankle extension during the stance phase was constant at approximately 65% of stance duration. Ankle movements during the swing phase were the most variable of any of the limb joint movements, with the only general similarity being the minimum ankle flexion of approximately 54–73°.

High walks versus sprawls

Femoral retraction movements

The timing of femoral movements (relative to stride or stance duration) did not change significantly with posture (Table 4). Maximum protraction of the femur, which occurs prior to foot down, was significantly smaller (approximately

8°) in the high walks, but maximum femoral retraction angle did not vary with posture. Accordingly, the overall excursion of femoral movements relative to the pelvis was significantly smaller in the high walks. Femoral movements during the stance phase begin from a more protracted position in sprawls (femoral retraction angle at foot down is significantly smaller) but converge to the same position in both postures at maximum retraction.

Femoral adduction movements

Stance phase femoral adduction kinematics differ in the two postures in ways not captured quantitatively by our kinematic variables. High walks have a static femoral adduction angle of approximately 55° throughout the stance phase (Fig. 4). The hip adduction angle at foot down is the same in both postures, but in sprawls the femur is rapidly abducted early in the stance phase to produce approximately 20° more abduction than in high walks, and this difference is maintained for the remainder of the stance phase. During the swing phase, femoral adduction angle in both postures is decreased slightly immediately after foot up, before increasing to the same maximum angle just prior to foot down. Therefore, the greater excursion of femoral abduction during the stance phase in sprawls is generated during a short period of abduction early in the stance phase.

Knee movements

Knee angles for both postures were essentially constant for

most of the stance phase but began to decrease at the end of the stance phase (Fig. 4). However, from foot down to foot up, high walks consistently had approximately 30° more knee extension than sprawls, as indicated by the significant difference in knee angle at foot down (Table 2; Fig. 4). This difference in knee extension is generated by differences in knee movements during the swing phase, as reflected by significant differences in five other knee variables during the swing phase (Table 4). The knee begins to flex before foot up and continues to flex to a minimum angle that is significantly smaller in sprawls (approximately 14° smaller). From this minimum, the knee extends in both postures until a critical kinematic event occurs in the last third of the swing phase. In high walks, the knee continues to extend until foot down. In sprawls, maximum extension occurs well before foot down, and the knee begins to flex prior to foot down. Thus, in sprawls, maximum knee extension is 25° smaller and occurs significantly earlier than in high walks, and the earlier onset of knee flexion results in a significantly smaller knee angle at foot down and during the stance phase. This shift in the timing of maximum knee extension (and its effect on the duration of knee flexion during the swing phase) is a crucial kinematic timing difference between the postures.

Ankle movements

Ankle movements during the stance phase are similar between postures (Fig. 4). During the swing phase, however,

Table 2. Angular variables for hindlimb joint and pelvic movements in alligators locomoting using sprawling and high walk postures at two speeds

Variable (degrees)	Sprawl		High walk	
	0.074 m s ⁻¹	0.146 m s ⁻¹	0.074 m s ⁻¹	0.146 m s ⁻¹
Ankle minimum (stance)	46±4	47±4	55±5	62±5
Ankle maximum (at approximately foot up)	113±5	126±4	112±4	124±4
Ankle excursion (stance)	66±4	79±4	58±5	57±4
Ankle minimum (swing)	54±2	62±3	66±1	73±1
Ankle at foot down	69±3	71±3	83±3	88±3
Knee minimum (swing)	39±1	48±1	52±2	64±1
Knee maximum (swing)	84±2	95±2	109±2	121±2
Knee excursion (swing)	44±2	47±3	57±3	57±2
Knee at foot down	80±2	90±2	109±2	121±2
Femoral adduction minimum (swing)	28±3	27±1	35±1	33±1
Femoral adduction maximum (swing)	59±1	57±1	59±1	59±1
Femoral adduction excursion (swing)	31±3	30±1	24±1	25±1
Femoral adduction at foot down	53±2	51±1	50±1	52±1
Femoral retraction maximum (stance)	127±3	128±2	126±2	123±1
Femoral retraction minimum (swing)	43±1	47±1	52±1	54±1
Femoral retraction excursion	84±2	81±2	74±2	69±2
Femoral retraction at foot down	52±2	53±1	64±1	67±1
Pelvic maximum (to right)	13±2	13±2	12±1	13±1
Pelvic excursion	27±2	26±1	24±1	26±1
Pelvic at foot down	-13±2	-13±2	-12±2	-13±1

Means (±S.E.M.) for each treatment (N=15) are pooled for three individuals (N=5 strides each).

