The Journal of Experimental Biology 203, 1241–1252 (2000)
Printed in Great Britain © The Company of Biologists Limited 2000
JEB2588

THE EFFECTS OF TEMPERATURE ON THE BURIAL PERFORMANCE AND AXIAL MOTOR PATTERN OF THE SAND-SWIMMING OF THE MOJAVE FRINGE-TOED LIZARD *UMA SCOPARIA*

BRUCE C. JAYNE* AND MATTHEW W. DAGGY
Department of Biological Sciences, PO Box 210006, University of Cincinnati, Cincinnati, OH 45221-0006, USA
*e-mail: jaynebc@email.uc.edu

Accepted 31 January; published on WWW 9 March 2000

Summary

Although lateral axial bending is widespread for the locomotion of ectothermic vertebrates, the axial motor patterns of terrestrial taxa are known only for a limited number of species and behaviors. Furthermore, the extent to which the trunk and tail of ectothermic tetrapods have similar motor patterns is poorly documented. We therefore recorded the activity of the epaxial muscles in the trunk and tail of sand-swimming Mojave fringe-toed lizards (*Uma scoparia*) to determine whether this specialized behavior has features of the motor pattern that differ from those of diverse ectothermic vertebrates. Muscle activity during initial sand-swimming was a standing-wave pattern in the trunk and tail. Next, the hind limbs moved alternately and the caudofemoralis muscles and nearby axial muscle in the trunk and tail had similar long-duration electromyographic bursts, whereas the anterior trunk had shorter, more frequent electromyographic bursts. The final tail burial involved a traveling wave of posteriorly propagated axial muscle activity within localized regions of the tail. With increased temperature (from 22 to 40 °C), the mean frequencies of axial oscillations increased from approximately 7 to 21 Hz, and the greatest value (33 Hz) was nearly twice the maximal limb cycling frequency during running. The mean burial time at the lowest temperature (3.8 s) was nearly twice that for a 10 °C higher temperature. For the axial electromyograms, a decrease in temperature of 18 °C more than doubled the electromyographic and cycle durations, whereas the duty factors and intersegmental phase lags changed only slightly with temperature.

Key words: locomotion, muscle, motor pattern, lizard, *Uma scoparia*, electromyography, temperature.

Introduction

Ectothermic vertebrates commonly bend their axial structures laterally during both aquatic and terrestrial locomotion, and their rhythmic axial motor patterns have been exemplary experimental systems for gaining insights into the neural control and muscle function responsible for locomotor movements. For aquatic vertebrate locomotion, which has been studied extensively, the axial motor pattern is generally rhythmic, alternating, unilateral and posteriorly propagated in lampreys (Wallén and Williams, 1984), sharks (Bone, 1966) and diverse teleost fishes (Gillis, 1998b; Jayne and Lauder, 1995; Knower et al., 1999; Rome et al., 1992). For the terrestrial locomotion of ectothermic vertebrates, the limited data available for the walking of lizards and salamanders indicate that the trunk muscles are activated rhythmically in an alternating, unilateral, standing-wave pattern (Carrier, 1990; Frolich and Biewener, 1992; Ritter, 1996). Tail muscle activity has been documented for the running of one species of lizard only, *Gekko gecko* (Rumping and Jayne, 1996), in which there is a rhythmic alternating unilateral pattern that is propagated posteriorly and is similar to that of the epaxial muscles of snakes during terrestrial lateral undulation (Jayne, 1988). We use unilateral to refer to electromyographic activity that occurs on one side of the animal only at a particular longitudinal location; however, in the examples above, electromyographic activity often occurs simultaneously on the left and right sides at different longitudinal locations.

Previous electromyographic studies of lizards have examined the role of the axial muscles only during normal surface locomotion (Carrier, 1990; Ritter, 1995, 1996), but the axial structures can be important for additional locomotor behaviors. For example, several sand-dwelling species of lizards use evolutionarily derived locomotor behaviors collectively referred to as either sand-swimming or sand-diving (Arnold, 1994a,b; Stebbins, 1944). Sand-swimming occurs in sands that are too loose to permit tunnel formation, and axial oscillations of the trunk and tail are commonly a conspicuous part of the burying movements (Arnold, 1994a,b). The subject of the present study, the Mojave fringe-toed lizard (*Uma scoparia*), occurs only in habitats with fine, loose sand, and it commonly uses sand-swimming both to evade predators and to thermoregulate (Arnold, 1995; Jayne and Ellis, 1998; Stebbins, 1944). Thus, the sand-swimming of *Uma scoparia* provides an interesting opportunity to study a behavior with considerable ecological relevance and to determine whether this specialized mode of axial locomotion has a motor pattern fundamentally different from the axial undulatory behaviors of other ectothermic vertebrates.

Ectothermic vertebrates, especially terrestrial groups such as lizards, commonly encounter a wide range of temperatures, which can affect both locomotor performance and muscle function (Bennett, 1984, 1990). For example, *Uma scoparia* lives in desert sand dunes where habitat and body temperatures can undergo daily fluctuations of approximately 30 and 20 °C, respectively (Jayne and Ellis, 1998; Stebbins, 1944). Decreased temperature commonly decreases the maximal frequencies and speeds of movement as well as decreasing the rates of force production and relaxation of muscle (Bennett, 1984, 1990). Consequently, to attain the same locomotor speed at two different body temperatures, both aquatic and terrestrial ectothermic vertebrates increase the recruitment of faster muscle fibers at lower temperatures (Jayne et al., 1990a; Rome et al., 1984, 1992). However, the effects of temperature on aspects of motor pattern other than fiber type recruitment have been studied only minimally.

We studied the sand-swimming of *Uma scoparia* with three specific objectives. First, we determined the effects of temperature on the speed of burial in laboratory performance trials. Second, we characterized the motor pattern used during sand-swimming and compared it with the axial motor patterns of diverse types of ectothermic vertebrate locomotion. Finally, we determined the effects of temperature on the sand-swimming motor pattern.

Materials and methods

Experimental subjects

The six *Uma scoparia* Baird for which performance (N=5) and electromyographic (N=4; one of these individuals was not used in performance trials) data were analyzed quantitatively were captured in San Bernadino County, California (CA permit 802030-01), and had snout–vent and tail lengths ranging from 7.6 to 10.1 cm and from 6.2 to 8.8 cm, respectively. Three lizards had a small amount of regenerated tail tissue (<1 cm), but the tails of all other individuals were complete. We housed the lizards individually in sand-filled 38 l tanks with incandescent lights on a 12 h:12 h light:dark cycle, which created a thermal gradient that allowed the lizards to attain active daytime body temperatures (40–43 °C) similar to those found in the field (Jayne and Ellis, 1998). We fed the lizards crickets dusted with a vitamin supplement. The lizards were held in captivity for approximately 1 month before performance trials were started and for approximately 2 months before the electromyographic experiments.

Performance trials

We tested burying performance using 7 cm of fine sand in a container 30 cm×30 cm with 40 cm high walls of white foam board. We used a NAC HSV-500 high-speed camera operating at 500 images s^{-1} to videotape dorsal views of performance trials. Among different performance trials, we varied the body temperature of the lizards within 2 °C of a low (22 °C), middle (32 °C) and high (40 °C) temperature. We used a combination of photoflood lights above the sand and ice or water beneath the test chamber to obtain the desired lizard and sand temperatures. For the low and middle temperature trials, two 200 W incandescent lights provided illumination, whereas two 500 W incandescent lights provided illumination and heat for the high-temperature trials.

We tested performance on three days within a total period of six days such that the lizards had one or two days of rest between each day of testing. On each testing day, we conducted trials for each of the three temperatures for each of the five lizards. Within each day, the order of temperatures tested was randomized among different lizards, and the order of testing lizards within a day was also randomized among different testing days. To elicit sand-swimming from the lizards at the low and middle temperatures, we either moved a hand rapidly towards the lizard or lightly touched its hindquarters. During high-temperature trials, the lizards were not disturbed because disturbance often caused running rather than sand-swimming. Thus, the spontaneous high-temperature sand-swims were presumably a result of thermoregulation. If the walls of the chamber substantially impeded sand-swimming or if the lizard was out of view of the camera, we quickly dug up the lizard and repeated the trial. We analyzed data only from the first unimpeded sand-swim that was successfully videotaped (usually within 1–3 attempts). After a successful trial, the cloacal temperature of the lizard was immediately measured using a thermocouple. The average resting time between trials at different temperatures for a single individual within a testing day was 3 h.

