Sprawling Locomotion in the Lizard Sceloporus clarkii: Speed Modulation of Motor Patterns in a Walking Trot

Abstract
Previous kinematic analyses in Sceloporus clarkii have shown that increased speed during trotting is attained by retracting the femur relatively faster (decreasing retraction time relative to stride duration) while all other aspects of axial and limb movements occur simply faster (scaling with stride duration). Thus, most of the limb muscles must be modulated to move the joints absolutely faster, while muscles effecting femoral retraction must be modulated differently to retract the femur relatively faster to increase speed. This prediction was examined by analyzing motor patterns in several key leg muscles in the spiny lizard running over a threefold increase in speed during a trot. The prediction is borne out in the limb muscles where the limb adductor (flexor tibialis), knee extender (femorotibialis), and plantar flexor of the ankle (gastrocnemius) have similar patterns of motor modulation that are different from that of the femoral retractor (caudofemoralis). To modulate a muscle to move simply faster (scaled with speed) the offset of the motor pattern is moved relatively earlier to decrease burst duration, while the intensity of electromyographical activation is ramped up. Increasing the relative speed of action is done by activating the muscle earlier, increasing the duration of the burst, and increasing the relative level of activation. Comparisons to other studies illustrate that the confounding effects that stance and swing duration have on stride duration with speed have important consequences for functional interpretations and that scaling locomotory data to stance duration is a more appropriate and useful convention because it relates information directly to the duty cycle when the propulsive effects of motor modulation are transmitted to the substrate. The ilio-costalis in Sceloporus clarkii has a pattern of activity indicating that it functions to rotate the pelvis to aid the contralateral duty cycle. This is strikingly different from the function of the ilio-costalis in the monitor lizard. Differences in axial function and differences among lizards in postures of the foot and crus during locomotion indicate that there are different ways that lizards run and that the functional and anatomical diversity of modes of locomotion in lizards is greater than is recognized at present.
Introduction

The functional morphology of quadruped terrestrial locomotion has been the focus of numerous studies approaching the problem from a variety of perspectives, including limb mechanics, muscle physiology, energetics, neural control, functional morphology, organismal performance and ecological morphology, to name a few [e.g. Gray, 1968; Alexander, 1968; Grillner, 1981; Bennett, 1983; McMahon, 1984; Hildebrand et al., 1985; Jayne et al., 1990a; Garland and Losos, 1994]. However, one facet of the study of locomotion that is of relevance to many of the above approaches but has received relatively little attention is the analysis of the muscle activity patterns (motor patterns) that drive limb movements and, more specifically, how motor patterns are modulated to increase locomotory speed. Most electromyographical studies to date have focused on the functions of specific muscles as they relate to certain tasks of the limbs (such as the paw shake, maintaining posture, or recruitment of synergistic ankle muscles) with a great preponderance of the work on cats, dogs, and rats. Some studies have focused on locomotion per se, providing data to describe motor patterns used when an animal walks or uses different gaits. Key mammalian works in this area are studies of Rasmussen et al. [1978] and Smith et al. [1993] on cats and studies of Goslow et al. [1981], Tokuriki [1973a, b, 1974], and Wentink [1976] on dogs which describe the motor patterns for numerous hind limb muscles in these species during walk, trot and gallop gaits. Although Grillner [1981] reviews ideas on the neural control of locomotion in vertebrates and presents a description of motor patterns in mammals, he admits that little work has been done on nonmammalian vertebrates and that only a qualitative description of a general vertebrate limb motor pattern is possible, lacking quantitative details even for mammals. Electromyographical studies of quadrupedal locomotion in nonmammalian species are limited to four studies: studies of motor patterns of forelimb muscles [Jenkins and Goslow, 1983] and epaxial muscles [Ritter, 1995] during a trot in monitor lizards (Varanus), a study of hind limb motor patterns in a trotting salamander [Dicamptodon, Ashley-Ross, 1995], and a study of hind limb and axial motor patterns during a trot in spiny lizards [Sceloporus, Reilly, 1995]. These data give us a basic picture of the motor patterns used by these few species for these specific gaits, but no study has specifically quantified how the onsets, offsets, durations, and amplitudes of electromyographical patterns change with speed within a gait. The goal of this study was to analyze how motor patterns are modulated over a range of trotting speeds in the spiny lizard, Sceloporus clarkii.

Analyses of the motor patterns [Reilly, 1995] and kinematics [Reilly and DeLancey, 1997a] of the hind limb in the spiny lizard trotting at a single speed have identified key muscles that function in limb propulsion and have shown that this species exhibits a truly sprawling posture in which the crus and foot never pass ventral to the knee. Analysis of the effects of speed on the kinematics of limb and axial movements [Reilly and DeLancey, 1997b] has shown that these lizards increase speed (while trotting over a threefold increase in speed) by increasing the rate of femoral retraction relative to stride duration (retraction occurs relatively faster as speed increases), while all other aspects of axial and limb kinematics remain unchanged except that all other movements increase in speed scaled with stride duration (movements occur simply faster as speed increases). This surprisingly simple pattern of kinematic change to increase speed indicates that most of the limb muscles must be modulated to move the pelvis, knee and ankle through the same range of motion more quickly but in concert with the stride duration, while muscles effecting femoral retraction must be modulated to retract the femur relatively faster (more quickly than stride duration) to increase speed.