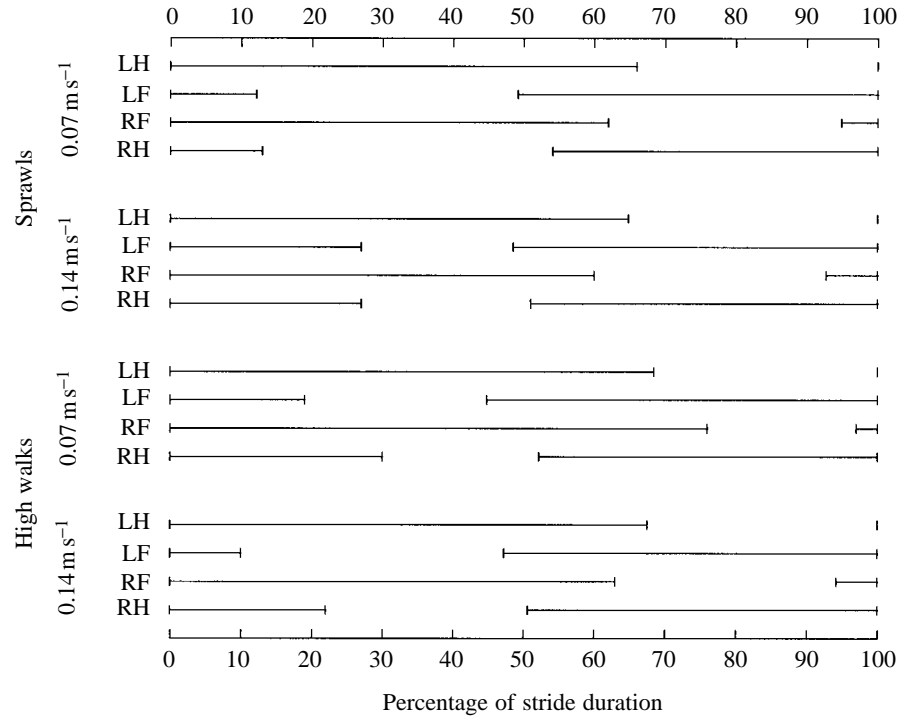


Fig. 5. Mean gait patterns (scaled to stride duration) based on footfall timing of all four limbs from one alligator using sprawl and high walk postures at two speeds ($N=5$ for each). L, left side; R, right side; H, hind foot; F, fore foot. Note the essentially identical gait (a walking trot) exhibited by all four combinations of speed and posture.

the high walks reach the minimum ankle angle significantly earlier and the ankle is then extended by $10\text{--}15^\circ$ before foot down (Tables 2–4). During sprawls, the ankle is extended less in late swing phase, which results in a significantly smaller ankle angle at foot down (approximately 15° smaller).

Speed effects

The height of the body above the treadmill at both the pelvis and pectoral girdles did not change significantly with speed (all $P>0.275$). Significant speed effects were found in only four kinematic variables, and these involved angular movements in the ankle and knee joints (Table 4). The maximum ankle extension, which occurred at approximately foot up, was significantly greater (by approximately 12°) at the higher speed within both postures. The minimum knee angle, maximum knee angle and knee angle at foot down were significantly greater (consistently by approximately 10°) at the higher speed, while the excursion from minimum to maximum remained constant within speeds. This indicates that the knee joint is more extended during the swing phase at the higher speed.

Discussion

Speed effects

Within postures, as the alligators moved faster, the stride length increased. With the doubling of speed, the stride length increased by approximately 4–4.5 cm or approximately 28–38%, while the stride duration decreased by approximately 30–40% in real time. Thus, speed was increased overall by moving the limb faster and over a greater distance during the

stride. Surprisingly, however, the duty factor did not change with speed (Table 4), with the stance phase comprising approximately 71% of the stride duration at both speeds and postures. Thus, the stance and swing phases shorten at the same rate. Gatesy (1997) reported the same duty factor over similar

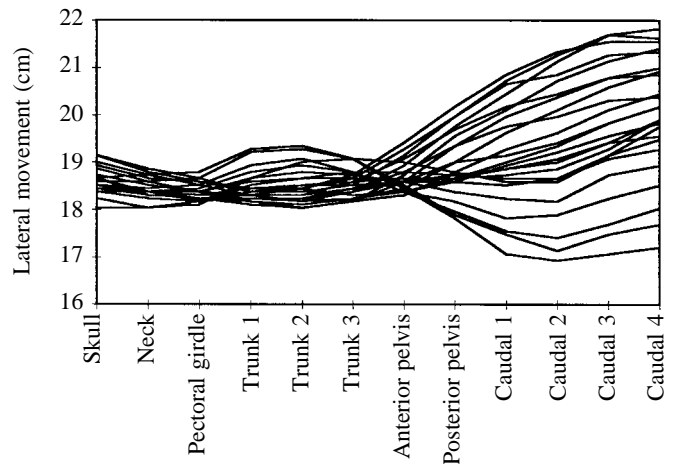


Fig. 6. Axial bending patterns for one individual stride of *Alligator mississippiensis* using a high walking trot at 0.146 m s^{-1} . This basic pattern was found in all four speed and posture combinations. Stick figures (lines through the axial landmarks) for 40 ms intervals during the stride are superimposed to illustrate the shape of the axial bending waves. y axis values are lateral movement values (in cm) from two-dimensional coordinates digitized from the axial landmarks indicated on the x axis. Note the approximate double-node standing wave with nodes just inside the appendicular girdles.