Electromyography

General procedures for the construction and implantation of bipolar electrodes were performed as in Jayne (1988). Electrodes were constructed using 0.051 mm diameter poly-coated stainless-steel wire with approximately 0.5 mm of insulation removed from the recording end. The average length of the wire from the lizard to the probes of the recorder was 1.5 m. After securing individual electrodes to the lizard, all wires were glued together using plastic model cement to form a main cable that was attached to the dorsal surface of the lizard near the pelvis in a manner that did not encumber the movements of the lizard in the recording arena.

We used Halothane to anesthetize the lizards prior to implanting 14 bipolar electrodes. We placed electrodes in the epaxial muscles at seven standardized longitudinal sites spaced at intervals of 4–5 vertebrae within both the trunk and tail. The most posterior of three longitudinal locations in the trunk was 4–5 vertebrae anterior to the sacrum, and the most anterior of four standardized sites in the tail was 4–5 vertebrae posterior to the sacrum. For the four lizards for which electromyographic data were analyzed quantitatively, the average numbers of cervical, trunk and caudal vertebrae were 4, 19 and 28, respectively. We placed six electrodes in the left and right longissimus dorsi muscles at the three standard longitudinal locations within the trunk. We also placed five electrodes in the epaxial muscles of the tail, including four in the left side at each of the four standard longitudinal locations and one additional electrode in the right side at the most anterior site. We also implanted each of two additional electrodes in the right and left caudofemoralis muscles. For each animal, we implanted one additional electrode in variable locations. The positions of the electrodes were confirmed by both radiographs and dissection. To facilitate visualizing the movements involved in the burial process, we placed paint marks on the ankles and along the middorsal line of the tail approximately every 4–5 vertebrae.

We waited more than an hour after the lizards appeared alert and to have recovered fully from the anesthesia before we recorded electromyograms (EMGs). We recorded and analyzed electromyographic data from three sand-swims for each of four individuals at a high temperature (40 °C); from two of the individuals used at high temperature, we obtained five sand-swims at a low temperature (22 °C). We only analyzed data for sand-swims that were not along the walls of the arena and for which the lizards had the desired body temperature. For the EMG experiments, the methods for eliciting sand-swims, the illumination and the test arena were as in the high- and low-temperature performance trials.

We only recorded EMGs for the low and high temperature because we wanted to obtain EMGs for the lowest and highest frequencies of movement, and logistical difficulties such as keeping electrodes in place made trials at additional temperatures impractical. During preliminary experiments, we obtained a few high-temperature sand-swims by startling lizards, but the resulting movements and EMGs appeared qualitatively indistinguishable from those of the spontaneous sand-swims at the high temperatures. We also incidentally obtained some EMGs from lizards at intermediate temperatures. All these EMGs fell along a continuum of variation spanned by the EMGs analyzed quantitatively for the low and high temperatures. Thus, for our final electromyographic experiments, different motivations (startled *versus* spontaneous) for sand-swimming during the low- and high-temperature trials did not appear to cause any fundamental differences in movements or motor pattern.

We amplified EMGs 10 000 times using Grass P511k series amplifiers with high and low bandpass settings of 100 Hz and 10 kHz, respectively, and a 60 Hz notch filter. A TEAC XR-7000 FM data recorder operating at 9.5 cm s^{-1} recorded the analog EMGs. A NAC HSV-500 high-speed video camera recorded a dorsal view at 250 images s^{-1}. A 100 Hz square-wave signal was recorded simultaneously on the videotape and with the EMGs to permit synchronization. We used custom-designed software (written by Garr Updegraff, San Clemente, CA, USA; e-mail: garru@uci.edu, garru@fea.net) for converting analog data to digital data, digital filtering of data and quantifying electromyographic variables. All analog-to-digital conversions used a sampling rate of 8 kHz (Jayne et al., 1990b). We filtered the digital EMGs using a finite impulse response filter that reduced frequencies below 100 Hz to less than 10 % of the original amplitude. We measured the onset and offset times of EMGs to the nearest millisecond.

Data analysis

We quantified the performance of sand-swimming by determining the total burial time from when the lizard started to burrow with its head until the tail was completely buried or stopped moving. The tail burial time was the time from the beginning to the end of tail oscillations or until the tail was completely buried. We calculated the frequency of oscillations from the inverse of the difference between successive times of maximal lateral displacement for a particular longitudinal location.

For the performance data, we used two-way analyses of variance (ANOVAs) with temperature (three levels) as a fixed, crossed factor and individual (five levels) as a random, crossed factor. Consequently, the F-test for a significant main effect of temperature was the mean square of temperature divided by the mean square of the temperature × individual interaction term. For these and all other analyses, the criterion for statistical significance was $P<0.05$.

We relied primarily on five quantities to characterize motor pattern. The duration of EMGs was the difference between the times of onset and offset of activity. Cycle duration was the difference between the times of successive EMG burst onsets at the same site. Duty factor was the percentage of burst duration divided by cycle duration. We calculated intersegmental (IS) lag times (ms segment^{-1}) between the EMG onsets from adjacent ipsilateral longitudinal sites by subtracting the value for the more anterior site from that for the more posterior site and dividing the result by the number of intervening vertebral segments. To determine IS phase lag (% cycles segment^{-1}), we divided each IS lag time by cycle duration. Values of IS lag times and IS phase lags greater than zero indicate posterior propagation, and the inverses of these quantities are the speeds of propagation expressed in absolute and relative time scales, respectively.

To test statistically whether muscle activity was a standing or a traveling wave, we calculated the mean values of IS lag time for each longitudinal location within single trials, within each individual and for data pooled across all individuals within a particular temperature. If the 95 % confidence limits (CL) spanned zero, then we concluded that activity was a standing wave. If both 95 % CLs were either negative or positive, then we concluded that activity was a traveling wave that was propagated anteriorly or posteriorly, respectively. Regardless of whether confidence limits were calculated within individuals or for data pooled across individuals, identical conclusions emerged. For the sake of simplicity, we only report the confidence limits calculated for all observations pooled across all individuals (see Tables 1, 2). For the EMG experiments, we were unable to obtain a balanced experimental design wellsuited for an ANOVA because only two of the four individuals with EMGs at the high temperature also had EMGs at the low temperature. Consequently, to test for significant effects of temperature on motor pattern, we used two-tailed paired *t*-tests to compare the mean values of longitudinal sites pooled across all individuals for each stage of the motor pattern.

Results are presented as means ± S.E.M., unless stated otherwise.

Results

General description of movement

Sand-swimming consistently showed the following sequence of movements. Initially, the lizard took two or three steps backwards. The body of the lizard moved posteriorly relative to the limbs such that the knee and elbow were usually substantially anterior to the hip and shoulder, respectively. Immediately after maximal posterior movement of the body, the neck flexed ventrally (Fig. 1A), and the snout then entered the sand and began a series of rapid, relatively small-amplitude (usually less than 5 mm) lateral oscillations (Fig. 1B). These initial movements of the head and neck also included a small amount of twisting about the longitudinal axis. Immediately after the head had begun to oscillate, all the limbs were retracted simultaneously, propelling the lizard forward until the head and neck were completely covered with sand (Fig. 1C). For the remainder of sand-swimming, the fore limbs remained retracted and tucked against the sides of the trunk.

The left and right hind limbs moved alternately for 2–3 additional steps as the trunk continued to oscillate laterally until the pelvis and hind limbs were completely buried (Fig. 1D–G). For a while (approximately 0.5–1.0 s at the high temperature) after the limbs had been completely beneath the sand, hind-limb movements continued and contributed to pulling the tail forwards and into the sand. After limb movements had ceased, the amount of the tail not covered by the sand was highly variable.

Forward movement of the tail stopped abruptly, and the tail then began to undulate laterally, usually until it was completely covered. The lateral undulations of the tail were propagated posteriorly, and the tail was covered from anterior to posterior (Fig. 2). The tail was covered by sand as a result of its undulations and being depressed rather than being pulled forward.