This leads to two interesting questions concerning the modulation of motor activity to increase speed. First, how do motor patterns change to make a muscle produce the same kinematic movements simply faster as most of the limb muscles are doing? And second, how would a motor pattern change to make a muscle do the same thing relatively faster? Answers to these questions are difficult to predict, given the paucity of data on speed effects on motor patterns during locomotion. Some idea of speed effects could be obtained by comparing motor patterns across gaits, but these comparisons would be influenced by the radical changes in limb movement dynamics when gaits change and not simply speed. One can predict that the relative intensity of electromyographical signals should increase with speed as motor units are activated more frequently and/or more motor units are activated to increase the force of muscle contraction [Basmajian and DeLuca, 1985; Corcos et al., 1989]. Although there is some evidence to suggest that muscle activation timing is modulated to increase the speed of movements [e.g. Buneo et al., 1994], it is difficult to predict how the timing of motor onsets, offsets and durations would change in the two modulatory scenarios discussed above. To examine these questions changes in motor patterns of several key leg muscles were analyzed over a threefold increase in speed during a trot. My general prediction is that muscles that act simply faster, without altering limb kinematics, should have a similar pattern of motor modulation with speed, a pattern that differs from...
that of the primary muscle involved with femoral retraction (the caudofemoralis) which must be modulated to act relatively faster.

**Materials and Methods**

Simultaneous kinematic and electromyographic (EMG) data were obtained from several adult *Sceloporus clarkii* collected in Molino Basin, Santa Catalina Mountains, 10 miles N. of Tucson, Arizona. *Sceloporus clarkii* was chosen because it is believed to use a generalized sprawling form of locomotion [Sukhanov, 1974], as it exhibits an extremely sprawling limb posture with the crus remaining lateral to the knee throughout the stride and represents the most sprawling quadrupedal vertebrate known [Reilly and DeLancey, 1997a], and because this species is morphologically generalized, possessing the primitive morphology for the family Phrynosomatidae [Miles, 1994].

Data from three individuals (snout-vent lengths, 90, 91, and 91 mm) for which the same key muscles were sampled at several speeds were used for this analysis. Lizards were filmed with a high speed video camera while running on a 70-cm long, speed controlled treadmill, while electromyograms were recorded via fine wire electrodes implanted into selected hind limb and axial muscles. Motor patterns for each muscle were quantified at speeds ranging from 0.303 m s\(^{-1}\) (1.09 km/h) to 1.070 m s\(^{-1}\) (3.85 km/h). Individual 1 was analyzed at 0.303, 0.476, 0.613, and 0.833 m s\(^{-1}\), individual 2 was studied at 0.476, 0.747, and 0.833 m s\(^{-1}\), and individual 3 was studied at 0.377, 0.907, and 1.070 m s\(^{-1}\) (n=five strides per speed for each individual). The lizards employed a trot (diagonal footfalls coincident) over this range of speeds. Quantitative analyses of kinematics [Reilly and DeLancey, 1997a] and motor patterns [Reilly, 1995] for the 0.833 m s\(^{-1}\) speed are presented elsewhere. Motor patterns quantified in the present study will be discussed in light of kinematic speed effects quantified in Reilly and DeLancey (1997b) for two individuals moving between 0.270 and 0.833 m s\(^{-1}\). All research was performed under Ohio University animal use guidelines.

**Myology**

Reilly [1995] studied 11 axial and hind limb muscles in *Sceloporus clarkii* and proposed primary functions of these muscles based on electromyographical and gross kinematic patterns. Five of these muscles (shown schematically in fig. 1), representing axial, thigh and crural muscles involved in locomotion, were chosen for the present study because of their relatively straightforward functions that relate to simple movements of joint segments (axial bending, knee extension, limb adduction, hip retraction, and plantar flexion).

Several lines of evidence indicate the caudofemoralis muscle is the primary muscle retracting the limb in sprawling vertebrates [Snyder, 1954; Gatesy, 1990; Reilly, 1995]. Although it is primarily an axial muscle, it is the largest muscle acting on the hind limb. The caudofemoralis extends from several postpelvic caudal vertebrae via a tendon that inserts primarily to the trochanteric fossa at the proximal posterior side of the femur, with an auxiliary tendon extending out along the posterior side of the femur to insert on the ligaments, cartilages and muscular insertions on the proximal and caudal aspects of the crus. From these insertions the caudofemoralis is hypothesized to act equally on the femur and crus early in the retraction phase and then, as the leg is moved laterally and posteriorly, its tension becomes progressively greater on the portion inserting on the femur [Snyder, 1954]. Kinematic and motor patterns in *Sceloporus clarkii* support this hypothesis, indicating that the caudofemoralis is the primary muscle impacting limb retraction because it flexes the knee and retracts the femur [Reilly, 1995; Reilly and DeLancey, 1997b]. Because the kinematic analysis of speed effects demonstrated that femoral retraction (and associated knee flexion) was the only movement to occur increasingly faster relative to stride duration, this muscle is predicted to have a different motor pattern than the four others studied, whose kinematic functions occur simply faster, scaling with stride duration. Electrodes in the caudofemoralis muscle were placed in the muscle about 2 vertebrae (4 mm) posterior to the pelvis which is approximately where the muscle has its greatest cross section.