Table 3. Scaled kinematic timing variables for joint and pelvic movements in alligators locomoting in sprawling and high walk postures at two speeds

Variable	Sprawl		High walk	
	0.074 m s ⁻¹	0.146 m s ⁻¹	0.074 m s ⁻¹	0.146 m s ⁻¹
Time to ankle minimum (stance)	0.38±0.03	0.42±0.03	0.34±0.02	0.35±0.03
Time to ankle maximum (at foot up)	1.02±0.02	1.03±0.02	1.03±0.01	0.99±0.01
Time to ankle minimum (swing)	1.30±0.03	1.32±0.02	1.25±0.02	1.22±0.02
Ankle excursion duration (stance)	0.64±0.04	0.61±0.04	0.69±0.02	0.65±0.03
Time to knee minimum (swing)	1.15±0.02	1.20±0.02	1.14±0.03	1.10±0.01
Time to knee maximum (swing)	1.31±0.02	1.36±0.02	1.40±0.03	1.43±0.02
Knee excursion duration (swing)	0.22±0.01	0.25±0.02	0.27±0.02	0.32±0.01
Time to femoral adduction maximum	1.09±0.02	1.13±0.03	1.08±0.02	1.10±0.02
Time to femoral adduction minimum	1.33±0.03	1.38±0.03	1.32±0.02	1.25±0.08
Femoral adduction excursion duration	0.24±0.02	0.25±0.02	0.24±0.14	0.15±0.07
Time to femoral retraction maximum	0.87±0.01	0.88±0.02	0.85±0.01	0.85±0.02
Time to femoral retraction minimum	1.32±0.03	1.39±0.03	1.30±0.02	1.29±0.01
Femoral retraction excursion duration	0.45±0.02	0.51±0.03	0.46±0.23	0.44±0.02
Time to pelvic maximum (to right)	0.71±0.02	0.73±0.02	0.73±0.02	0.77±0.01
Time to pelvic minimum (= to left)	0.00±0.02	0.04±0.04	0.03±0.02	0.03±0.01
Pelvic excursion duration	0.71±0.03	0.79±0.04	0.71±0.03	0.74±0.01

Means ± S.E.M. of raw times scaled to stance duration for each treatment ($N=15$) are pooled for three individuals ($N=5$ strides each).

Approximate mean raw timing values can be estimated by multiplying these values by the stance durations in Table 1.

speeds. A constant duty factor is contrary to the pattern usually observed in tetrapods where the duty factor decreases with speed and the relative proportions of stride duration made up by the swing and stance phases are altered (Reilly and DeLancey, 1997a).

How is a greater stride length accomplished in a shorter time? None of the scaled timing variables we measured changed significantly with speed, and axial bending patterns did not change with speed (Table 4). This indicates that, as stride duration decreased with speed, the time to minimum and maximum positions for each joint occurred at the same relative time during the stride. In addition, most of the angular variables did not change with speed. Thus, the joints moved through the same ranges of motion as speed increased, and in general the alligators simply moved the limb in the same way but faster to decrease the stride duration. However, two key kinematic changes that produce the greater stride length can be identified by those angular variables that did show significant changes with speed (Table 4). First, the ankle is significantly more plantar-flexed (by approximately 12°) towards the end of the stance phase at the higher speed. Because maximum ankle extension occurs at the same relative time (at foot up, Table 3), the rate at which ankle extension occurs during the stance phase must be relatively faster as well. Increased extension of the ankle adds directly to the limb (and thus stride) length, while faster ankle extension would increase the propulsive force generated during the stance phase. Both these effects can be expected to contribute to increasing stride length.

The second key kinematic effect of speed involves

movements of the knee during the swing phase. Three significant speed effects involved knee variables during the swing phase (Table 4). At the faster speed, both the minimum and maximum knee angles during the swing phase were significantly greater (by approximately 11°), while the excursion of knee movement remained the same, whereas the knee angle at foot down was significantly greater as well (by approximately 11°). These variables indicate that as speed increases the knee is flexed less during the swing phase, which results in the knee being more extended at foot down and during the stance phase. This effectively lengthens the limb, which increases the stride length. And because the duty factor did not change over this range of speeds, the effectively longer limb is retracted in the same amount of time, which would produce greater propulsive force as speed increases. So, overall, the speed is increased by retracting a longer limb (*via* greater knee extension) and by extending the ankle farther and relatively faster. This contrasts with data on other vertebrates in which femoral movements are the primary effectors of speed. In the salamander *Dicamptodon tenebrosus* (Ashley-Ross, 1994a), monkey *Cercopithecus aethiops* (Vilensky and Gankiewicz, 1990) and lizard *Sceloporus clarkii* (Reilly and DeLancey, 1997a), the femur is retracted through a constant range of motion but relatively faster as speed increases. In the only bird for which we have speed data (common guinea fowl *Numida meleagris*), it appears that speed is increased by retracting the femur farther and for a relatively longer time (Gatesy, 1994). Thus, alligators appear to be fundamentally different from more basal quadrupeds and guinea fowl and, therefore, cannot be considered intermediate between

sprawling and erect postural forms in the dynamics of speed production. However, information on speed effects in birds are lacking, and fully informed comparisons with birds cannot therefore be made at this time.

