2003

Motor control of locomotor hindlimb posture in the American alligator (Alligator mississippiensis)

Stephen M. Reilly

Richard W. Blob
Clemson University, rblob@clemson.edu

Recommended Citation

Please use publisher's recommended citation.

Motor control of locomotor hindlimb posture in the American alligator (*Alligator mississippiensis*)

Stephen M. Reilly[1] and Richard W. Blob[2,*]

[1]*Department of Biological Sciences, Ohio University, Athens, OH 45701, USA* and [2]*Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA*

*Author for correspondence (e-mail: rblob@clemson.edu)

Summary

Crocodilians are unusual among quadrupedal tetrapods in their frequent use of a wide variety of hindlimb postures, ranging from sprawling to a more erect high walk. In this study, we use synchronized kinematic videos and electromyographic recordings to test how the activity patterns of hindlimb muscles in American alligators (*Alligator mississippiensis* Daudin) differ between sprawling and more upright postures.

Previous force platform analyses suggested that upright posture in alligators would require greater activation by hindlimb extensors to counter increases in the flexor moments exerted about joints by the ground reaction force during upright stance. Consistent with these predictions, ankle extensors (gastrocnemius) and knee extensors (femorotibialis internus and iliotibialis 2) exhibit increases in signal intensity during the use of more upright stance. Bone loading data also predicted that activation patterns for hip adductors spanning the length of the femur would not differ between sprawling and more upright posture. Correspondingly, motor patterns of the adductor femoris were not altered as posture became more upright. However, the adductor puboischiofemoralis externus 3, which inserts far proximally on the femur, displays significant increases in burst intensity that could contribute to the greater femoral adduction that is integral to upright posture.

In contrast to patterns in alligators, in mammals EMG burst intensity typically decreases during the use of upright posture. This difference in the motor control of limb posture between these taxa may be related to differences in the relative sizes of their feet. Alligator feet are large relative to the hindlimb and, as a result, the ground reaction force shifts farther from the limb joints during upright steps than in mammals, increasing flexor moments at joints and requiring alligator extensor muscles to exert greater forces to keep the limb in equilibrium. However, several alligator hindlimb muscles show no differences in motor pattern between sprawling and upright posture. The wide range of motor pattern modulations between different postures in alligators suggests considerable independence of neural control among the muscles of the alligator hindlimb.

Key words: locomotion, biomechanics, kinematics, EMG, muscle, electromyography, modulation, neural control, bone stress, posture, evolution, vertebrate, alligator, Sauria, Crocodylia.

Introduction

Quadrupedal tetrapod species use a diverse variety of limb postures during terrestrial locomotion. In general terms, these postures range from sprawling (in which the limbs are held lateral to the body) to fully upright (in which the limbs are held beneath the body) (Gregory, 1912; Bakker, 1971; Jenkins, 1971; Charig, 1972). Most individual species typically employ a fairly narrow range of limb postures during normal locomotor behaviors (Jenkins, 1971; Reilly and DeLancey, 1997a,b; Irschick and Jayne, 1999). However, crocodilians are unusual among tetrapods in their ability to use a wide range of hindlimb postures, even over a restricted range of speeds (Cott, 1961; Brinkman, 1980; Gatesy, 1991; Reilly and Elias, 1998; Blob and Biewener, 1999). Crocodilians preferentially use a 'high walk' for sustained locomotion, with the femur adducted approximately 55° below horizontal during stance (Gatesy,
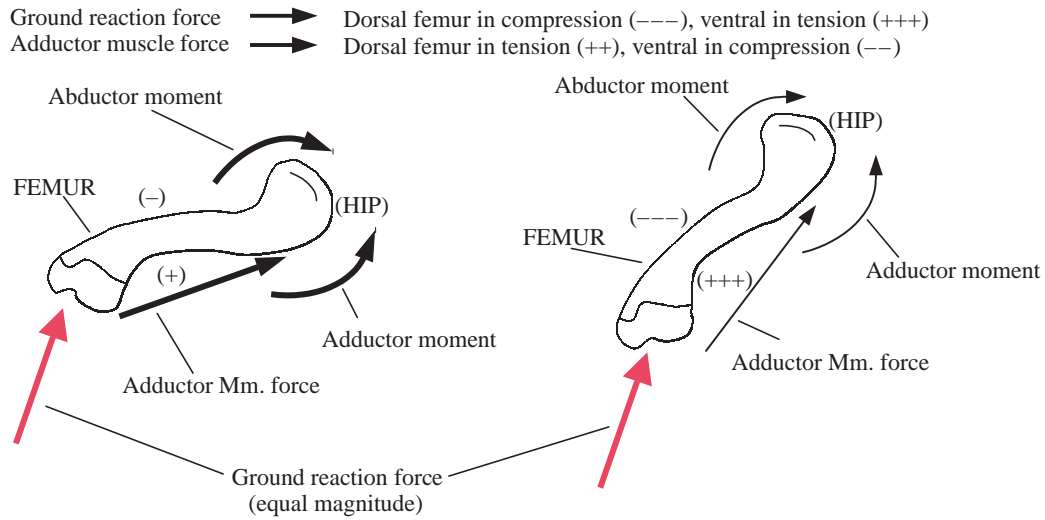
1991; Reilly and Elias, 1998), but they can also use more sprawling postures with as little as 20° femoral adduction (Brinkman, 1980; Reilly and Elias, 1998; Blob and Biewener, 1999). The kinematic changes required of crocodilians to accomplish these different hindlimb postures have been well characterized. During stance in sprawling steps, the femur is abducted more and protracted further while both the knee and ankle are flexed more than during high walk steps; in addition, a second phase of knee flexion begins during late swing phase in sprawling steps (Reilly and Elias, 1998). However, the neuromuscular basis underlying these different kinematic patterns has not been examined. How do crocodilians modulate hindlimb motor activity to achieve different hindlimb postures?

Crocodilian hindlimb musculature, like that of many

tetrapods, is highly redundant, with multiple muscles in different positions capable of producing each of the major movements (protraction/retraction, abduction/adduction, flexion/extension) at each joint (Romer, 1923; Gatesy, 1994,

1997). As a result, on the basis of anatomical data it is difficult to predict which muscle activity patterns might be required to change in order for crocodilians to use more upright posture. However, data on bone loading during locomotion by
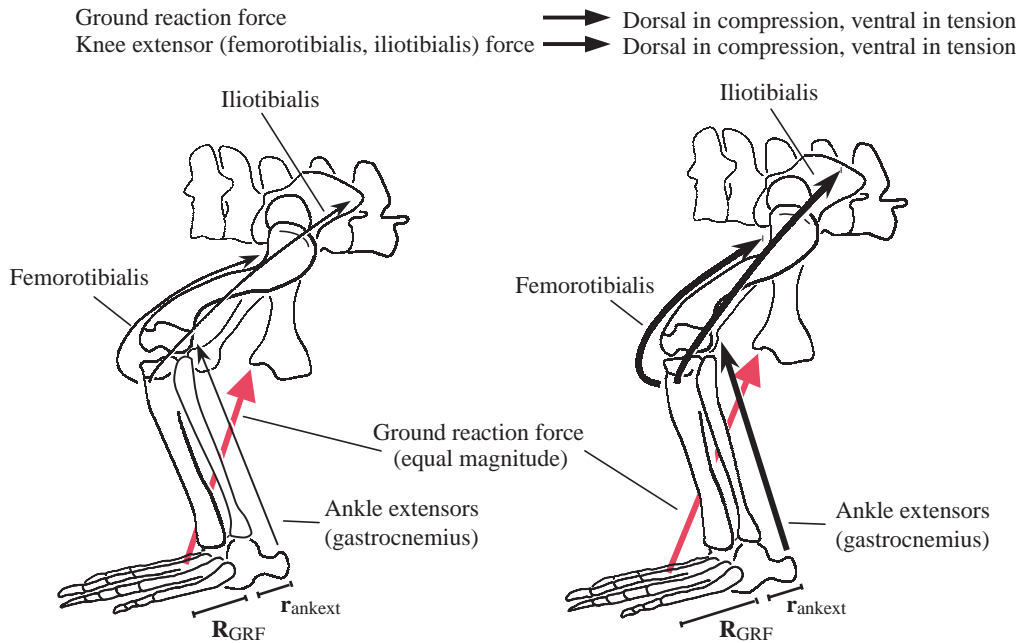
A MODEL 1: High femoral loads during upright posture related to adductor muscle function

Ground reaction force   Dorsal femur in compression (−−−), ventral in tension (+++)
Adductor muscle force   Dorsal femur in tension (++), ventral in compression (−−)