One other axial muscle, the iliocostalis, was studied (fig. 1). The iliocostalis is the lateral most epaxial muscle and runs lateral to the longissimus dorsi, extending all along the trunk to the pubis. Electrodes for this muscle were implanted approximately two vertebrae (about 4 mm) anterior to the pelvis between the pubis and the ribs. Contraction of this muscle bends the body to the right, which effectively rotates the pelvis to the left during the right side swing phase; thus it contributes to protraction of the right limb while simultaneously contributing to the retraction of the left limb.

Two thigh muscles were studied (fig. 1). The femorotibialis muscle is the largest muscle on the thigh and extends from the dorsal, lateral, and medial surfaces of the central shaft of the femur by means of a broad tendon over the surface of the knee to insert on the anterior tibial condyles. The femorotibialis exhibits bursts of activity when the knee is extended, with a small burst during swing phase extension and...
a large burst during knee extension with the stance phase [Reilly, 1995]. This study focuses only on femorotibialis activity that extends the knee during the stance phase (the portion of the stride when the foot is contacting the ground and thus effecting locomotion). Electrodes were placed in the belly of the muscle along the distal one-fourth of the femur.

The second thigh muscle studied (the flexor tibialis internus 2 deep) is part of the flexor tibialis internus group, a tripartite muscle lying along the posteroventral part of the thigh. The flexor tibialis internus 1 lies along the posterior aspect of the thigh and was not used in this study. Just anteromedial to this muscle is the flexor tibialis internus 2, which has separate superficial and deep portions. Both heads originate from the ilioischial ligament (along with the flexor tibialis internus 1), but the flexor tibialis internus 2 'superficialis' inserts on the lateral tibial condyle, sharing a wide tendon with the pubotibialis, while the flexor tibialis internus 2 'deep' inserts more distally on the posterior condyles of the tibia via a narrow tendon. Because both superficial and deep portions span the hip and knee joints, they have been hypothesized to adduct the limb during the swing phase, flex the knee during both the swing and stance phases, and retract the thigh at the onset of the stance phase [Snyder, 1954]. Electromyographical patterns for the flexor tibialis internus 2 superficialis suggest that this muscle does indeed contribute to all of these functions [Reilly, 1995]. The flexor tibialis internus 2 deep, however, has a large focused burst of activity during the middle portion of the stance phase, when the knee joint is extending, indicating that it cannot be flexing the knee during the stance phase (although it may contribute somewhat to femoral retraction). Rather, its primary function is hypothesized to be adduction of the hind limb as a means of counteracting the mass of the body during the middle third of the stance phase [Reilly, 1995]. In this study I focused on the deep portion of the flexor tibialis internus 2, which for simplicity will be referred to as the flexor tibialis in the text. Electrodes were placed in the belly of this muscle at mid femur level.

One muscle of the crucus, the medial gastrocnemius, was also analyzed (fig. 1). It is the largest muscle of the crucus, originating from the lateral and medial femoral condyles and the intervening fossa, the distal ventral femoral shaft, and along the medial side of the shaft of the tibia. Distally it inserts broadly on the plantar aponeurosis to the distal ends of metatarsal 3–5. It functions to plantar flex the foot. Electrodes were placed in the belly of the muscle at about the middle of the crus.

**Electromyography**

Muscle activity patterns (motor patterns) of the four limb and one axial muscle (all on the right side of the body) were quantified by simultaneously recording electrical activity patterns (EMG's) produced during locomotion. Electromyographical recordings were made from bipolar stainless steel electrodes implanted into each muscle as in previous research [Reilly, 1995]. All electrode implantations were done while the animals were under anesthesia, induced by placing the animals in a closed container containing 1 ml halothane for 5 min. The bared metal tips of each electrode were 0.5 mm long, and the insulated portions were glued together proximal to the bared ends with a cyanoacrylate adhesive to prevent tip displacement within the muscle [Jayne, 1988]. 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 on the midline dorsal to the pelvis. Animals completely recovered from anesthesia within two hours, and all synchronized EMG and kinematic data were recorded during the next 2 h. Body temperatures of the lizards during the runs was 27–29 °C. Lizards were rested (about 15–30 min) between bouts of running (20 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, and only preparations in which the electrode lay completely within the muscle were used.

The EMG signals were amplified 10,000 times, using AM Systems model 1700 differential AC amplifiers with a bandpass of 100 to 3000 Hz (and a 60 Hz notch filter), and recorded on a TEAC XR-5000 multichannel FM tape recorder along with a synchronization pulse simultaneously recorded on the video frames. The analog signals (5 EMG channels plus a synchronization pulse) for each stride were converted to a digital data file using custom software with a Keithley analog-to-digital converter and a microcomputer. The effective sample rate for each of the channels was 10,000 Hz at 12 bit resolution. This sample rate was chosen because of the results of a separate study which showed that 10 kHz allowed the faithful reproduction of spikes present in the EMG's from lizard locomotory muscles [Jayne et al.,
Table 1. Regression statistics for the effects of speed on the relative timing of hind limb movements during the duty cycle in *Sceloporus clarkii* based on means [data from Reilly and DeLancey, 1997b] scaled to stance duration for two individuals moving at three speeds (0.270, 0.476, and 0.833 m s⁻¹, n = 5 each speed per individual). Note that significant speed effects are observed in only three variables: two variables indicate relatively faster femoral retraction, and one describes relatively faster flexion of the knee during limb retraction, all of which can be attributed to the action of the caudofemoralis muscle.