Effects of temperature on performance

Increased temperature significantly decreased total burial time ($F_{2,8}$=21.9, P<0.001) and significantly increased the frequency of the first tail vibration ($F_{2,8}$=260, P<0.001). For an increase of approximately 10 °C from the low to the middle

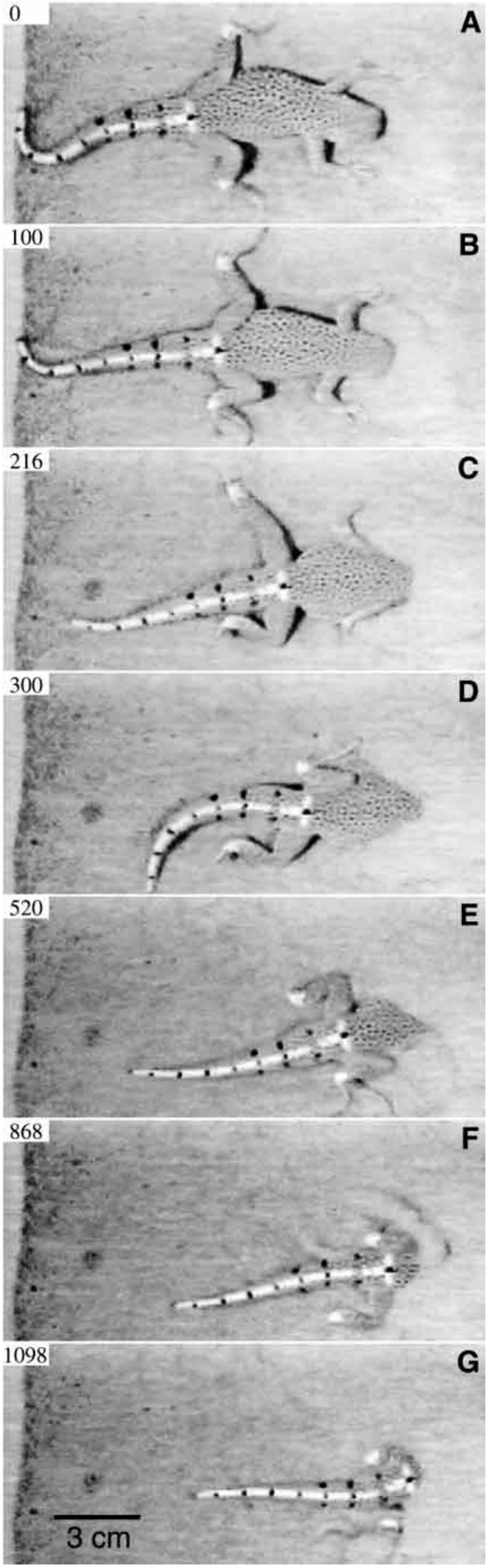

Fig. 1. (A–G) The progression of movements during sand-swimming prior to tail vibration for a *Uma scoparia* with a body temperature of 39 °C. Numbers in the upper left-hand corner of each panel indicate elapsed time (ms) from the beginning of the sand-swimming behavior. The white paint marks on the tail and ankles are clearly visible.

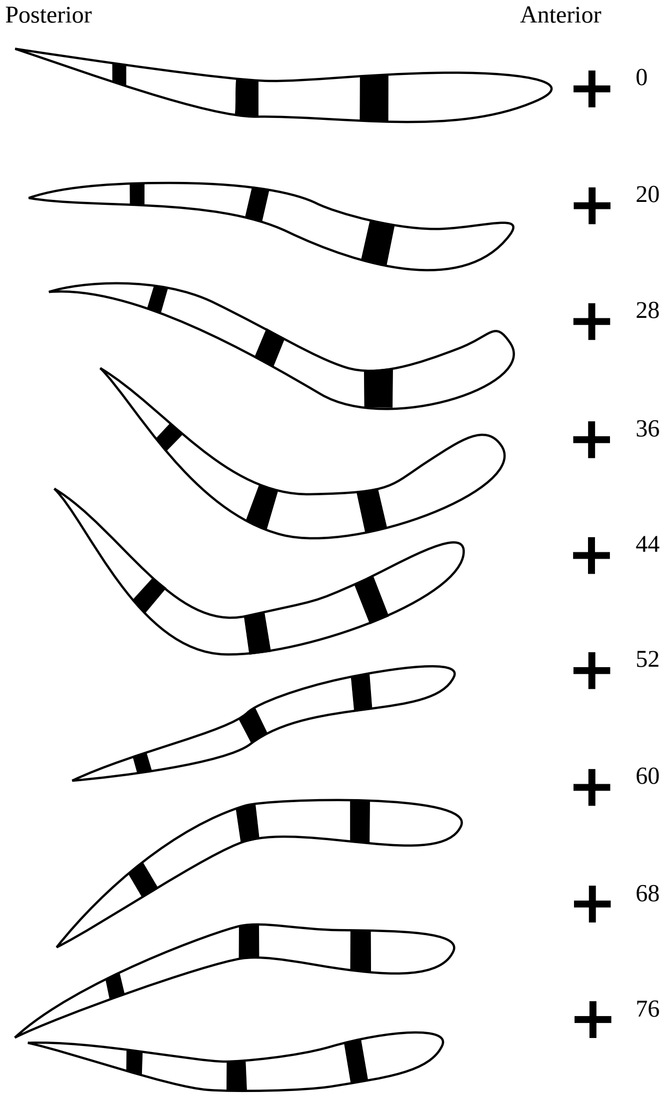

Fig. 2. Initial tail vibrations for a high-temperature trial (39 °C). The drawing is of a different individual from that depicted in Fig. 1. The plus sign indicates a fixed point of reference in the test chamber. Lateral flexion of the tail is propagated posteriorly, and the tail is covered with sand from anterior to posterior. Numbers indicate elapsed time (ms) from the beginning of tail vibration. The black bars are paint marks on the tail.

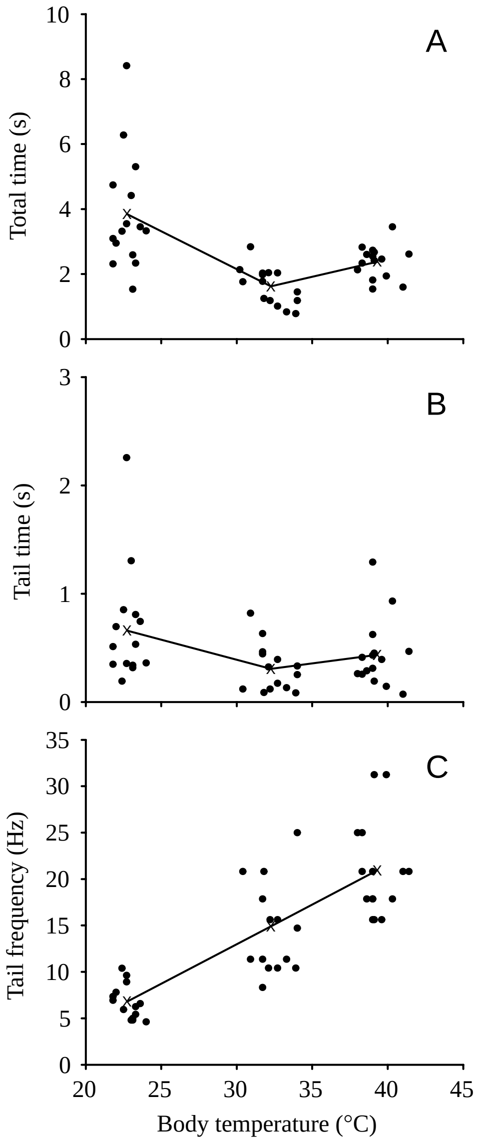

Fig. 3. The effects of body temperature on total burial times (A), tail burial times (B) and the frequencies of tail vibrations (C). The average temperatures for the low-, middle- and high-temperature categories were 22.7, 32.3 and 39.3 °C respectively. For each temperature category, the mean value of temperature and performance is indicated by a cross, and individual observations are indicated by filled circles.

temperature, mean (for 15 observations from five individuals) total burial time was approximately halved (3.84±0.46 *versus* 1.62±0.15 s), whereas the mean value at the high temperature (2.38±0.13 s) was slightly greater than that at the middle temperature (Fig. 3). Unlike the similar total burial times at the middle and high temperatures, the mean values of tail vibration frequency increased substantially with each successive increase in temperature (6.8±0.5, 14.9±1.3 and 20.9±1.3 Hz). The mean tail burial times for the low, middle and high temperatures were 0.69±0.14, 0.31±0.06 and 0.44±0.08 s, respectively, and these values did not quite differ significantly among the three temperatures ($F_{2,8}$=3.3, 0.05<P<0.10). Although all sand-swims ended with tail vibrations, the tail was occasionally partially exposed after the tail vibrations had ceased. The percentage of trials with complete burial at the low temperature (67 %) was less than that at both the middle (100 %) and high (85 %) temperatures. At the cold temperature, the mean value of tail burial time for incompletely buried tails (0.95±0.34 s, N=6) tended to be higher than that for completely buried tails (0.54±0.11 s, N=9), but this was not a statistically significant difference (two-tailed t=2.01, P=0.3).