SPRAWL
- Larger abductor moment induced by GRF
- Larger adductor force counters GRF more
- *Lower femoral stresses and strains*

UPRIGHT
- Smaller abductor moment induced by GRF
- Smaller adductor force counters GRF less
- *Higher femoral stresses and strains*

B MODEL 2: High femoral loads during upright posture related to chain of events starting at foot

Ground reaction force   Dorsal in compression, ventral in tension
Knee extensor (femorotibialis, iliotibialis) force   Dorsal in compression, ventral in tension

SPRAWL
- Smaller $\mathbf{R}_{GRF}$ at ankle
- Low ankle and knee extensor forces
- *Lower femoral stresses and strains*

UPRIGHT
- Larger $\mathbf{R}_{GRF}$ at ankle
- High ankle and knee extensor forces
- *Higher femoral stresses and strains*

American alligators (*Alligator mississippiensis*; Blob and Biewener 1999, 2001) provide a biomechanical basis for predicting differences in motor control between sprawling and upright stance (Zernicke and Smith, 1996). In alligators, *in vivo* bending strains and stresses are greater on dorsal and ventral femoral cortices when more upright posture is used (Blob and Biewener, 1999, 2001). Because the magnitude of the ground reaction force does not change significantly as alligators use more upright posture, these changes in bone loading must be the result of changes in the forces exerted by limb muscles (Blob and Biewener, 2001). One possibility is that hip adductors (on the ventral aspect of the femur) might exert less force during more upright steps (Fig. 1A). This would cause

---

Fig. 1. Diagrammatic illustrations of alternative models to explain increases in femoral loading during upright locomotion in alligators (adapted from Blob, 1998, 2001; Blob and Biewener, 1999, 2001). For visual clarity of the forces and moments bearing on the model, the views are presented from an oblique posterolateral perspective (this causes the femur to appear not to project perpendicular to the vertebral axis as it does at mid-stance). For each arrow depicting a force or moment, a difference in thickness (not length) between the left and right sides of a panel indicates a difference in force or moment magnitude between the postures illustrated in those panels (with thicker arrows indicating larger forces or moments). Note that panels A and B are drawn to different scales (A is magnified for clarity), and that comparisons of force and moment magnitudes are not intended between A and B. Because the ground reaction force (GRF) does not differ in magnitude between sprawling and upright steps (Blob and Biewener, 2001), both models are based on changes in the action of hindlimb muscles between these postures. (A) Bending induced by the ground reaction force (red arrow) places the dorsal femur in compression (–), and the ventral femur in tension (+). In sprawling posture (left), the GRF might have a longer moment arm about the hip than in upright posture (right), resulting in a larger abductor moment that would tend to rotate the femur dorsally. To keep the hip joint in equilibrium, the hip adductors might exert a larger force in sprawling posture (left) and a smaller force in upright posture (right). Because the hip adductors bend the femur in the opposite direction from the GRF, larger adductor forces during sprawling steps could more effectively mitigate strains induced by the GRF, resulting in lower dorsal and ventral stresses and strains during sprawling steps. (B) As limb posture becomes more upright, the center of pressure of the GRF shifts away from the ankle, increasing the moment arm of the GRF at the ankle (R_{GRF}). Consequently, ankle extensors (e.g. gastrocnemius) must exert higher forces during upright steps in order to counter the larger ankle flexor moment and maintain joint equilibrium. Because gastrocnemius also spans the knee, it makes a greater contribution to the flexor moment at the knee during more upright steps, and knee extensors (femorotibialis and iliotibialis, on the dorsal aspect of the femur) must exert greater force to counter this moment and maintain equilibrium at the knee. Increases in knee extensor forces could then raise dorsal and ventral femoral strains and stresses as alligators use more upright posture. Data from previous force platform studies (Blob and Biewener, 2001) are consistent with the model proposed in B, but changes in muscle activity patterns have not been tested prior to this study. r_{ankext}, moment arm of ankle extensor muscles at ankle (no change between sprawling and upright stance).

the adductors to mitigate bending due to the ground reaction force less effectively, contributing to higher dorsal and ventral femoral bending loads (Blob, 1998; Blob and Biewener, 2001). However, analyses of joint equilibrium based on force platform data do not indicate posture-related changes in adductor force. Instead, force platform data indicate a cascade of changes in locomotor mechanics during upright posture that begin at the ankle (Blob and Biewener, 2001; Fig. 1B). During the use of more upright limb posture, the center of pressure of the ground reaction force is shifted anteriorly, away from the ankle. This shift increases the moment arm of the ground reaction force at the ankle; as a result, ankle extensors (e.g. gastrocnemius) must exert higher forces to maintain joint equilibrium by countering the larger ankle flexor moment during more upright steps. Because gastrocnemius also spans the knee, it makes a greater contribution to the flexor moment at the knee during more upright steps, and knee extensors (femorotibialis and iliotibialis, on the dorsal aspect of the femur) must exert greater force to counter this moment and prevent the knee from collapsing. These increases in knee extensor forces could then raise dorsal and ventral femoral strains and stresses as alligators use more upright posture (Blob and Biewener, 1999, 2001).

Although force platform data suggest that the activity patterns of several hindlimb muscles might be modulated between sprawling steps and high walk steps in crocodilians, force platforms provide only an indirect indication of muscle action. In the present study, we use electromyographic (EMG) recordings from the hindlimb muscles of American alligators synchronized with video of locomotor kinematics to test for modulations of hindlimb motor patterns correlated with the use of different limb postures. EMG patterns have been recorded for alligator hindlimb muscles during the high walk (Gatesy, 1994, 1997), but explicit analyses of postural effects on muscle motor patterns have not been performed previously. Our analyses will, therefore, provide insight into the basis for the ability to use both sprawling and more upright limb postures, a trait that has made crocodilians feature prominently in many analyses of the evolution of tetrapod locomotion (e.g. Bakker, 1971; Charig, 1972; Kemp, 1978; Brinkman, 1980; Parrish, 1987; Gatesy, 1991; Reilly and Elias, 1998; Blob and Biewener, 1999, 2001). In addition, our analyses of motor pattern modulation across limb postures in alligators will provide a new data set for comparison with other studies of behavioral modulation of motor patterns (e.g. Gruner and Altman, 1980; Nilsson et al., 1985; Buchanan et al., 1986; Macpherson, 1991; Johnston and Bekoff, 1996; Gillis and Blob, 2001), allowing us to explore potential general patterns in how muscle activity and patterns of recruitment change to allow the same morphological structure to perform a variety of tasks.

In performing these analyses, we recognize that the relationship between EMG and force production in muscles is not necessarily direct and can be complicated by several factors (Loeb and Gans, 1986). However, force/length curves that could clarify these relationships are not currently available for

alligator limb muscles. Therefore, our premise that increases in the force exerted by a muscle would be reflected in increases in the intensity of EMG bursts for that muscle must be regarded as an assumption. However, in the absence of contradictory evidence, we believe that this assumption is a reasonable starting point from which to generate and test hypotheses about how the activation of alligator limb muscles should be expected to differ during the use of sprawling and more upright limb posture.

Materials and methods

Synchronized kinematic and electromyographic (EMG) data were collected from hindlimb muscles of five *Alligator mississippiensis* Daudin (total length, 0.48–0.54 m; body mass, 247–333 g) during treadmill locomotion. The animals were obtained from the Department of Wildlife and Fisheries of the Rockefeller Wildlife Refuge, Grand Chenier, LA, USA. All experimental procedures followed Ohio University IACUC guidelines. To control for speed effects, only strides during which the animals very nearly matched a treadmill speed of 0.146 m s^{-1} were analyzed. We selected strides in which the position of the hip landmark stayed within a 1 cm zone (i.e. $\pm 0.005 \text{ m}$) during the stride. Based on the durations of these strides, the complete range of speed variation among strides for all individuals was $0.141–0.151 \text{ m s}^{-1}$. This is less than 10% variation among strides, which is well within the range of variation reported in previous studies of alligator kinematics (Gatesy, 1991) and EMGs (Gatesy, 1997). Cloacal body temperatures of the alligators during treadmill recording ranged from 22°C to 29°C, which is within the range of both daily and seasonal fluctuations of field body temperature in this species (Seebacher et al., 2003).