<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Effective muscle</th>
<th>R²</th>
<th>F₁₄₋₁₄</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time from foot down to maximum femoral retraction</td>
<td>Caudofemoralis</td>
<td>0.973</td>
<td>106.49</td>
<td>0.002*</td>
</tr>
<tr>
<td>Total femoral retraction time</td>
<td>Caudofemoralis</td>
<td>0.917</td>
<td>33.94</td>
<td>0.011*</td>
</tr>
<tr>
<td>Time from foot down to minimum knee flexion</td>
<td>Caudofemoralis</td>
<td>0.887</td>
<td>23.62</td>
<td>0.017*</td>
</tr>
<tr>
<td>Time from foot down to maximum knee extension</td>
<td>Femorotibialis</td>
<td>0.000</td>
<td>0.001</td>
<td>0.983</td>
</tr>
<tr>
<td>Duration of knee extension</td>
<td>Femorotibialis</td>
<td>0.305</td>
<td>1.32</td>
<td>0.334</td>
</tr>
<tr>
<td>Degree of femoral abduction (extent of lateral knee displacement amplitude)</td>
<td>Flexor tibialis internus</td>
<td>0.057</td>
<td>0.06</td>
<td>0.847</td>
</tr>
<tr>
<td>Time from foot down to maximum ankle extension</td>
<td>Gastrocnemius</td>
<td>0.378</td>
<td>0.18</td>
<td>0.270</td>
</tr>
<tr>
<td>Duration of ankle extension</td>
<td>Gastrocnemius</td>
<td>0.111</td>
<td>0.38</td>
<td>0.583</td>
</tr>
<tr>
<td>Time from foot down to maximum pelvic rotation to right</td>
<td>Iliocostalis</td>
<td>0.186</td>
<td>0.69</td>
<td>0.468</td>
</tr>
</tbody>
</table>

* = Significant with muscle-wide sequential Bonferroni test [Rice, 1989]; ** = from maximum forward protraction of the limb which occurs before foot down.

Baseline noise was eliminated at a threshold voltage of +12 μV in the unamplified signal. Prior to the experiments an extensive calibration of the system revealed no crosstalk down stream of the electrodes, and crosstalk has not been a problem in previous work using the same electrode materials, construction, and placement protocols. Single EMG profiles were inspected for possible patterns revealing crosstral, and none were found.

Custom software was used to digitize the onset time, offset time, duration, and the rectified integrated area for each burst for each muscle at each speed. The goal was to quantitatively describe the muscle activity patterns (motor patterns) during locomotion at a given speed by averaging the motor pattern variables for five strides each from each speed. Burst onset and offset values were compared to the timing of foot down (time zero) within each stride to calculate the relative onset and relative offset times. Burst area was divided by burst duration to calculate the mean EMG amplitude for each burst. Burst duration, relative onset, and relative offset values were divided by the stance duration for each stride to scale the timing variables to the duty cycle. This was done to assess changes in muscle activity patterns relative to the portion of the stride when the foot is contacting the ground, when resulting limb movements directly effect the propulsive phase of the limb cycle. Mean amplitude values for each burst were scaled to the highest value observed within each muscle within each individual at the highest speed studied for each individual. This gives a measure of the amplitude at each speed compared to the maximum recorded amplitude for each individual.

To quantify the timing of motor patterns for each speed the values for each stride were divided by the stance duration for that stride and averaged for the five strides for each speed. The means were then plotted with standard errors to illustrate motor pattern changes with speed relative to stance duration. Mean EMG amplitude was not scaled to stance duration. To identify motor pattern variables that differed with speed, individual variable means at each speed for the three individuals (total n = 10) were regressed against speed. Significant regressions were used to indicate which EMG variables differed with speed. Variables that differed with speed were then compared to significant kinematic speed effects [based on a reanalysis of data in Reilly and DeLancey, 1997b, see below] to describe how these lizards modulate motor patterns to increase their velocity.

**Kinematic Analysis**

Details of kinematic methods and data on speed effects are presented in Reilly and DeLancey [1997b]. In the present study the only kinematic measures taken from high-speed video recordings were the times of foot down (when the foot meets the substrate), foot up (when the toes leave the ground) and the following foot down for each stride. These times were used to calculate the stance duration (from foot down to foot up) when the propulsive retraction of the limb occurs (also termed the duty cycle, stance phase, and support phase), the swing duration (foot up to the next foot down) when the limb is protracted and swung forward to recover before the next propulsive stroke (the swing phase or transport phase), and the stride duration (foot down to foot down) for each stride and to correlate foot down times to EMG onset and offset times.