Motor pattern

The overall motor pattern for the entire event of sand-

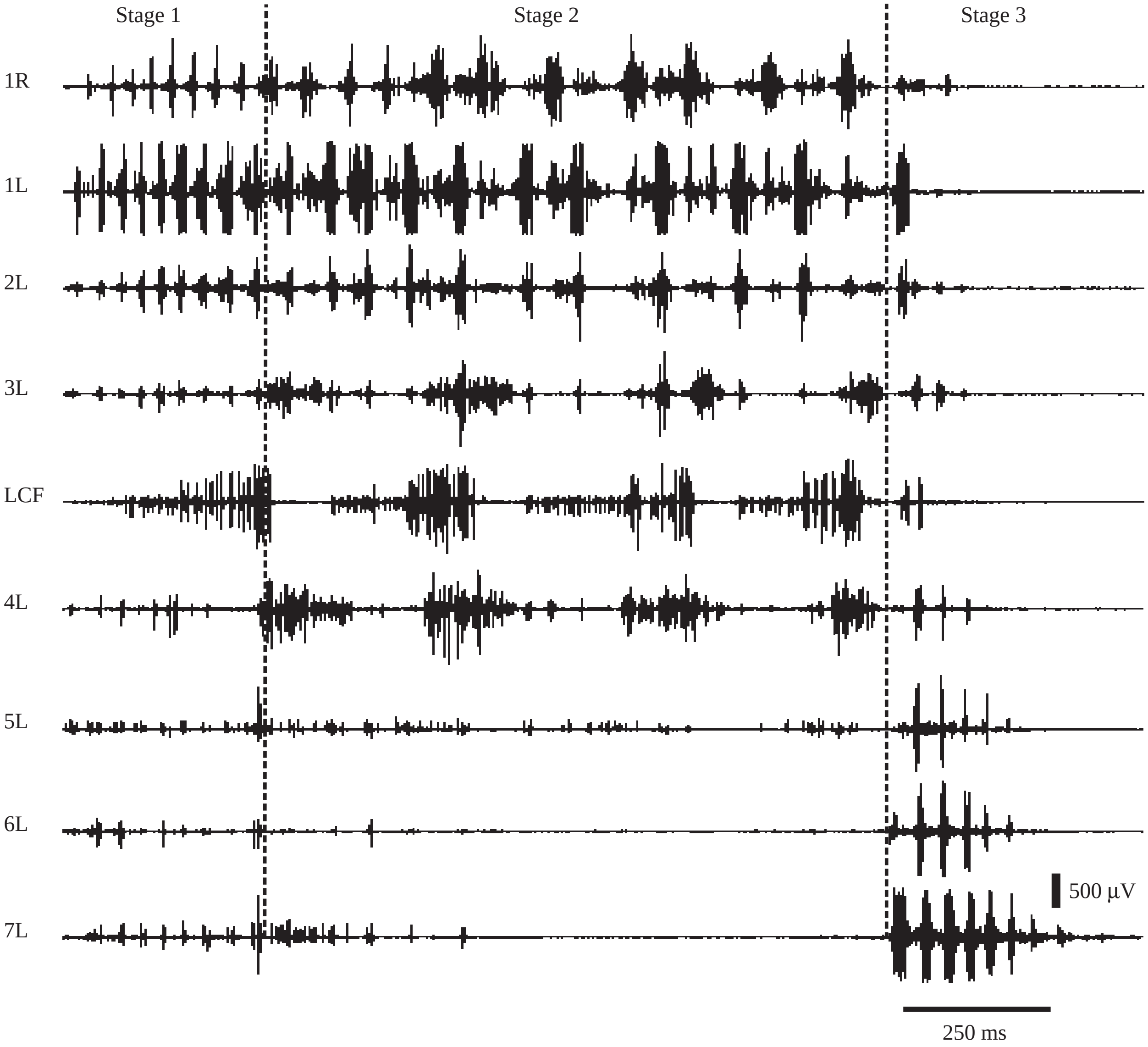

Fig. 4. The overall motor pattern for a sand-swim at high temperature (40.4 °C). To the left of each electromyogram, numbers indicate longitudinal positions (1 is the most anterior) for electrodes in epaxial muscles. L and R indicate the left and right sides of the body, respectively. LCF indicates the left caudofemoralis site. Sites 1R and 1L show an alternating pattern of right- and left-side activity. Stage 1 involves the initial penetration and burial of the head and neck as all the limbs are retracted simultaneously. During stage 2, the hindlimbs move alternately as the trunk moves forward and below the surface of the sand. During stage 3, none of the limbs moves as the exposed portion of the tail is buried using a series of rapid vibrations.

swimming had three distinct stages (Fig. 4). During the first stage, EMGs of the epaxial muscles had short burst and cycle durations (Table 1) and their amplitudes were greatest in the anterior trunk (Fig. 4). During stage 1, the intersegmental (IS) lag times of the epaxial EMGs in the trunk and tail were not significantly different from zero. For example, for the 12 high-temperature trials and data pooled across all four individuals and all observations, the mean lag times between sites 2 and 3 (N=100) and between sites 5 and 6 (N=83) were -0.04 ± 0.10 and 0.4 ± 0.12 ms segment^{-1} (means ± 95 % CL) respectively. Thus, the epaxial muscle activity in both the trunk and tail formed a standing wave (Fig. 5A). The stage 1 epaxial muscle activity was also rhythmic and unilateral, and alternated between the left and right sides at a single longitudinal location (Figs 4, 5A). The three epaxial trunk sites had an average of approximately eight EMG bursts during stage 1 (Fig. 6A). In contrast, the caudofemoralis muscles had a single long-duration burst (Fig. 4) that occurred simultaneously on the left and right sides as the limbs retracted and helped to push the head into the sand during stage 1.

During stage 2, the epaxial muscles in the anterior trunk had several (more than 10) EMG bursts (Fig. 6B) of relatively high amplitude and intermediate duration (Fig. 4; Table 1), whereas the posterior tail sites often had little or no muscle activity. The epaxial muscle sites in the trunk (site 3) and tail (site 4) that were nearest to the pelvis generally had 3–4 EMG bursts of

Table 1. *Epaxial electromyographic variables at different longitudinal locations for each stage (see Fig. 4) of sand-swimming at the high (40 °C) and low (22 °C) temperatures*

	EMG duration (ms)		Cycle duration (ms)		Duty factor (% cycle)	
Site	High	Low	High	Low	High	Low
Stage 1	*t*=13.6, *P*<0.001, d.f.=6		*t*=16.7, *P*<0.001, d.f.=6		*t*=–0.2, *P*=0.88, d.f.=6	
1	16.1±1.0 (113)	46.2±6.2 (33)	49.9±5.4 (100)	128±19 (29)	33.8±2.2 (100)	34.8±3.6 (29)
2	16.1±1.0 (110)	37.3±6.6 (23)	46.4±3.0 (95)	99±11 (15)	34.0±1.7 (95)	32.6±5.5 (15)
3	15.5±1.1 (105)	38.7±6.6 (20)	46.4±4.0 (87)	115±20 (14)	33.2±2.0 (87)	32.7±6.1 (14)
4	12.4±1.4 (39)	30.4±6.7 (14)	42.1±4.2 (23)	93±18 (6)	30.6±4.4 (23)	31.7±8.8 (6)
5	15.3±1.0 (98)	32.6±4.3 (27)	51.9±7.2 (80)	112±16 (22)	31.4±2.1 (80)	27.9±3.8 (22)
6	14.2±1.1 (83)	35.0±4.7 (23)	48.0±7.0 (61)	105±16 (18)	29.6±2.3 (61)	32.0±3.8 (18)
7	14.1±1.2 (68)	35.4±6.4 (19)	47.0±9.4 (46)	114±20 (13)	31.0±2.3 (46)	31.1±4.8 (13)
Stage 2	*t*=2.54, *P*=0.085, d.f.=3		*t*=3.6, *P*=0.037, d.f.=3		*t*=0.06, *P*=0.95, d.f.=3	
1	29.0±1.9 (108)	65.0±11.0 (39)	114±8 (104)	253±30 (37)	28.4±2.7 (97)	30.5±3.9 (37)
2	27.3±1.8 (98)	70.0±9.0 (28)	114±9 (89)	245±37 (26)	28.0±3.2 (84)	30.9±5.5 (26)
3	191±21 (37)	410±58 (12)	365±36 (26)	772±198 (8)	57.3±4.8 (26)	56.6±8.9 (8)
4	168±24 (15)	355±99 (7)	315±35 (10)	677±274 (5)	55.9±5.8 (10)	51.1±8.4 (5)
Stage 3	*t*=17.5, *P*<0.001, d.f.=6		*t*=17.2, *P*<0.001, d.f.=4		*t*=–3.7, *P*=0.010, d.f.=4	
1	11.9±4.4 (7)	36±19.6 (5)	43.1±38.9 (2)	–	30.6±16.5 (2)	–
2	10.3±1.4 (23)	36.3±6.0 (6)	35.7±3.2 (15)	–	31.1±6.2 (15)	–
3	13.3±1.7 (30)	31.2±3.9 (9)	38.9±3.2 (20)	131±41 (4)	37.2±4.7 (20)	24.7±13.3 (4)
4	14.0±2.3 (31)	31.4±5.2 (14)	41.9±3.6 (21)	118±25 (8)	35.6±4.7 (21)	30.6±9.7 (8)
5	14.6±1.1 (76)	36.5±3.5 (37)	38.9±1.8 (62)	108±8 (31)	37.9±2.4 (63)	34.5±2.5 (31)
6	14.8±1.0 (97)	39.6±4.0 (45)	37.4±1.5 (84)	107±7 (39)	39.8±2.1 (85)	36.7±2.9 (39)
7	14.1±0.8 (121)	36.6±3.2 (45)	36.8±1.4 (108)	105±7 (39)	38.8±1.5 (109)	35.3±2.3 (39)

