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Biomechanical Modeling of Forelimb Adduction in the Eastern Mole, *Scalopus aquaticus*

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Senior Thesis

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Approved by:

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Table of Contents

Figures and Tables

Abstract

The hypertrophied musculoskeletal system driving adduction of *Scalopus aquaticus*'s forelimb supports the locomotion of these burrowing subterranean mammals. Due to the excessive bulk of the major muscles contributing to this action, it was thought that this particular species may represent a rare case of a mammalian species with a greatly enhanced force contribution from each muscle, correlating with a reduction in the potential for the forelimb to adduct at a high velocity. By assessing the lever ratios of five significant muscles contributing to forelimb adduction, combined with vector analyses for the angles of these muscles' insertions, a model was established that represents all significant sources of force reduction along the path of transduction in the forelimb of *Scalopus aquaticus*.

Introduction

The heavily developed musculature contributing to forelimb adduction in many fossorial mammals makes these species excellent for establishing a model of large-scale forelimb force transduction. Previous studies (Powell et al. 1984) have given rise to models that use measurements of muscle mass, angle of pinnation, fiber length, muscle density and specific tension to calculate the maximum tetanic force that an individual mammalian muscle dissected from a cadaver can produce. Our goal was to establish a model that would produce an accurate value of the muscle's effective force by accounting for major reductions along the path of force transduction. To quantify these sources of reduction, a vector analysis of all force components parallel and perpendicular to the forelimb's line of action was conducted and the lever mechanics of each contributing muscle were analyzed.

The underground environment is thought to be responsible for many of the derived characteristics of fossorial mammals. Examples include the hypertrophied mallei and the unique orientation of the stapes found in certain species of golden moles (family Chrysochloridae) (Mason 2003), which are thought to be adaptations that contribute to the detection of seismic vibrations. The atrophied eyes of mole rats represent another example (Fong et al. 1995). These small, skin-covered eyes are functionally blind and seem to be the result of evolutionary forces on a structure that is essentially useless in an underground habitat. Similarly, the eastern mole, *Scalopus aquaticus,* has evolved a hypertrophied musculoskeletal system that contributes to forelimb adduction. While some species rely upon gnawing or lateral undulations to burrow underground, *Scalopus* *aquaticus* uses its forelimbs and shovel-like paws to tunnel through the soil (Yalden 1966).

The eastern mole utilizes its forelimbs to dig away at the earth while burrowing by thrusting its forelimbs into undisturbed soil and 'swimming' through the soil using alternate rowing movements. In contrast, the hindlimbs are primarily used to kick loose dirt behind the animal and to help propel its body forward once the path has been cleared. This heavy reliance on the muscles used for adduction of the forelimbs demonstrates the need for the disproportionate muscle mass between the two sets of limbs. Dissection of the shoulder girdle of the eastern mole revealed five large muscles that functioned in forelimb adduction. It was surmised that this relatively large group of muscles would make an excellent model for force transduction through a mammalian limb. Data collected from thirty eastern mole carcasses were used to determine the maximum tetanic tension that each muscle could produce; all functional reductions of this theoretical force along the path of transduction were then be assessed in order to quantify the maximum realized force produced by the forelimb.

Materials and Methods

Thirty eastern mole cadavers were obtained from a nuisance animal trapper in southern Ohio with the use of commercial traps. Relatively little damage occurred to the trunk and forelimbs. The weight of the mole was recorded along with the total and snout-vent length.

Muscle Dissection

The dissection began with the removal of the skin by making an incision along the dorsal midline and pulling the skin from the carcass. After removing the excess adipose tissue from the right flank, the body of the latissimus dorsi was separated from the underlying muscles using a blunt probe. Once cleared from the rest of the specimen, a scalpel was used to sever the latissimus dorsi at its origin from the neural spines of the posterior thoracic vertebrae and the lumbodorsal fascia (Whidden 2000). The latissimus dorsi's fused insertion with the teres major was divided by carefully lifting the latissimus dorsi away from the teres major at a 120° angle while splitting the fascicles that contribute to each of the two muscles. This separated the fused insertion into two distinct units: the superficial portion, which attaches the latissimus dorsi, and the deep portion, which connects the teres major. Both of these muscles insert on the teres tubercle of the humerus.