Kinematics

The alligators were filmed on a treadmill under strobe lights at $200 \text{ fields s}^{-1}$ using a NAC HSV-400 high-speed video system, while muscle activity patterns were simultaneously recorded. Both lateral and dorsal views of the alligators were filmed (using mirrors) during locomotion on a 70 cm-long canvas treadmill. Reflective landmarks (2 mm-diameter dots visible in both the lateral and dorsal views) were painted on the skin of the alligators to mark a position on the vertebral column, the position of each hip joint (directly over the acetabulum) 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–phalangeal articulation). Three-dimensional coordinates of each landmark were digitized using stereo Measurement TV (sMTV: Updegraff, 1990), and kinematic angles were calculated from these coordinates with an accuracy of $\pm 1°$ for each joint, following the conventions of Reilly and Elias (1998).

The knee and ankle angles calculated were the actual three-dimensional angles for these joints based on the landmarks above. Femoral movements were quantified using two three-dimensional angular variables: hip retraction (indicating retraction/protraction movements relative to the longitudinal axis of the pelvis) and hip adduction (indicating adduction/abduction position relative to the mediolateral axis of the pelvis). Femoral retraction angle was measured relative to a line from the acetabulum to the trunk landmark. This calculation produces angles that are 5–10° greater (not 15° as indicated by Reilly and Elias, 1998) than those that would be calculated if femoral position were measured relative to the sagittal plane (e.g. Gatesy, 1991) but produces kinematic profiles that are essentially identical (within 5–10%: Reilly and Elias, 1998). Femoral adduction was measured as the angle between the femur and a transverse axis through the acetabula (based on three-dimensional coordinates of both hips), with 0° indicating no femoral adduction (the femur held straight out laterally from the acetabulum) and 90° indicating a position parallel to the sagittal plane of the alligator (Reilly and Elias, 1998). This convention for reporting femoral adduction angles follows the evolutionary sprawling-to-erect paradigm, which categorizes sprawling femoral angles as 0° and erect angles as 90° (Bakker, 1971; Charig, 1972; Parrish, 1987; Blob, 2001). Our method of calculating femoral adduction also accounts for the slight roll of the pelvis about a longitudinal axis (≤6° to each side: Gatesy, 1991) and, thus, effectively represents the angle between the femur and the horizontal plane of the body of the alligator. This convention for calculating femoral adduction was chosen over reference to the absolute horizontal and sagittal planes because it represents limb motion with reference to the body of the animal, which should be most relevant to the actions of muscles (attached to the body) that are examined in this study. However, from a practical perspective, because pelvic roll is not very large in alligators (Gatesy, 1991) the difference between the convention we employ here and conventions that refer to absolute planes (e.g. Blob and Biewener, 2001) are minimal. Although other studies (e.g. Gatesy, 1991; Irschick and Jayne, 1999) have used different conventions for some of the angular calculations we report here, the conventions we have used are appropriate for the purposes of this study. Most kinematic angles were calculated and graphed to indicate the general position and direction of movement of limb segments for comparison with patterns of muscle activation (e.g. to determine whether a muscle was active during swing-phase protraction or stance-phase retraction). The only quantitative kinematic data that we extracted for use in further analyses were values of femoral adduction at mid-stance (see Analyses and statistical considerations below), a time during the stride cycle when any differences in results among approaches for angular calculations would be minimized.

Electromyography

We examined the activity patterns of 12 different alligator hindlimb muscles (Fig. 2) during strides in which alligators used a range of femoral posture angles (ranges for each individual are presented in Table 1). Femoral adduction angle at mid-stance was used as the 'postural angle' for each stride
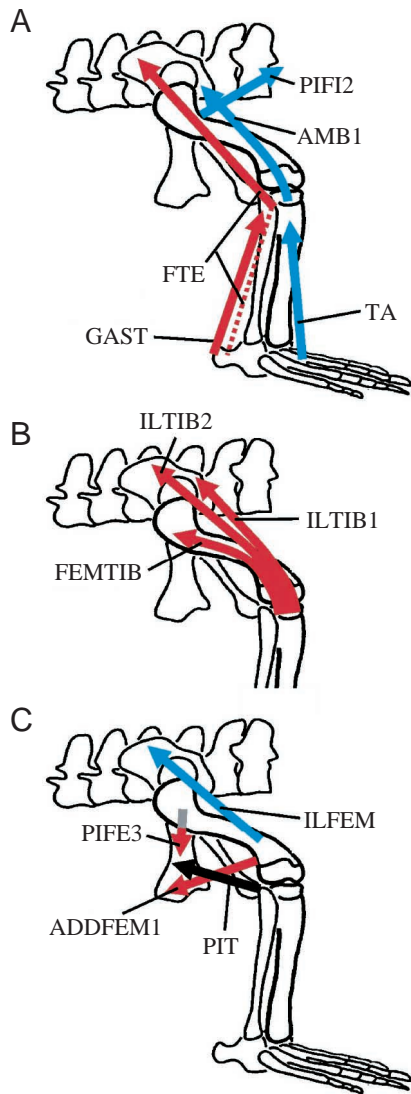
Fig. 2. Hindlimb muscles from which electromyographic (EMG) data were collected in alligators walking with a range of postures. Lines of actions are indicated for muscles primarily active in either stance phase (red), swing phase (blue) or with activity in both phases (black). Muscle abbreviations are indicated in the text (under Myology).

to reflect the degree of adduction when the femur is approximately perpendicular to the pelvis. Although we did not record from all of these muscles in each of our five experimental alligators, we recorded data from seven of these muscles in multiple individuals (see Myology), and it is upon these data that our primary conclusions are based (see Results). Muscle activity patterns (motor patterns) of limb muscles (all on the right side of the body) were quantified by recording electrical activity patterns (EMGs) during treadmill locomotion. Electromyographical recordings were made from bipolar stainless steel electrodes implanted into each muscle as in previous research (Reilly, 1995). All electrodes were implanted while the animals were under anesthesia. The bared metal tips of each bifilar insulated electrode were 0.5 mm long. Electrodes were implanted percutaneously through the skin directly into the belly of each muscle. The bundle of electrodes was glued together and sutured to a scale on the midline of the animal, dorsal to the pelvis. Animals completely recovered from anesthesia within two hours, and all synchronized EMG and kinematic data were recorded during the following two hours. Animals were rested (approximately 15–30 min) between bouts of walking (45 s maximum). Immediately following the experiment the animal was euthanized by overdose of anesthetic and preserved in 10% formalin. Electrode position was then confirmed by dissection. EMG data were considered valid for analysis only for preparations in which the electrode lay completely within the muscle.

EMG signals were amplified 10 000 times using differential AC amplifiers (model 1700; AM Systems, Carlsborg, WA, USA) with a bandpass of 100–3000 Hz (and a 60 Hz notch filter) and then recorded on a multichannel FM tape recorder (XR-5000; TEAC, Montebello, CA, USA) along with a synchronization pulse simultaneously recorded on the video frames. The analog signals (EMG channels plus a synchronization pulse) for each stride were converted to a digital data file using custom software with an analog-to-digital converter (Keithley, Cleveland, OH, USA) and a microcomputer. The effective sample rate for each channel was 10 000 Hz at 12-bit resolution. Prior to the experiments, an extensive calibration of the system revealed no crosstalk downstream of the electrodes, and crosstalk has not been a problem in previous work using the same electrode materials,

Table 1. *Correlation coefficients and significance levels for regressions of limb cycle time parameters on femoral posture in five alligators*

	Individual 1		Individual 2		Individual 3		Individual 4		Individual 5	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Stride duration	−0.352	0.057	−0.521	0.003*	−0.033	0.858	−0.165	0.383	−0.152	0.424
Stance duration	−0.388	0.034	−0.442	0.014*	−0.092	0.623	−0.101	0.594	0.186	0.326
Swing duration	−0.201	0.286	−0.380	0.038	0.099	0.596	−0.194	0.304	−0.415	0.023
Posture range (deg.)	28–48		31–55		31–53		19–44		39–55	

Postural ranges are the femoral adduction angle at mid-stance phase.
*Significant ($P<0.05$) with sequential Bonferroni correction for $N=3$ variables per individual.

construction and placement protocols. EMG profiles were inspected for possible patterns revealing crosstalk, and none were found.

Custom software was used to digitize several standard EMG variables to quantify motor patterns from each muscle for each stride analyzed. For all muscles, these included: times of burst onset and offset, relative to the beginning of stance; burst duration; burst duration normalized by stance duration; the integrated area of rectified burst signals; mean burst amplitude (integrated area divided by burst duration); and integrated area normalized by stance duration. For muscles active primarily during the swing phase of strides, the integrated areas and durations of activity bursts normalized by the duration of swing phase were also calculated. These last two variables were calculated to control for possible changes in stance (or swing) duration between different postures.