Values are means ± 95 % confidence limits. *N*, the total number of observations, is given in parentheses.

Sites 1–3 and 4–7 are in the trunk and tail, respectively.

For each variable and stage, values of *t* and *P* are for two-tailed *t*-tests on pairs of mean values for each temperature among all sites.

For the high and low temperatures, the numbers of sand-swims and individuals were 12 and 4 and 5 and 2, respectively.

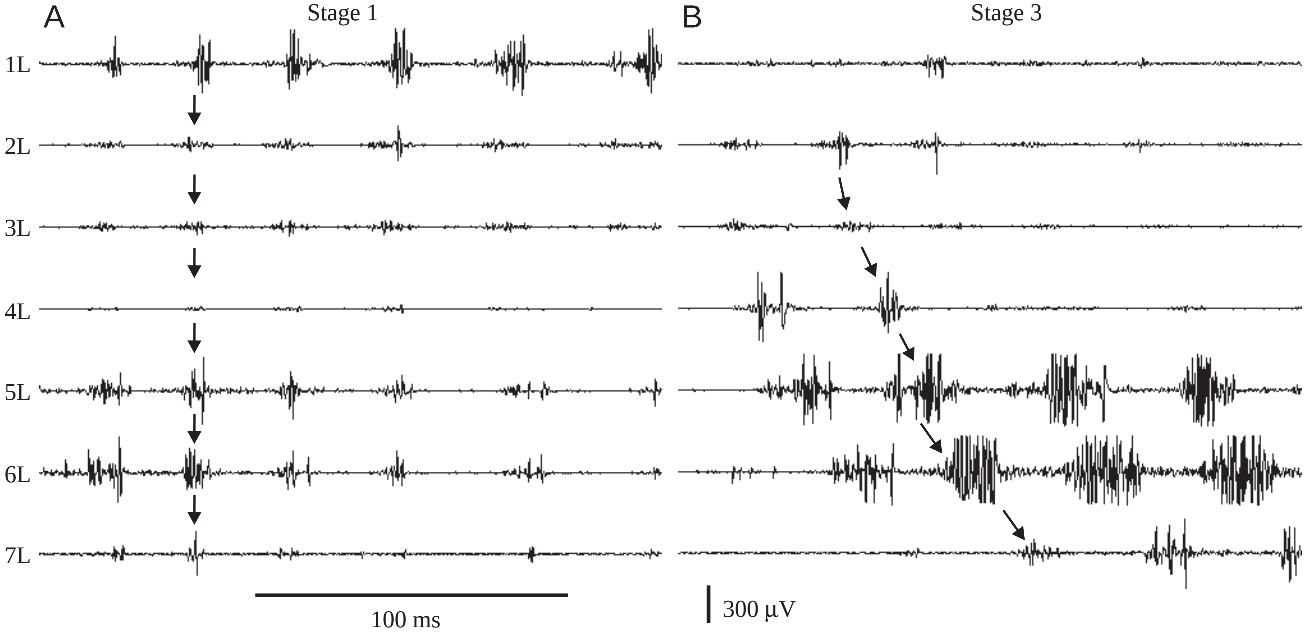

Fig. 5. Motor patterns for stage 1 (A) and stage 3 (B) at high temperature (40 °C). Abbreviations for the locations of electromyographic electrodes are as in Fig. 4. The arrows show the standing (A) and posteriorly propagated (B) waves of epaxial muscle activity.

relatively long duration (Table 1) and high amplitude (Fig. 4). The onset and offset times of the epaxial muscles at sites 3 and 4 were nearly synchronous during stage 2 (Fig. 4), and activity at these sites overlapped considerably with high-amplitude activity of the ipsilateral caudofemoralis muscle (Fig. 4).

Stage 3 was characterized by EMGs with short duration (Table 1) and high amplitude for the tail epaxial muscles and little regular activity in either the trunk epaxial muscles or the caudofemoralis muscles (Fig. 4). The absence of substantial activity in the caudofemoralis muscles suggests that the hind legs do not move significantly while they are beneath the sand during this final stage of the behavior. The EMGs of the tail epaxial muscles were rhythmic and alternated in a unilateral fashion between the left and right sides (Fig. 5B). The EMGs of the posterior trunk and entire tail had IS lag times significantly greater than zero, indicating a posterior propagation of activity (Table 2). From anterior to posterior, the values of IS lag times generally increased (Table 2); hence, the speed of propagation decreased posteriorly. The speed of EMG propagation in the posterior portion of the tail site was so slow that sites only five vertebrae apart had EMGs that were nearly half a cycle out of phase (Fig. 5B). The number of epaxial EMG bursts in the anterior tail during stage 3 was generally two or three, increasing steadily to more than 10 bursts for the most posterior sites (Fig. 6C). In the caudal epaxial muscles, activity began and ended earliest for the most anterior sites, and the first and last bursts for more posterior sites occurred progressively later (Figs 4, 5B). Within a single longitudinal location, the amplitude of the caudal epaxial EMGs was commonly small for the initial burst or two and, after increasing to a maximum, the amplitude declined progressively for the last few bursts (Figs 4, 5B, 7). Consequently, since the frequency of the EMGs from the caudal epaxial muscle was nearly constant, the amplitude and frequency of the epaxial EMGs were commonly decoupled.

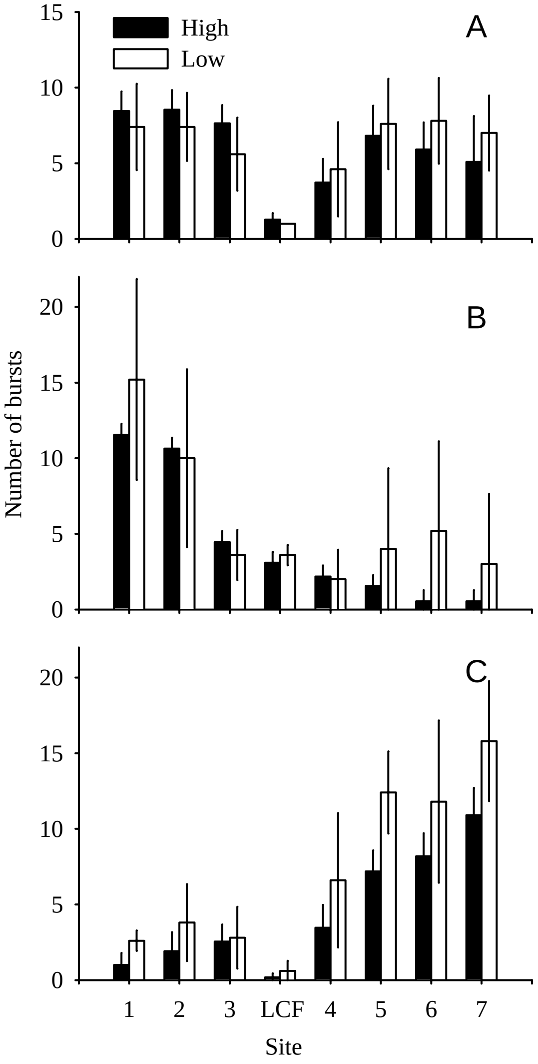

Fig. 6. Mean values (±95 % confidence limits) for the numbers of left-side electromyographic bursts during stage 1 (A), stage 2 (B) and stage 3 (C) at high (*N*=12) and low (*N*=5) temperatures. Abbreviations for the locations of electromyographic electrodes are as in Fig. 4. All sites were usually active during stage 1. During stage 2, the tail sites often lacked measurable muscle activity, whereas during stage 3 the trunk sites often lacked measurable activity.