Locomotor behavior in the alligator

Our extensive film sampling showed that alligators use the

high walk posture when moving more than one or two strides and they often 'stand up' and use the high walk immediately. The sprawling posture is used only for short distances, usually involving one and rarely two or three strides, or as a transitional behavior used in going from resting to a high walk or when slowing to a stop from a high walk. This corresponds with field observations that the sprawl is used primarily for

Table 4. Analysis of variance statistics for the effects of speed and posture on the hindlimb joint movements and pelvic rotation in alligators

Variable	Speed d.f.=1, 2	Posture d.f.=1, 2	Individual d.f.=2, 48	Speed × posture d.f.=1, 2
Stance duration	0.003*	0.006*	0.003*	0.026*
Swing duration	0.010*	0.028*	0.001*	0.950
Stride duration	0.001*	0.003*	0.0002*	0.124
Stride length	0.011*	0.021*	0.211	0.244
Stride width	0.957	0.974	0.757	0.974
Duty factor	0.219	0.881	0.002*	0.463
Ankle minimum (stance)	0.082	0.071	0.001*	0.950
Time to ankle minimum (stance)	0.759	0.243	0.575	0.689
Ankle maximum	0.007*	0.392	0.0001*	0.459
Time to ankle maximum	0.384	0.479	0.169	0.128
Ankle excursion (stance)	0.400	0.142	0.0001*	0.249
Ankle excursion duration (stance)	0.674	0.734	0.184	0.844
Ankle minimum (swing)	0.110	0.151	0.0006*	0.794
Time to ankle minimum (swing)	0.986	0.001*	0.0001*	0.279
Ankle at foot down	0.509	0.036*	0.011*	0.442
Knee minimum (swing)	0.048*	0.021*	0.0001*	0.739
Time to knee minimum (swing)	0.757	0.152	0.0001*	0.215
Knee maximum (swing)	0.012*	0.008*	0.003*	0.844
Time to knee maximum (swing)	0.287	0.019*	0.004*	0.684
Knee excursion (swing)	0.655	0.018*	0.105	0.878
Knee excursion duration (swing)	0.095	0.016*	0.0001*	0.783
Knee at foot down	0.005*	0.006*	0.046*	0.731
Femoral adduction minimum (swing)	0.161	0.006*	0.003*	0.867
Time to femoral adduction maximum (swing)	0.380	0.592	0.0001*	0.757
Femoral adduction maximum (swing)	0.126	0.486	0.0001*	0.380
Time to femoral adduction minimum (swing)	0.914	0.361	0.098	0.433
Femoral adduction excursion (swing)	0.740	0.004*	0.620	0.529
Femoral adduction excursion duration (swing)	0.398	0.286	0.973	0.240
Femoral adduction at foot down	0.869	0.683	0.0001*	0.378
Femoral retraction maximum (stance)	0.548	0.668	0.0001*	0.295
Time to femoral retraction maximum	0.698	0.358	0.193	0.619
Femoral retraction minimum (swing)	0.057	0.046*	0.0001*	0.731
Time to femoral retraction minimum	0.353	0.144	0.0001*	0.179
Femoral retraction excursion	0.187	0.0001*	0.888	0.676
Femoral retraction excursion duration	0.656	0.345	0.031*	0.345
Femoral retraction at foot down	0.525	0.011*	0.0001*	0.425
Pelvic maximum (to the right)	0.592	0.319	0.089	0.126
Time to pelvic maximum	0.138	0.148	0.0002*	0.430
Time to pelvic minimum (= to left)	0.452	0.423	0.344	0.155
Pelvic excursion	0.760	0.640	0.001*	0.130
Pelvic excursion duration	0.362	0.080	0.0001*	0.703
Pelvic at foot down	0.729	0.340	0.002*	0.303

Significance at $P < 0.05$ is indicated with an asterisk.

hauling out or slipping into the water (Cott, 1961) and in muddy shoreline conditions (Webb and Gans, 1982) and is supported by laboratory observations as well (Gatesy, 1997). Therefore, the high walk posture in a walking trot gait (*sensu* Hildebrand, 1985) is the primary means by which alligators locomote continuously over land.

Kinematics of the high walk

Gatesy (1991, 1997) has described the high walk in the alligator moving over the ground past a cineradiograph. Our results in general agree with Gatesy's (1991, 1997) kinematic overview, and we present the following additional and contrasting information about high walk kinematics.

Gatesy's (1991, 1997) pattern of pelvic movements was similar to that reported here, and we found mean pelvic rotation angle (13°) to fall in the middle of the range he reported ($10\text{--}15^\circ$). In contrast, however, we found that time to peak pelvic rotation to the left coincided with foot down as opposed to being slightly after foot down. Time to peak pelvic rotation to the right occurred at 75% of the stance phase.

The ankle movements detailed here parallel those described by Gatesy (1991, 1997), except that we found less plantar flexion of the ankle at the end of the stance phase (120° versus $130\text{--}134^\circ$) and less ankle flexion during the swing phase (70° versus 40°).