Myology

The 12 muscles from which we recorded EMGs (Fig. 2) included muscles that spanned the hip, knee and ankle joints, allowing us to test the hypotheses of muscular control of limb posture that were suggested by force platform analyses of alligator locomotion (Blob and Biewener, 2001). Detailed descriptions of the anatomy of these structures are provided in a number of studies. To facilitate understanding of the analyses we present in this report, in this section we briefly summarize the origins, insertions and hypothesized functions of these muscles that have been outlined in previous anatomical (Romer, 1923) and electromyographic (Gatesy, 1997) research. For each muscle, we list an abbreviation, together with the figure in which the muscle is illustrated and the number of individuals from which we recorded data in parentheses.

Stance-phase femoral retractors

Flexor tibialis externus (FTE; Fig. 2A; 1 individual). Origin: postacetabular process of ilium. Insertion: proximally on proximal tibia, distally *via* auxiliary tendon to ankle.

Stance-phase femoral adductors

Adductor femoris, head 1 (ADDFEM1; Fig. 2C; 3 individuals). Origin: ventral aspect of ischium. Insertion: ventral femoral shaft.

Puboischiofemoralis externus, head 3 (PIFE3; Fig. 2C; 2 individuals). Origin: ventral aspect of ischium. Insertion: postero-ventral aspect of the proximal femur.

Puboischiotibialis (PIT; Fig. 2C; 1 individual). Origin: anterior aspect of ischium, ventral to acetabulum. Insertion: medial aspect of proximal tibia. Additional hypothesized functions: knee flexor at stance–swing transition.

Stance-phase knee extensors

Femorotibialis internus (FEMTIB; Fig. 2B; 3 individuals). Origin: most of the femoral shaft. Insertion: knee extensor tendon.

Iliotibialis, head 1 (ILTIB1; Fig. 2B; 1 individual). Origin: anterior aspect of the rim of the iliac blade. Insertion: surface of the femorotibialis leading into the knee extensor tendon. Additional notes: no previous EMG data.

Iliotibialis, head 2 (ILTIB2; Fig. 2B; 2 individuals). Origin: central aspect of the rim of the iliac blade. Insertion: surface of the femorotibialis leading into the knee extensor tendon.

Stance-phase ankle extensors

Gastrocnemius (GAST; Fig. 2A; 3 individuals). Origin: ventral aspect of distal femur. Insertion: tuber calcis of ankle. Additional notes: no previous EMG data.

Swing-phase femoral protractors

Puboischiofemoralis internus, head 2 (PIFI2; Fig. 2A; 1 individual). Origin: ventral aspect of lumbar vertebrae. Insertion: dorsal aspect of the proximal femur. Additional hypothesized functions: adducts femur during late swing.

Swing-phase femoral abductors

Iliofemoralis (ILFEM; Fig. 2C; 1 individual). Origin: blade of the ilium posterior to acetabulum, deep to iliotibialis. Insertion: lateral and posterior femoral shaft.

Swing-phase knee extensors

Ambiens, head 1 (AMB1; Fig. 2A; 2 individuals). Origin: junction of the ilium and preacetabular ischium, anterior to the acetabulum. Insertion: extensor tendon attaching to the tibia.

Swing-phase ankle flexors

Tibialis anterior (TA; Fig. 2A; 2 individuals). Origin: anterior aspect of tibia and fibula. Insertion: dorsal aspect of metatarsals. Additional notes: no previous EMG data.

Analyses and statistical considerations

We performed two analyses to examine how alligators modulate muscle activity between low- (sprawling) and high-walk limb postures. First, we compared mean patterns of EMG burst timing for low (~30° femoral adduction) and high (~50° femoral adduction) postured strides with mean kinematic profiles for three-dimensional joint movements reported in the detailed analyses of alligator joint kinematics (at 0.146 m s^{-1}) by Reilly and Elias (1998). Second, for each individual animal we regressed the values of each EMG variable for each muscle on femoral posture angle at mid-stance (ranges in Table 1). The correlation coefficients and probabilities of significance from these regressions allowed us to evaluate whether changes in the timing or intensity of activation of individual muscles were required for alligators to use sprawling *versus* upright postures. Because we examined multiple correlations for each muscle, we adjusted for multiple comparisons within individuals using the more conservative sequential Bonferroni tests (Rice, 1989) to determine which EMG variables exhibited significant changes with posture.

Results

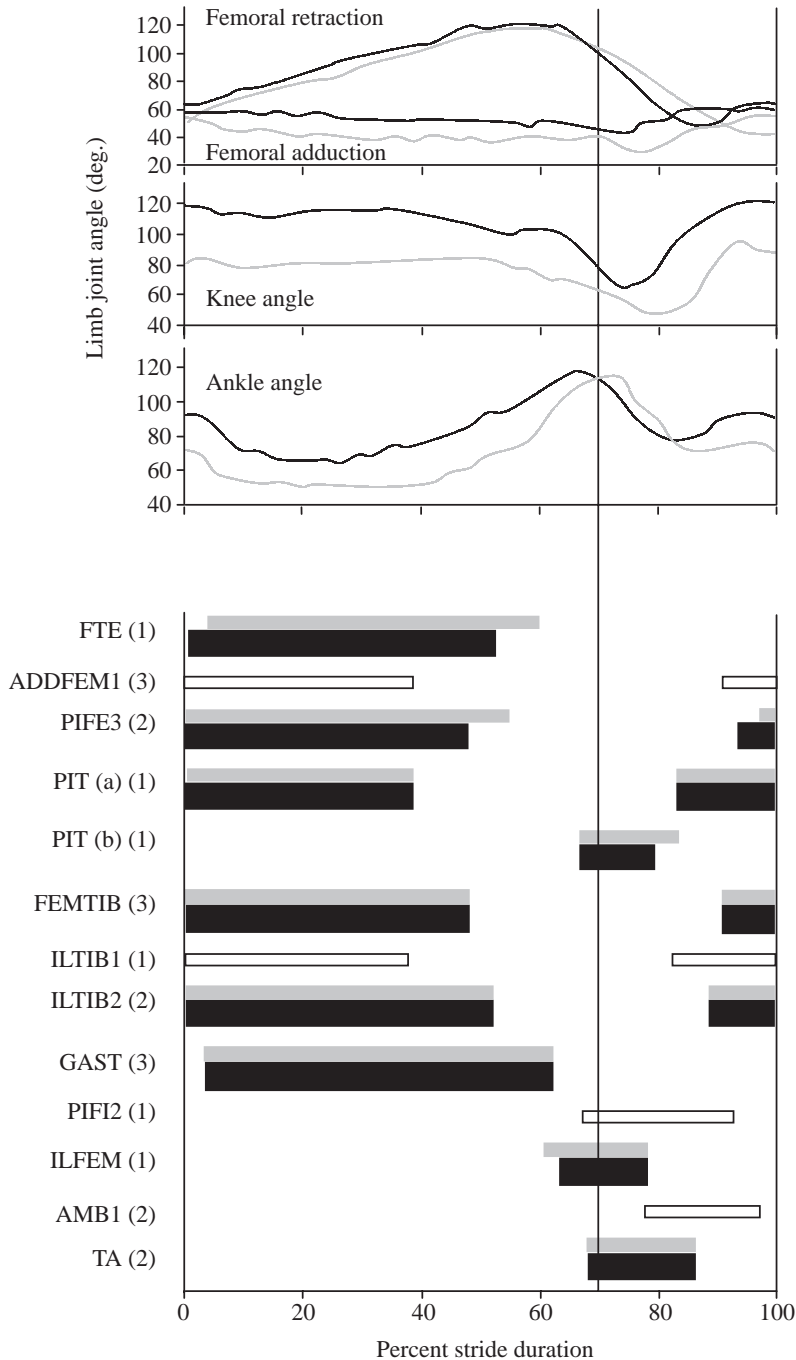Several hindlimb muscles exhibited changes in burst timing