Effects of temperature on motor pattern

For a decrease in temperature of approximately 18 °C, the EMG burst and cycle durations more than doubled for all sites in all stages (Table 1; Fig. 7), and the IS lag times increased significantly (Table 2). The numbers of epaxial EMG bursts (Fig. 6) during stage 1 (two-tailed paired t=0.3, P=0.78, N=7 sites) and stage 2 (t=1.9, P=0.95, N=7) were unaffected by changing temperature. The number of epaxial EMG bursts during stage 3 increased significantly (t=4.3, P=0.005, N=7), and the most conspicuous differences between the high- and low-temperature values were for the caudal sites. Duty factor during stages 1 and 2 did not change significantly with decreased temperature, whereas during stage 3 both duty factor (Table 1) and IS phase lags (Table 2) showed small but statistically significant decreases. Thus, characterizing motor pattern on a relative time scale (% cycles) was not sufficient to explain all the effects of decreased temperature.

Discussion

Effects of temperature on performance

The mean total burial time at the middle *versus* the low temperature largely conformed to the expectation that physiological rate processes approximately double with an increase of 10 °C in body temperature (for a review, see Bennett, 1985). However, the burials at the high temperature were unexpectedly slow, which might be explained either by the behavior of the lizards or by the mechanism of burrowing.

The unexpectedly slow sand-swims at the high experimental temperature may indicate that themoregulatory sand-swims are slower than those used to escape from a threat. In the field study of Jayne and Ellis (1998), *U. scoparia* with active body temperatures ranging from 34 to 45 °C ran to escape from a

Table 2. *Intersegmental variables for epaxial muscle activity at pairs of adjacent, ipsilateral longitudinal sites during stage 3 (see Fig. 4) of sand-swimming at the high (40 °C) and low (22 °C) temperatures*

	Intersegmental lag time (ms segment^{-1})		Intersegmental phase lag (% cycles segment^{-1})	
Sites	High	Low	High	Low
	t=2.83, P=0.037, d.f.=5		t=4.92, P=0.016, d.f.=3	
2–1	0.17±1.04 (6)	1.08±1.54 (5)	0.65±5.66 (4)	–
3–2	0.50±0.27 (21)	0.69±0.97 (4)	1.49±1.27 (15)	–
4–3	0.99±0.21 (25)	2.01±0.93 (9)	2.32±0.45 (18)	1.29±1.71 (4)
5–4	1.71±0.67 (30)	2.74±0.65 (13)	4.15±1.53 (29)	2.32±0.54 (7)
6–5	1.52±0.18 (76)	3.56±0.75 (37)	4.05±0.49 (68)	3.05±0.46 (31)
7–6	2.35±0.41 (95)	6.26±1.34 (43)	6.37±0.98 (89)	5.62±1.17 (39)

Values are means ± 95 % confidence limits. *N*, the total number of observations, is given in parentheses.

Sites 1–3 and 4–7 are in the trunk and tail, respectively.

Positive values indicate posterior propagation.

For each variable, values of *t* and *P* are for two-tailed *t*-tests on pairs of mean values for high and low temperatures among all sites.

For the high and low temperatures, the numbers of sand-swims and individuals were 12 and 4 and 5 and 2, respectively.

threat, and escape paths usually only terminated in a sand-swim when the escape destination lacked a burrow opening. Thus, in the wild, running may be the preferred escape tactic for animals near their preferred active body temperature, but whether *U. scoparia* switch to sand-swimming as the primary means of escape at colder temperatures remains to be determined.

The mechanical properties of sand may also change for the low frequencies (<10 Hz) of the lizard vibrations at the coolest temperature. Arnold (1995) suggested that the rapid (30 Hz) vibrations of warm *U. scoparia* liquefy sand and hence facilitate the burying process. Vibratory pile drivers commonly use frequencies of 10–40 Hz to facilitate penetration, and the predominant frequency of sand is between 30 and 40 Hz (Carter and Seed, 1988). Furthermore, our preliminary experiments with vibrating cylinders suggest that frequencies near or below 10 Hz were either insufficient or minimally effective for liquefying the dry, loose sand that we used, whereas frequencies above 15 Hz quickly caused liquefaction. Quantifying the exact frequencies that induce liquefaction poses a considerable technical challenge (Carter and Seed, 1988) and is beyond the scope of the present study. However, if the temperature-induced range of tail vibration frequencies of *U. scoparia* bracketed a threshold frequency for the liquefaction of sand, then this might explain a large improvement in performance from the low to the middle temperature with less change in performance from the middle to the high temperature.

Comparisons of vertebrate axial motor patterns

Axial muscle activity for sand-swimming in *U. scoparia* was rhythmic and alternated unilaterally between the left and right

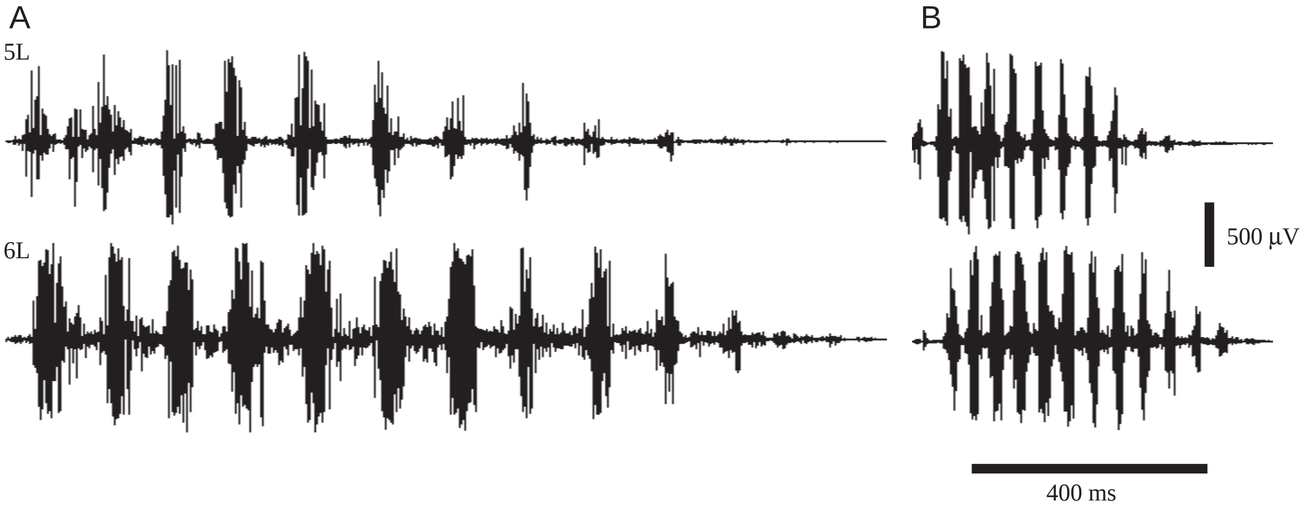

Fig. 7. Electromyograms from a single individual at low (A) and high temperature (B) during stage 3. Abbreviations for the locations of electromyographic electrodes are as in Fig. 4. See Tables 1 and 2 for statistical analyses of the significant effects of temperature on motor pattern.

sides; these characteristics are similar to those found nearly universally in previous studies of steady aquatic and terrestrial locomotion of diverse fishes, amphibians and reptiles (Bone, 1966; Carrier, 1990; Frolich and Biewener, 1992; Gillis, 1998b; Jayne, 1988; Rome et al., 1992; Jayne and Lauder, 1995; Knower et al., 1999; Ritter, 1996; Wallén and Williams, 1984). The axial motor patterns for steady swimming of ectothermic vertebrates also uniformly have posterior propagation, whereas those for the terrestrial locomotion of limbed ectothermic vertebrates often have a standing-wave pattern. However, unlike the standing-wave patterns described for the trunk muscles of walking lizards and salamanders (Carrier, 1990; Frolich and Biewener, 1992; Ritter, 1996), the tail muscles of the lizard *Gekko gecko* have posteriorly propagated activity during running (Rumping and Jayne, 1996). Thus, for *U. scoparia*, recording EMGs from several sites allowed us to determine whether the activity of the axial muscles was propagated and how it varied between or within the trunk and tail.