Gatesy's (1991, 1997) reported femoral retraction patterns are similar to those reported here for the high walk, showing the femur protracted to 53° just prior to foot down, then retracted to 66° at foot down, with a maximum retraction of 125° at 85% of the stance duration. Our femoral adduction angle (0° is sprawling, 90° is erect), which can be exactly correlated with Gatesy's abduction variable (0° is erect, 90° is sprawling), showed some differences in femoral adduction movements. Converting Gatesy's angles to our angles for direct comparison, we found the femur to be less adducted at foot down (51° versus $60\text{--}70^\circ$) with no change in adduction during the stance phase as opposed to the $15\text{--}25^\circ$ of abduction that Gatesy (1991, 1997) observed. Thus, although Gatesy's (1991, 1997) alligators were apparently using more adducted femora, they exhibited femoral abduction during the stance, which is something we found to be characteristic of sprawls, as did Brinkman (1980) in the caiman *Caiman sclerops*. During the swing phase, we found a consistent pulse of femoral abduction to occur just after foot up (to 35° at approximately 1.1 stance durations), followed by a rapid 24° adduction of the femur to its minimum abduction (of 59°) just before foot down and then by abduction prior to foot down (Fig. 4). Gatesy's (1991, 1997) peak femoral abduction occurred just before or coincident with foot up. We found the knee angle at foot down to be $109\text{--}121^\circ$ in the high walk, which decreased by approximately 10° early in the stance phase, was constant during the middle stance phase and then began to decrease, similar to patterns found in *Caiman sclerops* (Brinkman, 1980). Gatesy's (1991, 1997) kinematics differ considerably from these, showing a $30\text{--}40^\circ$ increase in knee angle during the stance phase starting from 90° at foot down.

While femoral retraction kinematics were similar in the two studies, some differences between Gatesy's (1991, 1997) data and ours are significant. At both speeds studied, our alligators high-walked with a constant femoral adduction angle and gradually decreasing knee angle over the stance phase. Gatesy (1991, 1997) found that they adducted the femur and greatly increased the knee angle, suggesting that there may be two different ways in which the hip and knee can be used during the stance phase. Gatesy's (1991, 1997) high walk involved a greatly adducted femur with the knee at a right angle, while our high walk had a moderately adducted femur with a somewhat extended knee. These differences may be due to the differences in experimental techniques (e.g. differences in controlling for speed) or alligators may truly exhibit significant variation in locomotor behaviors as Gatesy (1991) has suggested.

Changing a high walk to a sprawl

Changing a high walk to a sprawl had significant effects on each of the limb joints but did not affect pelvic rotation or the width of the stride (Tables 1–4). Our data show that the primary difference between the high walk and sprawl is that the femur was more abducted and the knee more flexed during the stance phase in the sprawl (Fig. 4), and thus the limb was more compressed vertically. This had consequences for limb joint movements during the swing phase. Most of the swing phase changes were purely a consequence of a more sprawled limb posture. But several key behavioral shifts during the swing phase and one during the early stance phase interact to create the sprawling posture in alligators. We present evidence for this observation in the following sections, reviewing the postural changes that occur in each limb joint.

Femoral movements

Although the relative timing of femoral retraction movements did not change, changing to a sprawl produced significantly greater femoral excursion as a result of significantly greater protraction of the femur during the swing phase. This resulted in an increase in the femoral protraction angle at foot down. The maximum retraction angle of the femur did not change and femoral positions converged in the two postures at foot up. Greater femoral excursion in sprawls is generated by greater protraction of the femur just prior to foot down.

The amount of femoral adduction was the same at foot down in the two postures, but the femur was rapidly abducted during the first third of the stance phase (Fig. 4) during sprawls. Femoral abduction in sprawls is therefore greater at foot up and during the immediate pulse of abduction when the limb is lifted after foot up. The femur then adducts back to the same maximum angle just before foot down that is seen in the high walks. Hip adduction excursion during the swing phase is, therefore, greater in sprawls. The rapid abduction of the femur early in stance phase is the key behavior that causes the more sprawling femoral position in sprawls relative to the static hip adduction angle seen in the high walk. Thus, femoral abduction

during the early stance phase appears to be a behavioral characteristic of the sprawling posture in alligators and it contributes, in part, to lowering the posture.

Knee movements

Through 90% of the stride, the knee angle profiles for high walks and sprawls were approximately parallel, with the sprawls having consistently greater knee flexion. Sprawls had significantly more knee flexion at foot down and throughout the stance phase. As the knee is flexed during the swing phase, the difference decreased but sprawls maintained a significantly lower minimum knee flexion. Sprawls maintained approximately 30° more flexion during the stance phase but converged to an approximately 10° difference as the knee reached peak flexion during the swing phase. Late in the swing phase, there is a key behavioral shift in the sprawls that increases knee flexion to generate the difference observed at foot down. From the point of minimum knee flexion in the swing phase, high walks simply re-extend the knee to the position observed at foot down and during the stance phase. Sprawls, however, begin to re-extend the knee during mid-swing, but then flex the knee at the end of the swing phase to the position observed for sprawls at foot down. This key change is what produces the more flexed knee position that is maintained throughout the stance phase of sprawls. This change (earlier onset of knee flexion), in concert with the more abducted femur, generates the more sprawling posture. In order to walk 2 cm lower (with the belly dragging), alligators have to abduct the femur and flex the knee. And because the stride width did not change, the late swing knee flexion behavior is, in effect, a way to pull the foot back into the same sagittal 'landing' plane with a femur that is protracted more in the same amount of time.