Fig. 3. Modulation of the timing and intensity of hindlimb muscle activity between sprawling and high-walk locomotion in alligators. Significant changes in motor patterns (Table 2) as limb posture becomes more erect are illustrated by comparing mean electromyographic (EMG) patterns for more sprawling postures (about 30° of femoral adduction; gray bars) to those for more erect postures (about 50° of femoral adduction; black bars). Open bars indicate muscle patterns for which there was no significant change in motor patterns (timing or amplitude) as femoral adduction angle increased. Differences in bar thickness between sprawling and upright stance indicate significant differences in mean amplitude (in all cases where such differences occur, black bars for upright posture are thicker than gray bars for sprawling posture). The number of individuals from which EMG data were collected is listed in parentheses after each muscle name. In the top panel, mean three-dimensional limb segmental kinematics for the low (gray line) and high (black lines) walking postures are shown, illustrating differences between these postures (from Reilly and Elias, 1998). Note that more erect postures are produced by consistently greater femoral adduction, knee extension and ankle extension during the stance phase. Abbreviations: FTE, flexor tibialis externus; ADDFEM1, adductor femoris, head 1; PIFE3, puboischiofemoralis externus, head 3; PIT (a), puboischiotibialis (stance burst); PIT (b), puboischiotibialis (swing burst); FEMTIB, femorotibialis internus; ILTIB1, iliotibialis, head 1; ILTIB2, iliotibialis, head 2; GAST, gastrocnemius; PIFI2, puboischiofemoralis internus, head 2; ILFEM, iliofemoralis; AMB 1, ambiens, head 1; TA, tibialis anterior.

or intensity during the use of more upright posture in alligators. However, in no case did the activity pattern of a muscle change so substantially as to suggest that its functional role differed fundamentally between the use of sprawling and upright postures. Therefore, we first present an overview of alligator hindlimb muscle activation patterns derived from data obtained over the full range of postures used by the animals in our study, with a particular focus on patterns of synchronicity in muscle activation. We then detail the specific differences in the timing and intensity of alligator hindlimb muscle bursts between sprawling and upright locomotion.

Our primary conclusions are based upon the seven muscles in which we recorded EMGs from multiple individuals. We report supplementary data from single individuals for additional muscles in order to provide a more comprehensive picture of how muscle activation patterns must change in order for alligators to use a high walk *versus* a sprawl. EMG data from single individuals must be interpreted cautiously. However, none of the muscles that were tested in multiple individuals showed markedly different changes in EMG pattern between sprawling and upright posture among those individuals. Given this consistency in EMGs among

individuals, we are confident that even the patterns we report for muscles recorded in single individuals are likely to be reliable indicators of general patterns in alligators.

General patterns of alligator hindlimb muscle activation
Stance phase

Seven of the alligator thigh muscles that we examined show major EMG bursts during the stance phase of locomotion (Fig. 3). For several muscles, the onset of activation is nearly synchronous, so that stance-phase muscles are activated in four groups, three of which begin activity during the swing phase prior to stance. The first group consists of ILTIB1 (knee extensor) and PIT (hip adductor and knee flexor), which onset together midway through swing phase. The second group, including the hip adductor ADDFEM1 and the knee extensors ILTIB2 and FEMTIB, onset together two-thirds of the way through swing phase. The third group consists of the hip adductor PIFE3, which is activated near 85% swing-phase duration, and the fourth group consists of the femoral retractor FTE, which is activated at the beginning of stance.

The offset of muscle activity also occurs nearly synchronously for several muscles, although the groups produced are not the same as those during onsets (Fig. 3). The first group to cease activity (at nearly 60% through stance duration) includes ILTIB1 and PIT (the first onset group) but also ADDFEM1. The second offset group includes FEMTIB and PIFE3 (members of the second and third onset groups), which cease activity 70% through stance duration. The third offset group includes ILTIB2 and FTE (members of the second and fourth onset groups) and ceases activity at 80% stance duration.

One of the crural muscles examined, the ankle extensor GAST, is active during stance, with an onset just after that of FTE (<10% stance duration) and an offset just after that of ILTIB2 and FTE (>80% stance duration).

Gatesy (1997) measured EMGs for many of the same stance-phase muscles during walking in alligators, including ADDFEM1, FEMTIB, FTE, ILTIB2, PIFE3 and PIT. Patterns measured for those muscles in the present study were largely consistent with those described by Gatesy (1997), although ILTIB2 was active for a somewhat longer portion of the stride in the present study (offset at almost 60% stride cycle) than in Gatesy's study (offset at 30–50% stride cycle).

Swing phase

Four of the alligator thigh muscles we examined show major EMG bursts during swing phase (Fig. 3). ILFEM, a hypothesized femoral abductor, is activated nearly 90% through stance duration and ceases activity nearly 30% through swing duration. PIT, the hypothesized hip adductor and knee flexor that is active during stance, shows a second burst of activity that is almost synchronous with that of ILFEM. PIFI2 (a hypothesized hip protractor) and AMB1 (a hypothesized hip protractor and knee extensor) are activated nearly synchronously just at the offset of activity by ILFEM and PIT; both PIFI2 and AMB1 remain active for almost all of the rest of swing phase.

One of the crural muscles examined, the hypothesized ankle flexor TA, is activated just after the start of swing phase and ceases activity at nearly 70% through swing duration.

Gatesy (1997) also measured EMGs for some of the same swing-phase muscles during walking in alligators, including AMB1, ILFEM and PIFI2. Patterns measured for these swing-phase muscles were also generally consistent with those described by Gatesy (1997), although the offset of ILFEM was somewhat earlier in the present study (nearly 80% stride cycle) than in Gatesy's study (90–95% stride cycle).

Changes in hindlimb motor patterns accompanying the use of more upright posture

Four of the five alligators tested showed no significant relationship between limb posture and the duration of swing phase, stance phase or the entire stride (Table 1). In a single alligator (Individual 2), stride duration and stance duration decreased significantly with the use of upright posture. However, with the exception of EMG changes for FTE (for which Individual 2 was the only animal recorded), all of the changes in muscle motor pattern exhibited by Individual 2 were also exhibited by at least one additional individual in which phase and stride durations were not correlated with posture (Table 2). Therefore, we are confident that the motor pattern changes we observed were related to differences in limb posture rather than differences in footfall timing.

Stance phase

Several stance-phase muscles exhibit significant changes in EMG burst timing, intensity or both as posture becomes more upright, but a few maintain constant patterns as different postures are used (Fig. 3). These patterns of change (or lack of change) in EMGs were remarkably consistent among the individual alligators examined. For example, in both individuals in which EMGs were measured for the ankle extensor GAST, neither burst timing nor duration changed during the use of more upright postures; however, all three indicators of burst intensity (rectified burst area, mean burst amplitude and mean burst amplitude normalized by stance duration) increased significantly as posture became more upright (Fig. 4; Table 2). Two of the three knee extensors examined, FEMTIB and ILTIB2, showed similar patterns. Neither muscle showed significant changes in burst timing or duration as different postures were used. However, both individuals in which ILTIB2 was examined showed increases in burst area, mean burst amplitude and mean burst amplitude normalized by stance duration (Table 2). In addition, all three individuals in which FEMTIB was examined showed significant increases in mean burst amplitude and normalized mean burst amplitude during the use of more upright posture, and two of these three also showed significant increases in rectified area (with the third showing a nearly significant increase; Fig. 4; Table 2). The third knee extensor examined, ILTIB1, was only recorded in one individual but showed no significant changes in activity as posture became more upright (Fig. 3; Table 2).
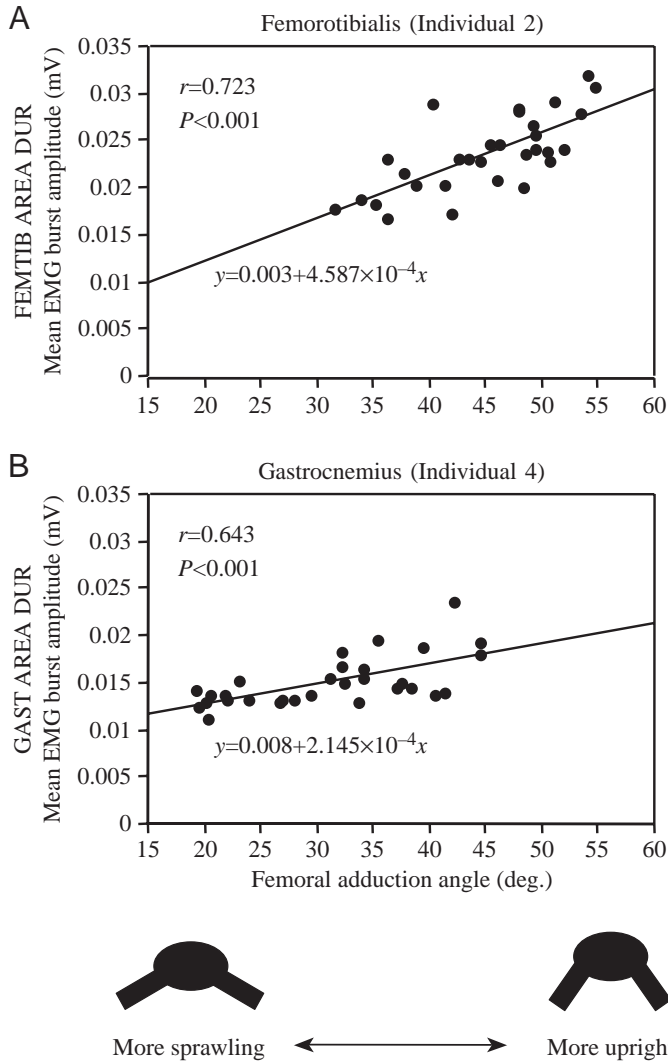
Fig. 4. Representative regressions of electromyographic (EMG) variables on femoral adduction angle for hindlimb extensor muscles of individual experimental alligators. Larger angles indicate more upright posture, as illustrated by the sketches at the bottom of the figure. *N*=30 for both regressions. (A) Mean burst amplitude for the femorotibialis of Alligator 2 (=FEMTIB AREA DUR of Table 2). (B) Mean burst amplitude for the gastrocnemius of Alligator 4 (=GAST AREA DUR of Table 2). Burst amplitudes increase significantly with the use of upright posture for both muscles.