Upon dissection, the pectoralis profundus and pectoralis superficialis pars posticus muscles appeared to be a single unit. Two previous studies failed to identify these muscles as being separate (Campbell 1939; Reed 1951), whereas a more recent study recognized them as independent (Whidden 2000). Due to the near fusion of these muscles and the similarity of their actions, it was assumed that they act as a single functional unit, and dissections and calculations were carried out as such (beginning here, this pair is referred to as the pectoral complex). To remove the pectoral complex, an incision was made along the right lateral side of the sternum to separate the pectoral muscles at their origin (Whidden 2000). A blunt probe was used to begin the separation of the pectoral complex from the rib cage, and then a scalpel was used to sever tendons connecting this muscle to the ribs. Once the posterior portion of the pectoral complex was freed, an incision was made ventral to the right clavicle along the border between this muscle complex and the pectoralis superficialis pars anticus. The muscle was then completely removed from the body by severing it at its insertion on the lateral side of the pectoral crest of the humerus (Whidden 2000).

The teres major had to be teased away from the subscapularis, supraspinatus, and the miniscule infraspinatus with a blunt probe. The teres major has a long origin along the entire teres fossa and on the lateral surface of the vertebral border of the scapula (Whidden 2000; Campbell 1939); this muscle was separated from the scapula with great care due to the complexity and extent of its origin. The insertion of the teres major on the teres tubercle of the humerus could then be revealed and detached, freeing the muscle.

The body of the subscapularis was lifted with a blunt probe to expose its origin at the subscapular fossa on the scapula (Whidden 2000; Campbell 1939). After severing the origin, the muscle was pulled away from the scapula to better expose this muscle's dual neighboring tendons that insert upon the lesser tuberosity of the humerus.

Once these muscles were removed from the carcass, they were wetted with a cloth saturated in water. The wet weights were measured using a digital scale. The forelimbs of the carcass were set to a fixed position pointing anterior to the body, as they would be located prior to adduction of the forelimbs (i.e. at the onset of a power stroke). The carcass was then placed in a 10% formaldehyde solution for at least 48 hours.

Forelimb Dissection

During the second portion of the contralateral shoulder girdle dissection, inlever measurements were identified from the point of articulation of the humeral head with the clavicle to the points of insertion for each of the aforementioned muscles. The origin of the latissimus dorsi was severed, and using a scalpel, the scapula was cleared of all other muscles attaching it to the dorsal surface of the ribcage. The origin of the pectoral complex was freed by making an incision along the lateral surface of the sternum. Another incision was made ventral to the clavicle to fully separate the pectoral complex from the pectoralis superficialis pars anticus. The space between the pectoral complex and the ventral ribcage was cleared using a blunt probe and scalpel. With the four relevant muscles still attached to the left forelimb, a scalpel was used to fracture the middle of the clavicle, freeing the left forelimb from the rest of the carcass.

The distal remnant of the clavicle was removed from the humeral head using a scalpel and forceps to sever the ligaments holding it in place. With the head of the humerus exposed, three measurements were made with digital calipers from this articulation point to the insertion of each muscle for inlever distances. The two insertions of the subscapularis were measured as two distinct units and were later averaged for calculations. Three measurements for outlever distance were also obtained from the articulation point of the humeral head to the tip of the middle digit of the left forelimb. The muscles removed from this dissection were stored in water until further analysis could be conducted, usually within 48 hours.

Muscle Fiber Data Collection

Initially, Powell's guinea pig model (1984) was mimicked as a preparatory step for muscle fiber data collection. Connective tissue was digested using an acid bath prior to the determination of fiber lengths and angle of pinnation. However, this method of soaking the individual muscles in 0.4 M sodium phosphate buffer solution prior to and following a 15-20% sulfuric acid bath (2-7 days) proved to be much too harsh for the smaller muscles of the mole. Even when the strength and duration of the sulfuric acid bath was drastically reduced, the muscles were too degraded to adequately collect data.

It proved to be more effective to examine the muscles after fixation alone, eliminating the buffer and acid baths. The muscle fibers could easily be visualized, and because they were fully intact, measurements could be recorded more efficiently. Angle of pinnation of the muscle fibers was determined by placing a protractor overtop the muscle and comparing the angle at which the fibers ran to the muscle's line of action between the origin and insertion. A total of ten measurements of angle of pinnation were recorded for each muscle from proximal, medial, and distal regions.

Individual muscle fiber length was not measured. Loeb et al. (1987) demonstrated that motor units tend to function simultaneously along the length of a muscle due to the distribution of the branches of alpha motor neurons, which innervate the motor unit's individual fibers. Due to this, the 'functional' fiber length was measured from the start of a series of fibers at a tendon to the end of the fiber series with the use of digital calipers. When these fiber series wrapped around the muscle or followed a line not parallel to the muscle, a series of fibers was teased from the muscle to allow for measurement of the effective fiber length.