The trunk and tail of *U. scoparia* had both standing and traveling patterns of epaxial muscle activity during different stages of sand-swimming (Fig. 5). Perhaps the loose sand behaves similarly to a very viscous fluid and thus elicits an ancestral, aquatic axial motor pattern with a traveling wave. If fluid-like behavior of the environment were sufficient to elicit an aquatic motor pattern, then one might expect a traveling wave of activity when most of the trunk was submerged in sand. However, the axial muscles had a standing-wave pattern of activity during stage 2. Two unique features of stage 3 were a traveling wave of muscle activity and an absence of limb movements. Thus, limb movements might be an important cue for eliciting a standing-wave pattern of activity during the first two stages.

The extent to which axial motor patterns vary longitudinally within vertebrates depends on the species, the behavior and the variables used to quantify motor pattern. For example, the duty factors for the axial muscles of swimming fishes commonly decrease from anterior to posterior in species with large longitudinal differences in surface area (Jayne and Lauder, 1995; Rome et al., 1992; Knower et al., 1999; van Leeuwen et al., 1990). In contrast, during the swimming of cylindrically shaped species such as lampreys (Wallén and Williams, 1984), eels (Gillis, 1998b; Grillner and Kashin, 1976) and snakes (Jayne, 1988), duty factors have little longitudinal variation similar to those of *U. scoparia* during stages 1 and 3 (Table 1). In contrast, during stage 2, the epaxial muscles near the pelvis of *U. scoparia* had duty factors and EMG durations substantially greater than those of the anterior trunk; in addition, the rhythmic activities of the axial muscles associated with trunk vibration and hind-limb movement simultaneously had different frequencies (approximately 10 and 3 Hz, respectively). The epaxial EMG durations of autotomized tails of the lizard *Gekko gecko* increase posteriorly in a continuous fashion while cycle duration remains constant (Rumping and Jayne, 1996) and, hence, this longitudinal variation differs fundamentally from the longitudinal discontinuity in axial motor pattern observed in *U. scoparia*.

The presence and absence of axial muscle activity also varied longitudinally in *U. scoparia*. For example, during stage 2, high-amplitude activity in the trunk commonly occurred without activity in the posterior half of the tail, and within the tail during stage 3, activity of the posterior sites continued substantially after activity had ceased in the more anterior sites. The axial muscle activity of steadily swimming fishes is often propagated from the front to the back of the vertebral column. However, in the eel, only posterior axial muscles are recruited at very slow speeds (Gillis, 1998b). Thus, the ability of *U. scoparia* to activate only a portion of its axial muscles segments is not unique, but has rarely been observed for the rhythmic locomotor behaviors of other ectothermic vertebrates.

Intersegmental phase lags of swimming fishes often show little apparent longitudinal variation (Grillner and Kashin, 1976; Grillner et al., 1991; Jayne and Lauder, 1995), but IS phase lags of swimming snakes tend to decrease posteriorly (Jayne, 1988). In contrast, during stage 3 of sand-swimming of *U. scoparia*, IS phase lags increased posteriorly (Table 2). For propagated EMGs, dividing duty factor by IS phase lag (when significantly different from zero) gives an estimate of the number of adjacent ipsilateral muscle segments that have simultaneous electrical activity. For sites 2–6 in *U. scoparia*, these estimates for the high temperature were 24, 16, 9, 9 and 6 segments, respectively, and for sites 3–6 at the low temperature values were 24, 13, 10 and 6 segments, respectively. Muscle force production lags behind electrical activity, and the times of relaxation are slower than those of force generation (Marsh and Bennet, 1985). Consequently, the longitudinal region of simultaneous force production in adjacent muscle segments would be longer and shifted anteriorly relative to the region of simultaneous EMGs, and decreased temperature would exaggerate the difference between the longitudinal extent of force and EMGs. The *U. scoparia* used in our experiments averaged 19 trunk and 28 tail vertebrae. Therefore, despite propagation of muscle activity between sites 2 and 3 during stage 3, all the ipsilateral trunk muscle segments had activity with substantial temporal overlap. In contrast to the trunk, propagated EMGs within the tail involved so few adjacent ipsilateral muscle segments that, from its base to its tip, the tail may simultaneously have EMGs on the left, right and left sides. Similar to the trunk muscle activity of *U. scoparia*, several species of diverse fishes have rapid propagation of EMGs compared with their duration such that a substantial fraction of the locomotor cycle has simultaneous activity of all the ipsilateral axial muscle segments from the head to the tip of the tail (Jayne and Lauder, 1995; Rome et al., 1992; Knower et al., 1999; van Leeuwen et al., 1990).

The effects of environment on axial locomotion have been widely studied for aquatic and terrestrial locomotion of ectothemic vertebrates (Carrier, 1993; Cohen, 1988; Frolich and Biewener, 1992; Gillis, 1998a; Jayne, 1988; Ritter, 1995), but previous EMG data for burrowing are available only for larval lampreys. During initial burrowing, the axial motor pattern of the unburied portion of a lamprey is grossly similar to that of rapid swimming, whereas later axial muscle activity has irregular, long-duration bursts of intense muscle activity that flex the body and pull it beneath the sand (Paggett et al., 1998). Compared with rapid swimming, the axial muscle activity of initial burrowing of the lamprey has significantly greater duty factors but similar intersegmental phase lags (Paggett et al., 1998). Like the sand-swimming of *U. scoparia*, localized longitudinal regions of axial muscle activity occur during the final portion of lamprey burrowing (Paggett et al., 1998). The frequency of EMG bursts of initial burrowing in lampreys is only slightly greater than that of rapid swimming (Paggett et al., 1998). In contrast, the highest axial frequencies observed for sand-swimming *U. scoparia* (approximately 33 Hz) were nearly twice those of the limbs during running at maximal speed (Irschick and Jayne, 1999).

Gatesy and Dial (1996) defined a locomotor module as an integrated anatomical region of the musculoskeletal system that acts as one unit during locomotion, and they suggested that decoupling of muscle activity in two anatomical regions implies more than one locomotor module. Since basal tetrapods such as salamanders move using both their appendages and lateral axial undulations, Gatesy and Dial (1996) suggested that these taxa have one locomotor module consisting of the trunk, tail and appendages. A striking finding for the axial muscle activity during the sand-swimming of *U. scoparia* was the extent to which activity varied among localized longitudinal regions including: (i) the anterior trunk (and probably the neck), (ii) trunk and tail segments within approximately five segments of the pelvis, and (iii) the tail and perhaps even subsets of the tail segments. In addition, the hind limbs moved while the front limbs remained still. Thus, *U. scoparia* may have five or more (more than three axial and two appendicular) locomotor modules. Clarifying the extent to which the versatility in the locomotor use of the axial and appendicular structures is unique to *Uma* and closely related taxa will require additional comparative data. However, this versatility and diversity of motor pattern in *U. scoparia* have not been described previously for any salamander or lizard and suggest two alternatives: either several locomotor modules evolved somewhere within the clade of lepidosaurian reptiles or perhaps the common ancestor of the lepidosaurs and theropods had more locomotor modules than previously supposed.

The effects of temperature on motor pattern

Decreasing the speed of undulatory swimming in fishes generally increases the absolute durations of events in axial motor patterns with little effect on duty factor and intersegmental phase lag (Gillis, 1998a; Grillner and Kashin, 1976; Jayne and Lauder, 1995). Thus, our null expectation was that decreased temperature would increase variables describing motor pattern in units of absolute time but not those using a relative time scale (% cycle). The most conspicuous temperature-induced changes in motor pattern did vary in this manner (Fig. 7; Tables 1, 2), similar to stretching the EMGs horizontally along the time axis. With decreased temperature, the stage 3 duty factors showed a statistically significant but small decrease (grand means of 35.9 % and 31.0 %). The most apparent effect of decreased temperature on a relative timing variable was for stage 3 IS phase lag. Shorter IS phase lags indicate the activation of more adjacent ipsilateral muscle segments simultaneously, which might help to compensate for lower rates of force production at lower temperatures. The effect of temperature on IS phase lag in *U. scoparia* is also noteworthy because this relative timing variable is often nearly constant during undulatory swimming of fishes (Grillner and Kashin, 1976; Grillner et al., 1991; Jayne and Lauder, 1995). At the lower temperature during stage 3, the greater number of cycles of activity might also compensate for each cycle having less mechanical effect in burying *U. scoparia*.