The stance-phase femoral retractor, FTE, displays a more complicated pattern of posture-related activation changes than the ankle or knee extensors (Fig. 3). The onset and offset of FTE bursts shift earlier relative to the beginning of stance during more upright steps (Fig. 3), but offset shifts more than onset, so that upright steps have shorter-duration FTE bursts (Table 2). Rectified burst area does not change, however, causing both mean burst amplitude and normalized mean burst amplitude to increase for FTE with the use of more upright posture (Table 2). Two stance-phase adductors (PIFE3 and PIT) also showed posture-related changes in burst pattern (Fig. 3). In both individuals in which PIFE3 was examined,

burst onset and offset shifted earlier, relative to the beginning of stance, among more upright steps. PIFE3 burst duration also decreased significantly in one individual (and nearly significantly in the other) during steps in which more upright posture was used. However, the rectified area of PIFE3 bursts increased as posture became more upright in both individuals, as did mean burst amplitude and mean normalized burst amplitude (Table 2). PIT activity was recorded in only one individual, but in that animal it also showed a significant increase in normalized mean amplitude among more upright steps (Table 2). Like the knee extensors, however, one of the femoral adductors, ADDFEM1 (sampled in three animals), showed no significant changes in burst timing or intensity as posture became more upright (Table 2).

Swing phase

One swing-phase muscle, the knee extensor AMB 1, exhibited no significant changes in burst timing or intensity during more upright steps (Table 2; Fig. 3). Another muscle, the limb protractor PIFI2, exhibited no significant changes in burst intensity, onset or offset with the use of upright posture and only a marginally significant increase in normalized burst duration (Table 2). However, the ankle flexor TA exhibited increases in burst area, mean burst amplitude and mean normalized burst amplitude that paralleled those observed in the stance-phase ankle extensor GAST (Table 2). The swing-phase burst by PIT also exhibited posture-correlated changes: the offset of the swing phase burst of this muscle shifted earlier relative to foot-down among more upright steps, producing a shorter burst duration with more upright posture (Table 2). The remaining swing-phase muscle examined, ILFEM, exhibited posture-related changes in both burst timing and intensity: burst duration [by a later shift in onset, which is marginally significant (P=0.027)] and rectified area both decreased as posture became more upright, but mean burst amplitude and mean normalized burst amplitude both increased as more upright posture was used.

Discussion
Motor control of alligator limb posture: tests of predictions and their implications for skeletal mechanics

Most of the stance-phase alligator hindlimb muscles that exhibit changes in activation between sprawling and upright steps, as well as those with no changes, closely match the patterns of modulation predicted based on force platform studies (Fig. 1B). Analyses of joint equilibrium based on force platform data indicated that both ankle and knee extensors should exert higher forces during more upright steps (Fig. 1B; Blob and Biewener, 2001). Consistent with force platform predictions, our EMG data show that the ankle extensor GAST and the two largest knee extensors FEMTIB and ILTIB2 (all three of which were recorded in multiple individuals) exhibit significant increases in all three measures of burst intensity as alligators use more upright posture (Table 2). By contrast, joint equilibrium analyses did not indicate that changes in the

Table 2. *Correlations between hindlimb motor patterns and the use of more upright limb postures in* Alligator

EMG variable	Individuals					
	r	P	r	P	r	P
Stance femoral retractors	INDIVIDUAL 2					
FTE REL ON	–0.669	<0.001*				
FTE REL OFF	–0.768	<0.001*				
FTE DUR	–0.661	<0.001*				
FTE DUR STANCE	–0.193	0.306				
FTE AREA	0.147	0.440				
FTE AREA DUR	0.612	<0.001*				
FTE AD STANCE	0.571	0.001*				
Stance femoral adductors						
ADDFEM	No significant correlations (Individuals 1, 4 and 5)					
	INDIVIDUAL 1		INDIVIDUAL 2			
PIFE3 REL ON	–0.609	<0.001*	–0.673	<0.001*		
PIFE3 REL OFF	–0.667	<0.001*	–0.675	<0.001*		
PIFE3 DUR	–0.426	0.019	–0.514	<0.001*		
PIFE3 DUR STANCE	–0.105	0.582	–0.130	0.494		
PIFE3 AREA	0.575	0.001*	0.679	<0.001*		
PIFE3 AREA DUR	0.768	<0.001*	0.751	<0.001*		
PIFE3 AD STANCE	0.719	<0.001*	0.679	<0.001*		
PIT (a) REL ON	0.018	0.924				
PIT (a) REL OFF	0.023	0.906				
PIT (a) DUR	0.143	0.451				
PIT (a) DUR STANCE	0.310	0.096				
PIT (a) AREA	0.334	0.071				
PIT (a) AREA DUR	0.474	0.008				
PIT (a) AD STANCE	0.528	0.003*				
Stance knee extensors	INDIVIDUAL 1		INDIVIDUAL 2		INDIVIDUAL 4	
FEMTIB REL ON	0.051	0.789	–0.089	0.639	0.053	0.779
FEMTIB REL OFF	–0.164	0.388	–0.222	0.239	0.208	0.271
FEMTIB DUR	–0.203	0.282	–0.146	0.440	0.211	0.263
FEMTIB DUR STANCE	0.294	0.115	0.336	0.070	0.291	0.119
FEMTIB AREA	0.370	0.044	0.694	<0.001*	0.802	<0.001*
FEMTIB AREA DUR	0.668	<0.001*	0.723	<0.001*	0.719	<0.001*
FEMTIB AD STANCE	0.669	<0.001*	0.653	<0.001*	0.590	0.001*
ILTIB1	No significant correlations (Individual 5)					
	INDIVIDUAL 4		INDIVIDUAL 5			
ILTIB2 REL ON	0.079	0.677	–0.287	0.123		
ILTIB2 REL OFF	0.333	0.072	0.056	0.770		
ILTIB2 DUR	0.128	0.500	0.197	0.296		
ILTIB2 DUR STANCE	0.147	0.439	0.061	0.747		
ILTIB2 AREA	0.863	<0.001*	0.840	<0.001*		
ILTIB2 AREA DUR	0.774	<0.001*	0.774	<0.001*		
ILTIB2 AD STANCE	0.622	<0.001*	0.651	<0.001*		
Stance ankle extensors	INDIVIDUAL 3		INDIVIDUAL 4		INDIVIDUAL 5	
GAST REL ON	0.169	0.363	0.116	0.540	–0.206	0.275
GAST REL OFF	0.118	0.529	–0.200	0.290	–0.041	0.828
GAST DUR	–0.077	0.681	–0.157	0.408	0.335	0.071
GAST DUR STANCE	–0.023	0.900	–0.086	0.652	0.178	0.347
GAST AREA	0.651	<0.001*	0.535	0.002*	0.760	<0.001*
GAST AREA DUR	0.702	<0.001*	0.643	<0.001*	0.790	<0.001*
GAST AD STANCE	0.640	<0.001*	0.602	<0.001*	0.518	0.003*

forces exerted by the femoral adductors would be expected as posture became more upright (Fig. 1A; Blob and Biewener, 2001). Consistent with this prediction, the primary femoral adductor ADDFEM1 showed no significant posture-correlated