Ankle movements

The late swing knee flexion of the sprawl has consequences for the ankle kinematics in sprawls as well. The late swing knee flexion in sprawls produces a parallel decrease (or lack of increase) in the ankle angle in late swing. This produced greater flexion of the ankle, folding the ankle under the leg to accommodate the increased flexion of the knee. Ankle flexion is therefore greater in sprawls at foot down and during the stance phase at a given speed.

In summary, in the stance phase of sprawls, the femur is protracted farther and abducted more, while the knee and ankle are flexed more relative to the high walk. Hip abduction is generated during the stance phase, while the other differences are attained by behavioral changes during the swing phase that result in differences at the beginning of the stance phase.

Consequences of a higher posture

In general, a change to a more erect posture will raise the hip joint, decreasing the effective limb length, which should decrease the stride length. Accordingly, elevating the posture at a given speed requires the limb to move faster to compensate for the loss in stride length. This is what we found in the

alligators. When changing to a high walk at a given speed, the alligators experienced a loss of 1.9–2.3 cm per stride or 10–16.5% of the stride length while stance duration decreased by 10–20%. Given that relative stance and swing durations (duty factor) did not change between postures, the swing phase duration decreased in proportion to the stance phase duration.

Comparisons with other vertebrates

Joint kinematics

Kinematic comparisons between the alligator postures and data available for other vertebrates provide information allowing us to examine the intermediate, primitive or derived status of extant crocodylian locomotion. Comparable quantitative kinematic data are only available for one salamander, *Dicamptodon tenebrosus* (Ashley-Ross, 1994a,b, 1995), a few cursorial mammals (e.g. cat *Felis domesticus*: Goslow *et al.* 1973; Smith *et al.* 1993), one lizard, *Sceloporus clarkii* (Reilly and DeLancey, 1997a,b), and two birds (chick *Callus* sp., Muir *et al.* 1990; *Numida meleagris*, Gatesy, 1990, 1994), and the following general synthesis is based on a comparison of our three-dimensional data with the two-dimensional kinematic data from these specific works.

Axial and pelvic movements in the alligators were similar to those known for the salamanders and lizards, with a double-node standing wave having nodes near the girdles. The alligator differs in having (1) the nodes shifted more towards the midtrunk and (2) considerably less total pelvic rotation (26° versus 40° in the salamander and lizard). All these sprawling species had peak pelvic rotation to the foot-down side occurring well before foot up, such that pelvic rotation to the opposite side leads the protraction of the limb.

Ankle and femoral protraction–retraction patterns are by their nature similar across vertebrates even when comparing sprawling and erect postures. Ankle movements commonly share a biphasic flexion and then extension movement during both the stance and swing phases. All vertebrates have strikingly similar femoral retraction kinematics as well. All show an approximately similar range of femoral excursion and a pattern of femoral retraction that peaks prior to foot up and protraction that peaks before foot down.

Data on femoral adduction angles are limited. Salamanders and lizards move with the femora extended laterally from the body. Alligators have adduction angles intermediate between these and those of totally erect mammals and birds, but they overlap considerably with those of non-cursorial mammals (Jenkins, 1971; Pridmore, 1985). It is important to note, however, that the degree of hip adduction in alligator sprawls is certainly greater than in the other sprawling forms studied to date.

Knee movements provide some of the most interesting differences among vertebrates. Salamanders, mammals and lizards show a biphasic pattern of knee movements within both the stance and swing phases, as described for the ankle. The knee is flexed then extended during the first two-thirds of the stance phase and then flexed and extended during the remainder of the stride. Knee flexion begins anew before foot

up in these species. Alligators and birds have the same biphasic knee movements as other vertebrates beginning with the onset of flexion in the late stance phase and during the swing phase. They differ, however, in knee movements in earlier portions of the stance phase. Alligators have little change in the knee angle for the first two-thirds of the stance phase, while birds actually flex the knee for the entire stance phase. The pattern of stance phase knee movements in alligators is thus kinematically intermediate between the primitive sprawling posture and patterns observed in birds.

Speed effects

Alligators increase speed differently using different limb segments from those used by other vertebrates. The sprawling vertebrates *Dicamptodon tenebrosus* and *Sceloporus clarkii* increase speed simply by retracting the femur and flexing the knee relatively faster during the stance phase, while joint excursions remain the same but are scaled temporally with speed (Reilly and DeLancey, 1997a). Similar patterns of speed changes are found in studies of mammals (Goslow *et al.* 1973, 1981; Grillner, 1975, 1981; Halbertsma, 1983), which report little or no change in angular excursions of the limbs with speed, but some timing changes. Our current understanding of sprawling vertebrates indicates that simply increasing femoral retraction rate may be a general mechanism by which speed is increased at walking speeds. Speed data on birds (Gatesy, 1990, 1994) show that knee excursion remains constant but femoral excursion increases greatly as speed increases. Thus, for the one species for which we have data, birds increase speed primarily by increasing the amplitude of femoral excursion, but it is at least similar to sprawling vertebrates and mammals in that the femur is the primary effector of increasing speed. Alligators employ a different mechanism to increase speed. In contrast to salamanders and lizards, which change the timing rather than the range of movements, several angular changes and one timing change were found in alligators. They extend the knee farther during the swing phase to increase the limb length and plantar-flex the ankle faster during the stance phase as speed increases. This suggests that the caudofemoralis muscle, which is critical to femoral retraction and increasing speed in salamanders and lizards, has changed its locomotory role in alligators and that ankle and knee extensors have assumed the primary role in increasing speed. Further evidence for a possible change in function of the caudofemoralis comes from a recent electromyographic study of the caudofemoralis in alligators that shows a peculiar pulsatile pattern of activity during femoral retraction (Gatesy, 1997), which is quite different from the strongly ramped-up and continuous activity patterns of this muscle during femoral retraction in lizards and salamanders (Ashley-Ross, 1995; Reilly, 1995).