Reilly and DeLancey [1997b] described the effects of speed on hind limb kinematics for *Sceloporus clarkii* by scaling their kinematic timing variables to stride duration. Scaling timing variables to stride duration, however, does not take into account the dynamics of changes in the stance and swing phases or, more importantly, the changes in kinematics relative to the stance phase during which locomotory forces are conveyed to the substrate (see discussion). Thus, to compare motor pattern data (scaled to stance duration) to kinematic changes with speed, the relevant kinematic timing data of Reilly and DeLancey [1997b] were reanalyzed after they were rescaled to stance duration with each variable then regressed against speed to test for the effects of speed on kinematics when compared to the duty cycle rather than the entire strides duration.
Changes of stance and swing phase timing with speed for *Scoloporus clarkii* are presented in figure 2. In real time, the stance phase (fig. 2 top: squares) decreases in duration as speed increases over the range studied while the swing phase (fig. 2 top: circles) decreases at a slower rate until it levels off at a duration of about 88 ms at a speed of about 0.6 m s\(^{-1}\). Calculating the relative contributions of the stance and swing phases to the entire stride (by dividing each by the stride duration) shows that the stance phase decreases from 58 to 44% of the stride (fig. 2 bottom: squares), while the swing phase increases from 42 to 55% of the stride (fig. 2 bottom: circles).

Results of regression analyses for the reanalysis of kinematic timing data [from Reilly and DeLancey, 1997b] scaled to stance duration versus speed are presented in table 1, with specific kinematic variables listed with the relevant muscles. Rescaling the kinematic timing variables...
to stance duration does not change any of the conclusions about speed effects on limb and pelvic kinematics. The extent of angular movements of joints and pelvic rotation do not change with speed. The timing of limb movements becomes absolutely faster with increasing speed, but it does not change relative to the stance phase timing, except for two features. During the stance phase, the time to minimum knee flexion and the time to maximum femoral retraction (whether from the time of maximum foot protraction or the time of foot down) occur relatively sooner as speed increases (table 1).

Motor Patterns
Means for the timing of EMG bursts relative to stance duration are presented in figures 3 through 5. Mean burst onset time (fig.3), offset time (fig.4), and burst duration (fig.5) illustrate the influence of speed on EMG timing variables. The effect of increased speed on mean EMG amplitude (integrated EMG area/burst duration) is presented in figure 6. Regression statistics for the timing variables scaled to stance duration (and mean amplitude unscaled) are pre-
sented in Table 2. Using the regression results to determine significant speed effects and the directions of change illustrated by the trends of the means (Fig. 3–6), a quantitative profile of the speed effects on the motor pattern for each muscle can be described. All five muscles exhibited a significant increase in mean amplitude with speed. Two muscles had significantly longer burst durations relative to the duty cycle as speed increased. The ilio-costalis and caudo-femoralis muscles developed significantly longer relative burst durations by moving the relative onset time significantly earlier. The other three muscles exhibited decreases in burst duration relative to the duty cycle as speed increased. The gastrocnemius and flexor tibialis developed significantly shorter burst durations by moving the relative offset significantly earlier while onset remained the same. The femorotibialis had significantly earlier relative onset and offset times but developed a significantly shorter burst duration by shifting the relative offset more than the relative onset.

**Discussion**

In studies of locomotion it is critical that the combined effects that stance and swing duration have on stride duration with speed are quantified and understood. As animals move faster using a trot the stance, swing, and stride durations generally decrease, but the relative contribution of the stance and swing phases to stride duration changes dynamically. As speed increases, the swing phase will level off at some minimum duration well before the stance phase does, but the percentage of the stride that is swing phase will continue to increase. This is illustrated in *Sceloporus clarkii*, where in real time the swing phase levels off after 0.6 m s$^{-1}$ while the stance phase continues to decrease (Fig. 2 top), but the relative contribution of the swing phase to the stride continues to increase (Fig. 2 bottom). At 0.833 m s$^{-1}$ *Sceloporus clarkii* has reached the crossover point seen in such plots (the 50:50 stance:swing ratio, Fig. 2 bottom), and with increasing speed, continued decrease in stance duration will produce a continuing increase in the relative proportion of the swing phase. Indeed, because the continued increase in proportion of the stride that is swing phase is due to the continuing decrease in the stance phase, the continuing decrease in the stride duration at higher speeds is solely due to the decrease in the stance phase. When the stance phase levels off, the stride duration will as well, and this appears to occur in trotting quadrupeds when the stance phase reaches a minimum of about 25% of the stride duration [e.g. Wisleder et al., 1990; Ashley-Ross, 1995]. This dynamic interaction of the swing and stance phases illustrates that scaling locomotory data to stride duration alone will likely lead to problematic functional interpretations, and comparisons across studies are difficult if not impossible without data on speed and stance/swing dynamics. Nonetheless, EMG data are often specifically scaled to stride duration to supposedly permit comparisons across species [e.g. Gatesy, 1994]. Ashley-Ross [1995] tried to address this problem in comparing salamander motor patterns to other vertebrates by scaling available comparative data to a standardized stride consisting of 75% stance: 25% swing. I would argue that scaling locomotory data to stance duration is a more appropriate and simple convention, because it relates information directly to the time when propulsive forces are transmitted to the substrate, and any motor modulation to increase speed has to be converted into propulsive forces. In addition, it is important for studies to gather

**Table 2.** Regression statistics for the effects of speed on motor patterns in *Sceloporus clarkii* based on means of three individuals moving at speeds between 0.303 and 1.070 m s$^{-1}$. The three timing variables were scaled to stance duration