Data Analysis

It was predicted that a majority of the lost force between muscle contraction and limb adduction was the result of either the deviance of the angles of muscle insertion from the forelimb's line of action or a decrease in the lever ratio (L_I/L_O) for these muscles. The vast majority of forelimb adduction force was assumed to primarily occur from the contributions of five muscles: the teres major, the latissimus dorsi, the subscapularis, the pectoralis superficialis pars posticus, and the pectoralis profundus (the latter two muscles were analyzed as a single functional unit due to their close proximity and lack of clear separation).

A modified version of Powell's model (1984) was used to determine the maximum tetanic tension of each individual muscle. Cross-sectional area can be calculated from the muscle's mass, the angle of pinnation of the myofibers(θ), the functional fiber length (Loeb et al. 1987), and muscle density using the following formula:

Eq. 1:

$$\mathrm{CSA} = \frac{\text{Muscle Mass} \bullet \mathrm{COS}(\theta)}{\text{Fiber Length} \bullet \text{Muscle Density}}$$

Mammalian muscle density was assumed to be ~$1.0\mathrm{g} \bullet \mathrm{cm}^{-3}$ (Close 1972; Spector et al. 1980). Specific tension, assumed to be $22.5\ \mathrm{N} \bullet \mathrm{cm}^{-2}$(Close 1972; Spector et al. 1980) was used to estimate the maximum tetanic force of a muscle (F_I) from its CSA:

Eq. 2:

$$F_I = \mathrm{CSA} \bullet \text{specific tension}$$

Results

The average values of the data that were collected from individual muscles is listed in Table 1. Force values for each muscle were calculated and listed here as well. Calculations were performed to represent overall muscle force (Force In) using equations 1 and 2. Muscle forces in the horizontal and vertical plane (Force In, X and Force In, Y, respectively) were calculated using equations 1 and 2, followed by vector analyses that account for the angle of the muscle's insertion. From these values, contributions to forelimb force from each muscle in both the horizontal and vertical planes (Force Out, X and Force Out, Y, respectively) were calculated by accounting for force vectors as well as each muscle's lever ratio (see equation 4).

Table 1. Average data values collected from the Latissimus Dorsi, Teres Major, Subscapularis, and Pectoral Complex of *Scalopus aquaticus*.

Muscle Data (Mean Values)				
	Latissimus Dorsi	Teres Major	Subscapularis	Pectoral Complex
In-Lever (mm)	12.63	11.39	8.30	10.52
Lever Ratio	0.34	0.32	0.23	0.28
Muscle Mass (g)	0.6	2.0	0.6	1.3
Angle of Pinnation (°)	7.6	14.7	12.2	17.0
Cross Sect. Area (cm^2)	0.00511	0.0358	0.0112	0.0239
Effective Fiber Length (mm)	53.14	24.72	23.07	24.13
Force In (N)	0.115	0.806	0.254	0.538
Force In, X (N)	0.113	0.796	0.248	0.522
Force Out, X (N)	0.0385	0.244	0.0551	0.147
Force In, Y (N)	0.0219	0.126	-0.0527	-0.130
Force Out, Y (N)	0.00748	0.0387	-0.0117	-0.0367
Muscle Insertion Angle (°)	11	9	12	14

Data and calculations that were not specific to a particular muscle have been listed in Table 2. The mean total forelimb force in the horizontal plane was found from the sum of the individual muscle contributions, both vertically and horizontally. This model predicts that the average eastern mole would be able to generate 0.4851N posteriorly with the adduction of one forelimb. With these four muscle complexes contracting simultaneously, a forelimb would generate only 0.0022N dorsally, a significantly lower value than the horizontal force component.

Table 2. Data and calculations from *Scalopus aquaticus* that were not specific to a particular muscle group.