Relevance to the sprawling-to-erect paradigm

Our results and comparisons with other vertebrates allow some inferences regarding the position and polarity of modern crocodilian locomotion in the sprawling-to-erect transition. First, the crocodilian sprawl is definitely not functionally

equivalent to the primitive sprawling behaviors exhibited by salamanders and lizards. Alligator sprawls differ in the degree of femoral adduction, in the lack of knee movements during the stance phase, in the way that speed is increased, in the pulsatile pattern of electrical activity in the caudofemoralis muscle and in the fact that the sprawl is not consistently used for overland travel. In fact, although the high walks and sprawls have kinematic differences, they are actually much more similar than expected. Both postures had femoral adduction angles that overlap and lie within 30–60° (0° is femur straight lateral to acetabulum), which is within the range for a semi-erect posture proposed by Charig (1972). Both were used at the same speeds, with the same duty factors and gaits, and had the same mechanisms to increase speed. Patterns of limb movements were similar and most of the kinematic variables we examined were not significantly different among the postures. Kinematic differences in sprawls were all essentially a consequence of changing to a lower body height, and key changes involved mechanisms to move the limbs to the same foot-fall plane with more abducted and functionally longer limbs. Essentially, one could say that the crocodilian sprawl is a lower version of a high walk or a 'low walk'. Crocodilians, therefore, momentarily switch between the semi-erect low walk and slightly more erect high walk and, thus, do not switch from a primitive sprawling posture to an intermediate semi-erect posture as posed in the Introduction. Furthermore, because it is used only to move short distances or in transitions to and from a high walk, the sprawl should perhaps not be used for comparisons made to understand the evolution of vertebrate postures.

In terms of the sprawling-to-erect transition, however, it is difficult to categorize the crocodilian high walk clearly. Because the femoral and ankle patterns among vertebrates known to date are so similar, they do not illuminate any key kinematic features that could be used to place or polarize the crocodilians. Alligator kinematics were intermediate between those of lizards and birds in femoral adduction angles, the amount of pelvic rotation and in the knee kinematics during the stance phase. Given the knee kinematics (albeit at an early stage of comparative understanding), one could hypothesize transformations in the knee kinematics that parallel the change to erect postures in diapsids: sprawling postures (salamanders and lizards) exemplified by highly flexing knees able to extend and flex during the stance phase, transforming to intermediate postures (alligator sprawl and high walk) in which more extended knees are held static during the stance phase, and finally to the erect posture (birds) where the knees are greatly extended and only flex during the stance phase. Generalized mammals as such are not as erect as birds and have apparently retained the primitive knee flexion movements. Such a hypothesis is dependent on the assumption that the alligator possesses (has retained or re-attained) the evolutionarily intermediate locomotory behavior. However, given that the modern crocodilians are secondarily semi-erect, the rather striking similarity and uniqueness of knee kinematics in birds and alligators may provide support for the secondary

development of semi-erect knee function in crocodylians; without a true transitional model, one cannot tell whether the knee patterns in alligators are novel or intermediate. Other evidence suggests that the crocodylians have evolved a novel form of a semi-erect posture. The striking difference in the way that the alligator increases speed (using the knee and ankle as opposed to the femur as primary effector) compared with other vertebrates suggests that the entire system, or at least the pattern of neural control of speed, may have been changed in the modern crocodylians as they returned to a semi-erect posture. Given the paleoanatomical evidence that modern crocodylians are secondarily sprawling and the kinematic evidence that they are functionally derived as well, we propose that the crocodylian low and high walk behaviors are not intermediate forms in the sprawling-to-erect continuum.

Studies such as these are vital to developing the database of kinematic studies on locomotion in vertebrates that is so critical to our understanding of the sprawling-to-erect posture paradigm. Many of the suggestions about the evolution of erect postures have been based on functional inferences from anatomical comparisons among taxa (extinct and extant) and functional studies of a few cursorial mammals. Few studies have detailed the locomotory kinematics and muscle function in birds or other lizards or mammals that use sprawling postures. Accordingly, it is not possible to make convincing inferences about the evolution of erect postures if the sprawling and erect conditions in extant species are not understood. Considerable further study of locomotion in other sprawling and erect vertebrates is needed to develop a sound functional foundation from which hypotheses and inferences about the evolution of locomotor function and the evolution of erect and bipedal locomotory postures can be forged and tested. However, on the basis of the comparison of our results with the few quantitative kinematic studies to date, it appears that sprawling and erect locomotion may be functionally more similar than has been thought in the past and that modern crocodylians are a problematic model for an evolutionarily intermediate semi-erect locomotory posture.