<table>
<thead>
<tr>
<th>EMG variable</th>
<th>$R^2$</th>
<th>$F_{df=1,5}$</th>
<th>p$^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iliocostalis</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>onset</td>
<td>0.815</td>
<td>35.344</td>
<td>0.00034*</td>
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<tr>
<td>offset</td>
<td>0.002</td>
<td>0.003</td>
<td>0.960</td>
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<tr>
<td>duration</td>
<td>0.854</td>
<td>46.777</td>
<td>0.00013*</td>
</tr>
<tr>
<td>area</td>
<td>0.802</td>
<td>32.311</td>
<td>0.00046*</td>
</tr>
<tr>
<td>Caudofemoralis</td>
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<td></td>
</tr>
<tr>
<td>onset</td>
<td>0.934</td>
<td>113.376</td>
<td>0.00001*</td>
</tr>
<tr>
<td>offset</td>
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<td>0.280</td>
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<tr>
<td>duration</td>
<td>0.867</td>
<td>52.017</td>
<td>0.00009*</td>
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<tr>
<td>area</td>
<td>0.866</td>
<td>51.748</td>
<td>0.00009*</td>
</tr>
<tr>
<td>Flexor tibialis internus</td>
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</tr>
<tr>
<td>onset</td>
<td>0.033</td>
<td>0.271</td>
<td>0.616</td>
</tr>
<tr>
<td>offset</td>
<td>0.803</td>
<td>60.561</td>
<td>0.00005*</td>
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<tr>
<td>duration</td>
<td>0.808</td>
<td>33.64</td>
<td>0.00041*</td>
</tr>
<tr>
<td>area</td>
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<td>202.077</td>
<td>0.00001*</td>
</tr>
<tr>
<td>Femorotibialis</td>
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<tr>
<td>onset</td>
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<td>85.999</td>
<td>0.00001*</td>
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<td>duration</td>
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<td>0.00202*</td>
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<tr>
<td>area</td>
<td>0.818</td>
<td>36.073</td>
<td>0.00032*</td>
</tr>
<tr>
<td>Gastrocnemius</td>
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<td></td>
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</tr>
<tr>
<td>onset</td>
<td>0.149</td>
<td>1.404</td>
<td>0.270</td>
</tr>
<tr>
<td>offset</td>
<td>0.871</td>
<td>54.033</td>
<td>0.00008*</td>
</tr>
<tr>
<td>duration</td>
<td>0.878</td>
<td>57.728</td>
<td>0.00006*</td>
</tr>
<tr>
<td>area</td>
<td>0.930</td>
<td>92.613</td>
<td>0.00003*</td>
</tr>
</tbody>
</table>

$^*$ = Significant with muscle-wide sequential Bonferroni test.
and present stance, swing, gait, and speed (or stride distance and timing) data for comparative purposes.

**Motor Modulation in Sceloporus clarkii**

To illustrate speed changes in motor patterns in *Sceloporus clarkii* schematic modulation patterns were constructed for the five muscles studied (fig. 7). Data for the motor pattern variables for the two individuals trotting at 0.476 m s⁻¹ (n = 5 each) and 0.833 m s⁻¹ (n = 5 each) were pooled to construct and superimpose mean motor patterns for these two speeds scaled to stance duration. Statistically significant changes in going from the slower to faster speed (table 2) show how motor patterns were modulated with speed, and these changes are compared to mean timing of kinematic events for the same individuals at the same speeds (table 1). The extent and direction of change in variables (i.e. earlier vs. later onset or offset times, stated as % of stance in figure 7) that vary significantly with speed (table 2) are calculated from differences in the pooled means across these two speeds.

To set the stage for interpreting the modulation of motor control, I must first review the kinematic patterns that
change over this range of speeds. Analyses of the speed effects on angular kinematics across these two speeds show that none of the ranges or extents of angular movements of the limb joints and pelvis change significantly with speed [Reilly and DeLancey, 1997b]. Thus, the range of movement displayed by the limb and its joints remains the same as speed increases. The timing of joint movements scales with both stride duration [Reilly and DeLancey, 1997b] and stance duration (table 1), except that the timing of femoral retraction and knee flexion occur relatively earlier as speed increases. The relative timing of kinematic events is indicated by vertical arrows on figure 7, with shaded arrows for kinematics that do not change relative to stance duration and the black arrow shifting to the white arrow indicating the relatively earlier time to maximum femoral retraction. Thus, the overall kinematic picture is that limb joints and pelvis are moved through the same motions simply faster as speed increases, except for femoral retraction (and knee flexion) which occurs relatively faster.

The prediction then is that the femoral retractor (the caudofemoralis), which moves its joint relatively faster as speed increases, will have a different modulatory pattern than the other muscles which scale their movements with stance duration. This prediction is borne out in the limb muscles but not the iliocostalis muscle. The limb adductor (flexor tibialis), knee extender (femoro Tibialis), and plantar flexor of the ankle (gastrocnemius) have essentially identical patterns of motor modulation. These three muscles exhibit significant decreases in the offset time that result in significant decreases in burst durations with speed. Thus, there seems to be a consistent pattern that to move a joint simply faster through the same range of motion, the timing of muscle activity is modulated to shorten the burst duration by moving the offset earlier. The same pattern is observed in the anterior deltoid muscle when human arms move faster through the same range of motion [Flanders and Herrmann, 1992]. Interestingly, the knee extensor (femoro Tibialis) exhibits a small but significantly earlier difference in onset time with speed that makes sense, in that because knee flexion occurs relatively earlier, knee extension should start relatively earlier as well.