Another system involving axial vibrations for which the effects of temperature have been quantified is the defensive tail-shaking of rattlesnakes, for which the rattling frequency at 35 °C (85 Hz) is approximately four times that at 10 °C (Schaeffer et al., 1996). Thus, although the high-temperature frequencies of the *U. scoparia* axial muscle activity (approximating 30 Hz) are rapid, they are exceeded by those of some other highly specialized vertebrate systems. The tailshaker muscle of rattlesnakes has only one motor unit potential per cycle at all temperatures (Schaeffer et al., 1996), whereas the much more complex epaxial EMGs of *U. scoparia* suggest recruitment of several motor units. Despite having single motor unit potentials, the frequency of EMGs in the rattlesnake is sufficiently fast for the muscle to exhibit an unfused tetanus rather than simple twitches (Rome et al., 1996). For the isometric twitches of fast glycolytic fibers from a limb muscle of the desert iguana *Dipsosaurus dorsalis*, the times from the beginning of force production to half-relaxation are 21 and 103 ms at temperatures of 40 and 20 °C, respectively (Marsh and Bennett, 1985). In the light of the cycle durations of sand-swimming muscle activity, which are approximately 50 and 100 ms at high and low temperatures, respectively, an unfused tetanus seems especially likely for the epaxial muscles of *U. scoparia* at lower temperatures.

NSF grants IBN 9514585 with a Research Experience for Undergraduates Supplement and BIR 9217409 to B.C.J. provided support for research and for the acquisition of the high-speed video system. D. Irschick and F. Nelson provided helpful comments on an earlier version of the manuscript. C. Luke and J. Andre facilitated the field portion of this research, which used the Sweeney Granite Mountains Desert Research Center. D. Scovill of the Mojave National Preserve and J. Brode of California Fish and Game provided timely processing of our permit applications.

References

Arnold, E. N. (1994a). Do ecological analogues assemble their common features in the same order? An investigation of regularities in evolution, using sand-dwelling lizards as examples. *Phil. Trans. R. Soc. Lond. B* **344**, 277–290.

Arnold, E. N. (1994b). Investigating the origins of performance advantage: adaptation, exaptation and lineage effects. In *Phylogenetics and Ecology* (ed. P. Eggleton and R. Vane-Wright), pp. 123–168. London: Academic Press.

Arnold, E. N. (1995). Identifying the effects of history on adaptation: origins of different sand-diving techniques in lizards. *J. Zool., Lond.* **235**, 351–388.

Bennett, A. F. (1984). Thermal dependence of muscle function. *Am. J. Physiol.* **247**, R217–R229.

Bennett, A. F. (1985). Temperature and muscle. *J. Exp. Biol.* **115**, 333–344.

Bennett, A. F. (1990). The thermal dependence of locomotor capacity. *Am. J. Physiol.* **259**, R253–R258.

Bone, Q. (1966). On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. Mar. Biol. Ass. UK* **46**, 321–349.

Carrier, D. R. (1990). Activity of the hypaxial muscles during walking in the lizard *Iguana iguana*. *J. Exp. Biol.* **152**, 453–470.

Carrier, D. R. (1993). Action of the hypaxial muscles during walking and swimming in the salamander *Dicamptodon ensatus*. *J. Exp. Biol.* **180**, 75–83.

Carter, D. P. and Seed, H. B. (1988). *Liquefaction Potential of Sand Deposits under Low Levels of Excitation.* Berkeley: College of Engineering University of California at Berkeley.

Cohen, A. H. (1988). Evolution of the vertebrate central pattern generator for locomotion. In *Neural Control of Rhythmic Movements in Vertebrates* (ed. A. H. Cohen, S. Rossignol and S. Grillner), pp. 129–166. New York: Wiley-Liss.

Frolich, L. M. and Biewener, A. A. (1992). Kinematic and electromyographic analysis of the functional role of the body axis during terrestrial and aquatic locomotion in the salamander *Ambystoma tigrinum*. *J. Exp. Biol.* **162**, 107–130.

Gatesy, S. M. and Dial, K. P. (1996). Locomotor modules and the evolution of avian flight. *Evolution* **50**, 331–340.

Gillis, G. B. (1998a). Environmental effects on undulatory locomotion in the American eel *Anguilla rostrata*: kinematics in water and on land. *J. Exp. Biol.* **201**, 949–961.

Gillis, G. B. (1998b). Neuromuscular control of anguilliform locomotion: patterns of red and white muscle activity during swimming in the American eel *Anguilla rostrata*. *J. Exp. Biol.* **201**, 3245–3256.

Grillner, S. and Kashin, S. (1976). On the generation and performance of swimming in fish. In *Neural Control of Locomotion* (ed. R. M. Herman, S. Grillner, P. S. G. Stein and D. G. Stuart), pp. 181–201. New York: Plenum Press.

Grillner, S., Wallén, P. and Brodin, L. (1991). Neuronal network generating locomotor behavior in lamprey: circuitry, transmitters, membrane properties and simulation. *Annu. Rev. Neurosci.* **14**, 169–199.

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.

Jayne, B. C. (1988). Muscular mechanisms of snake locomotion: an electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). *J. Morph.* **197**, 159–181.

Jayne, B. C., Bennett, A. F. and Lauder, G. V. (1990a). Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. Exp. Biol.* **152**, 101–128.

Jayne, B. C. and Ellis, R. V. (1998). How inclines affect the escape behaviour of a dune dwelling lizard, *Uma scoparia*. *Anim. Behav.* **55**, 1115–1130.

Jayne, B. C. and Lauder, G. V. (1995). Red muscle motor patterns during steady swimming in largemouth bass: effects of speed and correlations with axial kinematics. *J. Exp. Biol.* **198**, 1575–1587.

Jayne, B. C., Lauder, G. V., Reilly, S. M. and Wainwright, P. C. (1990b). The effect of sampling rate on the analysis of digital electromyograms from vertebrate muscle. *J. Exp. Biol.* **154**, 557–565.

Knower, T., Shadwick, R. E., Katz, S. L., Graham, J. B. and Wardle, C. S. (1999). Red muscle activation patterns in yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas during steady swimming. *J. Exp. Biol.* **202**, 2127–2138.

Marsh, R. L. and Bennett, A. F. (1985). Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis*. *J. Comp. Physiol.* B **155**, 541–551.

Paggett, K. C., Gupta, V. and McClellan, A. D. (1998). Adaptive variations of undulatory behaviors in larval lamprey: comparison of swimming and burrowing. *Exp. Brain Res.* **119**, 213–223.

Ritter, D. (1995). Epaxial muscle function during locomotion in a lizard (*Varanus salvator*) and the proposal of a key innovation in the vertebrate axial musculoskeletal system. *J. Exp. Biol.* **198**, 2477–2490.

Ritter, D. (1996). Axial muscle function during lizard locomotion. *J. Exp. Biol.* **199**, 2499–2510.

Rome, L. C., Choi, I., Lutz, G. and Sosnicki, A. (1992). The influence of temperature on muscle function in the fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. *J. Exp. Biol.* **163**, 259–279.

Rome, L. C., Loughna, P. T. and Goldspink, G. (1984). Muscle fiber activity in carp as a function of swimming speed and muscle temperature. *Am. J. Physiol.* **16**, R272–R279.

Rome, L. C., Syme, D. A., Hollingsworth, S., Lindstedt, S. L. and Baylor, S. M. (1996). The whistle and the rattle: the design of sound producing muscles. *Proc. Natl. Acad. Sci. USA* **93**, 8095–8100.

Rumping, J. M. and Jayne, B. C. (1996). Muscle activity in autotomized tails of lizard (*Gekko gecko*): a naturally occurring spinal preparation. *J. Comp. Physiol.* A **179**, 525–538.

Schaeffer, P. J., Conley, K. E. and Lindstedt, S. L. (1996). Structural correlates of speed and endurance in skeletal muscle: the rattlesnake tailshaker muscle. *J. Exp. Biol.* **199**, 351–358.

Stebbins, R. C. (1944). Some aspects of the ecology of the iguana genus *Uma*. *Ecol. Monogr.* **14**, 313–332.

van Leeuwen, J. L., Lankeet, M. J. M., Akster, H. A. and Osse, J. W. M. (1990). Function of red axial muscles of carp (*Cyprinus carpio*): recruitment and normalized power output during swimming in different modes. *J. Zool., Lond.* **220**, 123–145.

Wallén, P. and Williams, T. L. (1984). Fictive locomotion in the lamprey spinal cord *in vitro* compared with swimming in the intact and spinal animal. *J. Physiol., Lond.* **347**, 225–239.