Table 2. *Continued*

EMG variable	Individuals					
	r	*P*	*r*	*P*	*r*	*P*
Swing femoral protractors	INDIVIDUAL 5					
PIFI2 REL ON	0.289	0.122				
PIFI2 REL OFF	0.421	0.021				
PIFI2 DUR	0.296	0.112				
PIFI2 DUR SWING	0.488	0.006*				
PIFI2 AREA	0.412	0.024				
PIFI2 AREA DUR	0.144	0.449				
PIFI2 AD SWING	0.356	0.054				
Swing femoral abductors	INDIVIDUAL 4					
ILFEM REL ON	0.405	0.027				
ILFEM REL OFF	−0.212	0.261				
ILFEM DUR	−0.734	<0.001*				
ILFEM DUR SWING	−0.656	<0.001*				
ILFEM AREA	−0.586	0.001*				
ILFEM AREA DUR	0.649	<0.001*				
ILFEM AD SWING	0.540	0.002*				
Swing knee extensors						
AMB 1	No significant correlations (Individuals 3 and 5)					
Swing knee flexors	INDIVIDUAL 1					
PIT (b) REL ON	−0.288	0.122				
PIT (b) REL OFF	−0.494	0.005*				
PIT (b) DUR	−0.479	0.007*				
PIT (b) DUR SWING	−0.351	0.057				
PIT (b) AREA	−0.400	0.029				
PIT (b) AREA DUR	0.382	0.037				
PIT (b) AD SWING	0.335	0.070				
Swing ankle flexors	INDIVIDUAL 3		INDIVIDUAL 4			
TA REL ON	0.023	0.902	0.214	0.257		
TA REL OFF	0.038	0.839	−0.046	0.808		
TA DUR	0.137	0.462	−0.151	0.426		
TA DUR SWING	0.062	0.742	0.048	0.800		
TA AREA	0.634	<0.001*	0.875	<0.001*		
TA AREA DUR	0.804	<0.001*	0.862	<0.001*		
TA AD SWING	0.590	<0.001*	0.804	<0.001*		

Correlation coefficients (*r*) and significance levels (*P*) for regressions of electromyographic variables on femoral posture, based on *N*=30 strides per individual spanning the femoral posture ranges given in Table 1 (positive correlations indicate increases in the variable with more upright posture).

The prefix of each variable name is the abbreviation for the muscle (see Myology), and the suffix describes the EMG variable: REL ON, burst onset relative to foot-down; REL OFF, burst offset relative to foot-down; DUR, burst duration; DUR STANCE, burst duration normalized by stance duration; DUR SWING, burst duration normalized by swing duration; AREA, rectified burst area; AREA DUR, rectified area normalized by burst duration (i.e. mean burst amplitude); AD STANCE, mean burst amplitude normalized by stance duration; AD SWING, mean burst amplitude normalized by swing duration. For PIT, letters denote the stance (a) and swing (b) phase activity bursts for this muscle.

*Significant (*P*<0.05) with sequential Bonferroni correction, *N*=7 variables per muscle.

changes in motor pattern (Table 2). However, two other muscles situated in positions to adduct the femur both showed increases in burst intensity among more upright steps: PIT exhibited greater normalized mean burst amplitude with upright posture, and PIFE3 showed greater rectified area, mean burst amplitude and normalized mean burst amplitude during more upright steps (Table 2). What are the implications of these increases in burst intensity among femoral adductors

for the muscular mechanisms that have been proposed to explain increases in femoral strain during upright posture in alligators?

Although PIT and PIFE3 show burst intensity modulations that were not predicted by force platform analyses, *increases* in burst intensity by these muscles during upright stance are not inconsistent with the model that Blob and Biewener (2001) proposed, in which higher femoral strains during upright

posture result from correlated increases in forces exerted by ankle and knee extensor muscles (Fig. 1B). The clearest evidence for an increase in adductor force is in PIFE3, in which all three indicators of burst intensity increase during upright stance (Table 2). However, this muscle inserts on the proximal femur and does not span the femoral midshaft; thus, PIFE3 does not contribute directly to midshaft strains and stresses (Blob and Biewener, 2001). An increase in PIFE3 force (spanning the ventral aspect of the hip) might lead to a corresponding increase in ILTIB2 force (spanning the dorsal aspect of the hip) in order to maintain joint equilibrium but would not produce femoral bending that countered the dorsal compression of the femur imposed by ILTIB2 and the other knee extensors. As a result, an increase in PIFE3 force during upright posture can be accommodated by Blob and Biewener's model of femoral loading in alligators (Fig. 1B) because it either would not alter femoral load patterns or, if anything, would reinforce the pattern of strains and stresses identified in bone loading analyses. Even an increase in force exerted by PIT might not significantly counter the dorsal bending imposed on the femur by the knee extensors, because the cross-sectional area (proportional to the force the muscle exerts: Alexander, 1974) of PIT in alligators is only one-third that of adductor femoris (Blob and Biewener, 2001), which shows no change in activation as posture becomes more upright.

It should be noted that the alternative (Fig. 1A) to Blob and Biewener's favored model (Blob and Biewener, 2001) for how changes in muscle activation produce increases in femoral stress during upright posture in alligators required that adductor force decrease, thereby countering the ground reaction force less effectively and raising femoral stresses. Increases in PIT and PIFE3 burst intensity might not have been predicted by Blob and Biewener's preferred model, but they run distinctly counter to its alternative. In addition, the fact that at least some of the femoral adductors display more intense EMG bursts during upright stance is functionally reasonable, as more intense activity by these muscles could help to produce the greater femoral adduction that upright posture entails.

Specific muscular mechanisms underlying the use of different limb postures in alligators: interspecific comparisons and implications for neural control

In order for alligators to use upright locomotion rather than sprawling locomotion, changes in EMG burst timing and/or intensity are required for eight of the 12 hindlimb muscles that we studied, including both stance- and swing-phase muscles. A number of these changes in activation pattern between sprawling and upright stance directly reflect the kinematic differences between these two postures. For example, the earlier onset of activity by the retractor FTE during upright posture is probably responsible for the significantly smaller maximum protraction of the femur during high walks relative to sprawling steps (Reilly and Elias, 1998). In addition, as noted previously, the increased burst intensity of the hip adductors PIFE3 and PIT during upright steps probably contributes to the greater femoral adduction that is integral to

upright limb posture in alligators. Similarly, greater burst intensity by the knee extensors FEMTIB and ILTIB2 probably contributes to the greater stance-phase knee extension typical of high walks, and increased burst intensity of the swing-phase ankle flexor TA may contribute to the earlier attainment of maximum ankle flexion during upright steps (Fig. 3; Reilly and Elias, 1998). However, the mechanical requirements of locomotion with upright limb posture in alligators also appear to contribute to some changes in muscular activation between sprawling and upright stance in these animals (Zernicke and Smith, 1996), particularly for the stance-phase ankle extensor GAST. Ankle movements are similar between sprawling and high-walk steps for most of stance phase (Reilly and Elias, 1998), providing little kinematic basis to explain posture-related changes in GAST activity. However, in the context of the increased ankle flexor moment induced by the ground reaction force during upright steps in alligators (Blob and Biewener, 2001), an increase in GAST burst intensity is clearly explained as a mechanism for maintaining the equilibrium of ankle joint moments despite a change in limb posture (Fig. 1B).

Hindlimb motor pattern data through ranges of limb postures are available for two other species: domestic cats (Trank et al., 1996), which use a crouched posture during predatory stalking (Leyhausen, 1979), and humans (Grasso et al., 2000). In studies of each of these two species, motor patterns of hindlimb muscles were recorded for narrow ranges of speeds over a broad range of limb postures. In contrast to alligators, in both humans and cats the intensity of EMG bursts by hindlimb extensor muscles is typically greater during crouched posture than upright posture (Trank et al., 1996; Grasso et al., 2000). One possible explanation for these patterns in mammals is that crouched posture demands greater motor recruitment because it requires muscles to contract at lengths that are not optimal for force production (Trank et al., 1996). However, crouching might also lead to more intense bursts of motor activity in mammals because, in mammals, crouched posture increases the flexor moments of the ground reaction force about joints (Biewener, 1989, 1990), requiring extensor muscles to exert greater forces to keep the joints in equilibrium (Perell et al., 1993; Trank et al., 1996; Grasso et al., 2000). Because humans and cats have fairly small feet relative to the length of their hindlimb, when they use an upright limb posture they align the limb with the ground reaction force, decreasing its moment arms about the joints and, thereby, decreasing joint flexor moments and the extensor muscle forces needed to counter them in order to prevent the limb from collapsing (Biewener, 1989, 1990). Alligators, by contrast, have much longer feet (relative to their hindlimbs) than either humans or cats (Blob and Biewener, 2001). During upright steps, the ankle is lifted from the substrate earlier than in sprawling steps and, as a result, the ground reaction force shifts far anteriorly along the foot, increasing its flexor moment arm at the ankle and requiring greater ankle extensor forces for the maintenance of joint equilibrium during upright posture (Blob and Biewener, 2001). Thus, it is entirely possible that the same principles (i.e.

joint equilibrium) are ultimately mediating the modulation of muscle activity that produces different postures in mammals and alligators, but that differences in the limb anatomy of these animals lead to the different patterns of modulation that these species use in order to achieve upright and non-upright locomotor postures.