The femoral retractor exhibits a different pattern of modulation. The relative onset time for the caudofemoralis muscle is shifted significantly earlier, while in contrast to the other limb muscles, its offset does not change. Therefore, the caudofemoralis develops a relatively longer burst duration with increasing speed. Its relative onset time moves from just after to just before foot down, so that the muscle begins to shorten earlier in the stance phase or even before the foot hits the substrate. Interestingly, Reilly and DeLancey [1977a] describe that maximum femoral protraction occurs 5–10 ms before foot down, and therefore the femur begins to be retracted just before foot down (termed the terminal swing retraction phase). Thus, as speed increases, the relative onset of contraction in the caudofemoralis is modulated to move closer to the time of maximum femoral protraction, in effect causing the limb to begin to retract before foot down, thereby nullifying any decelerating (=braking) action at foot impact. Because the relative offset is constant, firing the muscle relatively earlier must be a primary modulatory timing mechanism to increase the speed of femoral retraction relative to stance phase.

The right side iliocostalis muscle bends the body to the right (concave to the right) which effectively rotates the pelvis to the left during the right side swing phase. This pelvic movement aids in swinging the right leg forward while moving the left leg backward. Thus, activity in the right iliocostalis is contributing to the duty cycle on the opposite side. Because the extent and timing of axial kinematics and pelvic rotation did not change with speed, except to speed up in concert with stance duration [Reilly and DeLancey, 1997b; table 1], it was expected to have a pattern similar to that of the flexor tibialis, femoro Tibialis and gastrocnemius. Instead it had a pattern identical to that of the caudofemoralis, with increase in duration produced by moving the onset time earlier. Given that the kinematics of the pelvis apparently do not change over this range of speeds, it is difficult to explain why the iliocostalis has the same pattern as a muscle that does produce a change in kinematics. One hypothesis is that the iliocostalis activity parallels that of the caudofemoralis to counteract the torque produced on the femur as it retracts relatively faster. I am confident in the pelvic rotation data, but it is possible is that real differences in axial kinematics were not detected by the variables used or by low statistical power in the kinematic analysis, or there may be some complex shift in axial waveforms that would change the dynamics of trunk bending. It is interesting, however, that both primarily axial muscles (iliocostalis and caudofemoralis) had similar patterns, while the three limb muscles shared a different but similar pattern. This may be due in part to possible differences in the physiological properties of axial vs. appendicular muscles.

The other primary mechanism to increase force over time is to increase the frequency of motor unit activation and/or the number of units firing, which will increase the amplitude of EMG signals. All of the muscles studied had significant and large increases in mean amplitude as speed increased (fig. 6). The magnitudes of these increases are indicated in figure 7 by the changes in the heights of the bars for each motor pattern, with percent increases in the mean...
amplitudes noted with plus signs. Similar increases in mean amplitude during trotting are seen in several limb muscles in rats (Roy et al., 1991; de Leon et al., 1994), the semitendinosus in cats (Smith et al., 1993), the gastrocnemius in turkeys (Roberts et al., 1997), and the iliofibrularis in desert iguanas (Jayne et al., 1990a). One interesting observation is that the limb muscles with significantly decreasing burst durations had the same order of magnitude increases in mean amplitude as did the axial muscles with significantly increased relative durations. This suggests that the muscles with shortening durations were exhibiting relatively greater overall EMG burst activity, which could be an indication that considerably more motor units were being recruited in these muscles.

Given this gross difference in EMG amplitude and the timing changes discussed above, the general question of how a muscle is modulated to act simply faster vs. relatively faster through the same range of motion can be answered for the limb muscles in Sceloporus clarkii. It appears that to modulate a muscle to move simply faster (scaled with stance duration), the offset is moved relatively earlier to decrease burst duration, while the area is ramped up to increase both the frequency of motor unit activation and the number of units recruited. Increasing the relative speed of action is accomplished by activating the muscle earlier, by increasing the duration of the burst, and by increasing the relative level of activation but not necessarily as much as in the former situation. Given the known kinematics of axial bending the iliofibularis does not fit this interpretation, and perhaps further study will show that this muscle is effecting a change in the timing of axial movements.

**Comparisons to Other Species**

As mentioned in the introduction, no other study has specifically addressed the effects of speed on quadrupedal locomotion within a gait and so comparisons to other species are difficult to make. Some speed related data have been presented for the stance phase EMG patterns of the semitendinosus muscle in trotting and galloping cats (Smith et al., 1993). However, their EMG data for within-trot speed changes are presented in real time, and the authors conclude that the stride duration, offset, and onset for this muscle do not change with speed (which is correct in real time). Using their stride duration data (none on stance duration is provided) and comments about the swing phase, their EMG data can be roughly scaled to stance duration to show that the relative onset and offset times actually increase dramatically with speed, resulting in a considerable increase in the burst duration as well. This increasing relative burst duration is similar to that of the caudofemoralis in lizards, but the burst moves in the opposite direction (later) in cats. These rough interpretations of the data for cats are difficult to use, given the lack of information on the specific function of the semitendinosus in cats, and the lack of limb joint kinematic data scaled to stance duration. Similarly, Roy et al. (1991) and de Leon et al. (1994) present EMG duration data for ankle and knee extensors in rats but do not provide any kinematic data from which the EMG durations can be correlated to stance timing to relate motor modulation to the duty cycle. In another study, Gatesy (1994) collected EMG data on four muscles in the guinea fowl during walking. Unfortunately, it is impossible to interpret the timing of muscle activity relative to the duty cycle, because EMG timing variables were measured relative to the onset time of the iliotrochantericus caudalis muscle (the only duty cycle muscle studied) rather than to some kinematic event, and again stance duration information is not provided. These studies illustrate that EMG patterns should be measured relative to a key kinematic reference point and scaled to stance duration to have interpretive and comparative utility in describing motor effects on speed. Therefore, at this time it is impossible to make any convincing conclusions about the generality of the modulatory patterns observed in Sceloporus clarkii relative to locomotor patterns in other vertebrates. These patterns do, however, have some relevance to two general hypotheses about EMG modulation with increasing speed based on studies of human limb movements.