Appendix

Calculation algorithms used to obtain three-dimensional coordinates

Measurement TV (MTV) is a video measurement program used for morphometric analysis. It allows point locations, line segment lengths, perpendicular distances, angles and areas to be recorded automatically from a single two-dimensional image on a video screen (Updegraff, 1990). A stereo version of MTV (sMTV) developed by Bruce Jayne (University of Cincinnati) and Peter Wainwright (Florida State University) allows three-dimensional coordinates to be calculated with respect to some absolute point existing in two separate camera views of the same object.

Background

A point in a television image on a computer screen actually represents a line in three-dimensional space from the furthest

point visible back to the original camera lens. Given the precise location, orientation and focal length of the camera, this line through three-dimensional space can be represented as a three-dimensional vector (X,Y,Z) anchored at the location of the camera. However, the actual location of a single point along that line cannot be identified accurately from a single image. Two different camera views of the same object, given the precise location and orientation of their respective cameras, allow two such lines to be mathematically characterized. The intersection between these two lines will give the precise coordinates (x,y,z) for a point in three-dimensional space.

In practice, because the location of a camera is difficult to identify precisely and the given resolution of a typical video image will only generate an approximate line, these sources of error mean that the two lines generated from two different views are unlikely to intersect, but there will be a point at which they are closest together. sMTV calculates this point on each line and then identifies the mid-point in the gap between the lines as the three-dimensional coordinates of that point on screen. The gap distance is also displayed by sMTV, indicating unacceptably high errors.

Camera locations

The largest source of error is in the exact location and orientation of a pair of cameras. First, an absolute reference point needs to be defined, origin point $(0,0,0)$, from which all other locations, including the points on the object to be measured and the cameras themselves, are defined. One must also specify the orientations of the X , Y and Z axes. Then, given the locations (x,y,z) of the cameras in space, one must also know precisely the orientation of each camera. This includes the camera's tilt angle from horizontal, pivot angle to the left or right with respect to the horizontal X axis, rotation from a normal vertical alignment and magnification.

In practice, it would be difficult and impractical to expect users to determine these parameters precisely on every occasion. Therefore, sMTV uses a process that makes this calculation semi-automatic. Users place a transparent, perfect cube shape within the field of view of both cameras then identify the eight corners of the cube in each view. In a two-step process, sMTV then calculates the camera's location, orientation and magnification, given those eight points that have been viewed in that perspective. In the first step, camera positions are calculated at 30° increments for all the camera orientation angles: tilt (-90 to 90°), pivot (0 – 330°) and rotation (0 – 330°). For each combination of these orientations, the program projects an imaginary cube centered and magnified to match the center and average spread of the actual eight points entered by the user. The program then records the differences between the eight points it projected and the actual eight points, and selects one orientation that is the closest to the correct orientation. The program next begins an iterative process in which each rotational parameter is adjusted by 5° in each direction to attempt to obtain a closer fit between the imaginary cube and the user's eight cube points. The program also varies the camera's distance from the cube. The program

chooses the adjustment that yields the closest fit, and then repeats the process. When no adjustment at that level yields an improvement, the program halves the percentage distance from the object and repeats the whole trial process for each adjustment. This cycle continues until there is negligible improvement. The program then knows the precise alignment and magnification of that camera.

The initial position of the user's cube, not the camera's position, defines the location of the three-dimensional axes used as an absolute reference by the program. Unless later changed by the user, the program's default is to set up the X, Y and Z axes so that they align with the cube's front face, with the X axis to the right, the Y axis straight up and the Z axis going into the cube.

Because each camera's position is determined independently of the other, the cameras can point from any direction; for maximum precision, they should be approximately at right angles to each other. Test computations on known angles are used to check the accuracy of the system. This calibration process is performed once for a given camera setup, and sMTV saves the camera alignment information with the data it records, so that users can reset the alignment information the next time they run sMTV by reloading a previously saved data file.

We extend sincerest thanks to Dr Ruth Elsey at the Rockefeller Wildlife Refuge, Department of Wildlife and Fisheries, for supplying the alligators, which were transported to Ohio University by Jim Barron. We thank Mike Lyons for the drawings in Fig. 1, and Cassy Kostizen, Rick Essner and Andrea Krug for assistance in data collection, digitizing and data analysis. Audrone Biknevičius, Ron Heinrich, Sandra Inouye, Larry Witmer and the Locolab Group at Ohio University provided mass quantities of critical and moral support for the research and provided comments on the manuscript. Phil Martin was excellent at keeping our alligators happy. We are especially grateful to Bruce Jayne and Peter Wainwright for letting us use stereo MTV, and we thank Garr Updegraff for the explanation of the three-dimensional algorithm in the Appendix. All credit for developing this program should go to Bruce Jayne, Garr Updegraff and Peter Wainwright. This research was supported by Ohio University Research Challenge Grant RC 95-025, a College of Osteopathic Medicine Summer Undergraduate Research Fellowship and two Ohio University Honors Tutorial College Summer Research Fellowships.

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