Changes in motor pattern between sprawling and upright posture are widespread in the alligator hindlimb but they are not universal. In fact, muscles belonging to the same functional group (e.g. the knee extensors ILTIB1 and ILTIB2), as well as muscles that typically burst on or off simultaneously (e.g. ILTIB1 and PIT), can display very different modulations of EMG pattern between sprawling and upright steps, with some muscles maintaining consistent motor patterns through the full range of limb postures. Such variety in the behavioral modulation of activity patterns among muscles has been documented in the limb muscles of a wide range of tetrapod species (Gillis and Blob, 2001) and suggests considerable independence of neural control among the muscles of the alligator hindlimb. Immutability of the motor pattern of a muscle between behaviors has been cited as evidence that central pattern generator input dominates its neural control, with supraspinal input and motion-related feedback playing less important roles (Buford and Smith, 1990; Pratt et al., 1996). Although some hindlimb muscles of alligators showed no difference in motor pattern with the use of different postures (e.g. ILTIB1, ADDFEM), the possibility that other behaviors (e.g. walking at faster speeds: Nilsson et al., 1985; Reilly, 1998) might elicit changes in the activation patterns of these muscles remains to be tested. The specific roles of some alligator hindlimb muscles may not be well understood until their actions have been measured in a wide range of behaviors that more completely sample the functional repertoires of these animals.

References

Alexander, R. McN. (1974). The mechanics of a dog jumping, *Canis familiaris. J. Zool. Lond.* **173**, 549-573.

Bakker, R. T. (1971). Dinosaur physiology and the origin of mammals. *Evolution* **25**, 636-658.

Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45-48.

Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097-1103.

Blob, R. W. (1998). Mechanics of Non-parasagittal locomotion in alligator and iguana: functional implications for the evolution of non-sprawling posture in the Therapsida. *PhD Thesis.* University of Chicago, IL, USA.

Blob, R. W. (2001). Evolution of hindlimb posture in nonmammalian therapsids: biomechanical tests of paleontological hypotheses. *Paleobiology* **27**, 14-38.

Blob, R. W. and Biewener, A. A. (1999). *In vivo* locomotor strain in the hindlimb bones of *Alligator mississippiensis* and *Iguana iguana*: implications for the evolution of limb bone safety factor and non-sprawling limb posture. *J. Exp. Biol.* **202**, 1023-1046.

Blob, R. W. and Biewener, A. A. (2001). Mechanics of limb bone loading during terrestrial locomotion in the green iguana (*Iguana iguana*) and American alligator (*Alligator mississippiensis*). *J. Exp. Biol.* **204**, 1099-1122.

Brinkman, D. (1980). The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Can. J. Zool.* **58**, 2187-2200.

Buchanan, T. S., Almdale, D. P. J., Lewis, J. L. and Rymer, W. Z. (1986). Characteristics of synergic relations during isometric contractions of human elbow muscles. *J. Neurophysiol.* **56**, 1225-1241.

Buford, J. A. and Smith, J. L. (1990). Adaptive control for backward quadrupedal walking II. Hindlimb muscle synergies. *J. Neurophysiol.* **64**, 756-766.

Charig, A. J. (1972). The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. In *Studies in Vertebrate Evolution* (ed. K. A. Joysey and T. S. Kemp), pp. 121-155. Edinburgh: Oliver & Boyd.

Cott, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. Lond.* **29**, 211-340.

Gatesy, S. M. (1991). Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *J. Zool. Lond.* **224**, 577-588.

Gatesy, S. M. (1994). Neuromuscular diversity in archosaur deep dorsal thigh muscles. *Brain Behav. Evol.* **43**, 1-14.

Gatesy, S. M. (1997). An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. *J. Morph.* **234**, 197-212.

Gillis, G. B. and Blob, R. W. (2001). How muscles accommodate movement in different physical environments: aquatic vs. terrestrial locomotion in vertebrates. *Comp. Biochem. Physiol. A* **131**, 61-75.

Grasso, R., Zago, M. and Lacquaniti, F. (2000). Interactions between posture and locomotion: motor patterns in humans walking with bent versus erect posture. *J. Neurophysiol.* **83**, 288-300.

Gregory, W. K. (1912). Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Ann. N. Y. Acad. Sci.* **22**, 287-294.

Gruner, J. A. and Altman, J. (1980). Swimming in the rat: analysis of locomotor performance in comparison to stepping. *Exp. Brain Res.* **40**, 374-382.

Irschick, D. J. and Jayne, B. C. (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.* **202**, 1047-1065.

Jenkins, F. A., Jr (1971). Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *J. Zool. Lond.* **165**, 303-315.

Johnston, R. M. and Bekoff, A. (1996). Patterns of muscle activity during different behaviors in chicks: implications for neural control. *J. Comp. Physiol. A* **179**, 169-184.

Kemp, T. S. (1978). Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *J. Zool. Lond.* **186**, 143-161.

Leyhausen, P. (1979). *Cat Behavior. The Predatory and Social Behavior of Domestic and Wild Cats.* New York: Garland.

Loeb, G. E. and Gans, C. (1986). *Electromyography for Experimentalists.* Chicago: University of Chicago Press.

Macpherson, J. M. (1991). How flexible are muscle synergies? In *Motor Control: Concepts and Issues* (ed. D. R. Humphrey and H. J. Freund), pp. 33-47. Chichester, UK: John Wiley & Sons, Ltd.

Nilsson, J., Thorstensson, A. and Halbertsma, J. (1985). Changes in leg movements and muscle activity with speed of locomotion and mode of progression in humans. *Acta Physiol. Scand.* **123**, 457-475.

Parrish, J. M. (1987). The origin of crocodilian locomotion. *Paleobiology* **13**, 396-414.

Perell, K. L., Gregor, R. J., Buford, J. A. and Smith, J. L. (1993). Adaptive control for backward quadrupedal walking. VI. Hindlimb kinetics during stance and swing. *J. Neurophysiol.* **70**, 2226-2240.

Pratt, C. A., Buford, J. A. and Smith, J. L. (1996). Adaptive control for backward quadrupedal walking. V. Mutable activation of bifunctional thigh muscles. *J. Neurophysiol.* **75**, 832-842.

Reilly, S. M. (1995). Quantitative electromyography and muscle function of

the hind limb during quadrupedal running in the lizard *Sceloporus clarkii*. *Zoology* **98**, 263-277.

Reilly, S. M. (1998). Sprawling locomotion in the lizard *Sceloporus clarkii*: speed modulation of motor patterns in a walking trot. *Brain Behav. Evol.* **52**, 126-138.

Reilly, S. M. and DeLancey, M. J. (1997a). Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. *J. Exp. Biol.* **200**, 753-765.

Reilly, S. M. and DeLancey, M. J. (1997b). Sprawling locomotion in the lizard *Sceloporus clarkii*: the effects of speed on gait, hindlimb kinematics, and axial bending during walking. *J. Zool. Lond.* **243**, 417-433.

Reilly, S. M. and Elias, J. A. (1998). Locomotion in *Alligator mississippiensis*: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. *J. Exp. Biol.* **201**, 2559-2574.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223-225.

Romer, A. S. (1923). Crocodilian pelvic muscles and their avian and reptilian homologues. *Bull. Am. Mus. Nat. Hist.* **48**, 533-552.

Seebacher, F., Guderley, H., Elsey, R. M. and Trosclair, P. L., III (2003). Seasonal acclimatisation of muscle metabolic enzymes in a reptile (*Alligator mississippiensis*). *J. Exp. Biol.* **206**, 1193-1200.

Trank, T. V., Chen, C. and Smith, J. L. (1996). Forms of quadrupedal locomotion. I. A comparison of posture, hindlimb kinematics, and motor patterns for normal and crouched walking. *J. Neurophysiol.* **76**, 2316-2326.

Updegraff, G. (1990). *Measurement TV: Video Analysis Software*. San Clemente, CA: Data Crunch.

Zernicke, R. F. and Smith, J. L. (1996). Biomechanical insights into neural control of movement. In *Handbook of Physiology Section 12: Exercise: Regulation and Integration of Multiple Systems*, (ed. L. B. Rowling and J. T. Shepherd), pp. 293-330. New York: American Physiological Society.