The first is the hypothesis of the speed-sensitive strategy for single joints [Gottlieb et al., 1989; Corcos et al., 1989] that states that changing movement velocity alone is accomplished primarily by modulating the EMG amplitudes and that burst duration may or may not change with speed. The Sceloporus data and those from several other studies [e.g. Gielen et al., 1985; Buneo et al., 1994] suggest that modulation of burst duration may be more the rule in the speed-sensitive strategy than an option. If so, the strategy becomes considerably more complex, because increasing EMG intensity while decreasing burst duration, as in Sceloporus limb muscles and human arm movements [Flanders and Herrmann, 1992], has quite different consequences for force and torque production than if burst duration increases, as in a lizard's axial muscles. In addition, changes in duration can involve shifts in onset and/or offset times, or the entire burst may shift without changing duration. Thus, both activation intensity and timing may take on equal roles in modulating movement velocity, and there may be more than one way to attain the same change in limb speed.
The second hypothesis, the dual component hypothesis of muscle activation [Flanders and Herrmann, 1992], separates the amplitude of EMG scaling into a tonic component (generating forces to counteract gravity) and a phasic component (generating forces to increase speed). Early work on this hypothesis [Flanders and Herrmann, 1992] assumed that the duration of EMG patterns scaled with speed, but more recent work has shown that burst duration does not scale with speed and that different muscles exhibit different time scaling factors with speed [Buneo et al., 1994]. Although these studies did not quantify onset and offset times, they found changes in burst durations involving both increases and decreases with speed in different muscles, as I found in Sceloporus. Interestingly, one of the muscles I studied in Sceloporus, the flexor tibialis internus, acts primarily to adduct the limb during the stance phase. It would be considered to be primarily a 'tonic' muscle in terms of the dual component model, and its intensity would not increase because the magnitude of the intensity needed to counteract gravity would not increase with speed. This muscle had an increase in intensity comparable to that of the muscles that act primarily to retract the femur and extend the knee and foot, and, thus, it does not seem to fit the predictions of the two component model (or it is not primarily an adductor).

The data for Sceloporus clarkii demonstrate that the motor pattern modulation of the three limb muscles was the same as speed increased. Although, these muscles are innervated by different nerves [oburator nerve - flexor tibialis and femorotibialis; tibial nerve - gastrocnemius; Gadow, 1882] and lie one each over the three major joints of the limb, their similar motor patterns suggest that they share a common neural drive pattern as speed increases. This would suggest that the same central pattern generator controls limb adduction, knee extension, and ankle extension as speed increases. A single central pattern generator for knee and ankle extension has been hypothesized in rats based on similarities of motor patterns in similar muscles [de Leon et al., 1994]. The caudofemoralis and iliocostalis muscles, which are innervated by pre- and postpelvic spinal nerves, respectively, share a different motor pattern which suggests that a different central pattern generator drives these axial muscles. Because the iliocostalis is activated one half of a stride out of phase from the other right side muscle it must be 'wired' to the opposite side pattern generator. Without any data on the details of the neural circuitry in these muscles, these ideas remain speculative, but the motor patterns seem to suggest that at least two central pattern generators are involved in driving the increase in speed in these lizards.

One striking functional contrast is evident from a comparison of iliocostalis motor patterns in Sceloporus and the monitor lizard. As described above and in Reilly [1995], the iliocostalis in Sceloporus clarkii is active during the contralateral stance phase, and this is completely out of phase from that of Varanus salvator [Ritter, 1995] where this muscle contracts during the ipsilateral stance phase. This may indicate a fundamental difference in the way these two lizards use the axial column during locomotion. Furthermore, the fact that monitor lizards exhibit iliocostalis activity coincident with the ipsilateral hind limb stance phase suggests that there may be a fundamental difference in the neural circuitry controlling axial bending in the monitor lizard that would explain the phase shift in the function of this muscle in these two lizards. In fact, Ritter [1995] concludes that the iliocostalis in the monitor lizard is not used in lateral bending but instead functions in a postural role to stabilize the trunk against ground reaction forces. Given this functional difference in axial function and the striking differences in the positions of the crus and foot during locomotion in the Sceloporus [Reilly and DeLancey, 1997a, b] versus that in other lizards [Sukhanov, 1974; Rewcastle, 1983; Bruce Jayne, pers. commun.], I would predict that there may be several fundamentally different ways that lizards have evolved to run and that we have only begun to learn about the functional and anatomical diversity of quadrupedal and bipedal modes of locomotion in lizards.

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