Project Data (Mean Values)	
Total Force, X (N)	0.4851
Total Force, Y (N)	-0.0022
Angle of Forelimb Adduction (°)	-0.317
Mole Mass (g)	112.8
Sum Forelimb Muscle Mass (g)	9.0
Forelimb Muscle Mass (% Body Mass)	8.06
Outlever (mm)	37.26
Average Lever Ratio	0.29

Figure 1. ***Scalopus aquaticus*** **(Dorsal)**

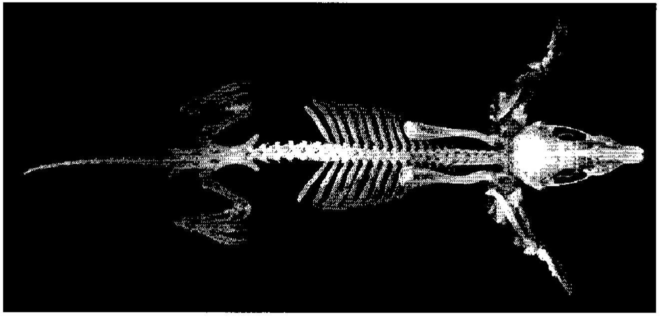


Figure 2. ***Scalopus aquaticus*** **(Ventral)**

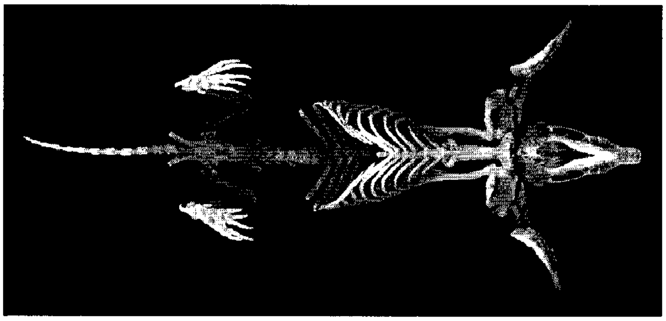


Figure 3. *Scalopus aquaticus* (Rostral)

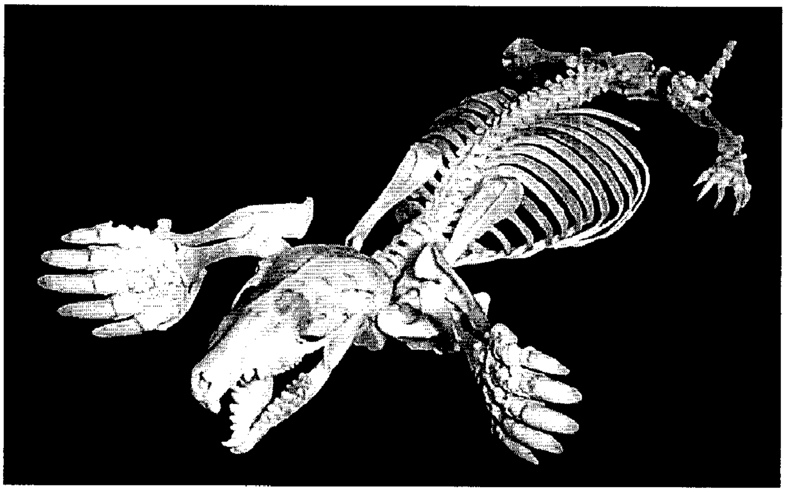


Figure 4. Humerus (Medial)

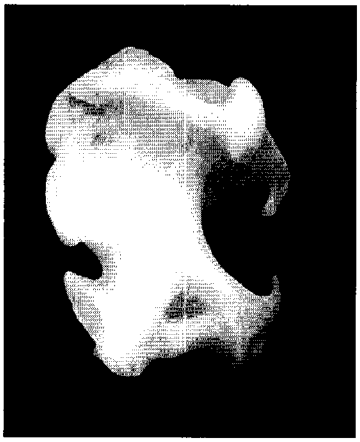
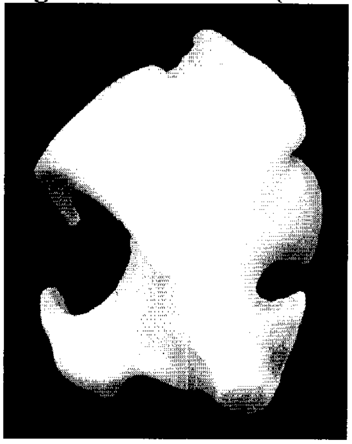


Figure 5. Humerus (Lateral)



Discussion

By analyzing the lever ratio (L_I / L_O) for each muscle that significantly contributes to forelimb adduction, we were able to draw several conclusions about the biomechanics that *Scalopus aquaticus* employs to burrow. Lever mechanics demonstrate that lower lever ratios will increase the velocity of a limb at the expense of force, while higher lever ratios emphasize the force of a limb while reducing its speed. The following equations display these principles mathematically by relating the out-lever and in-lever arms with their respective velocities (V_O and V_I) and their respective forces (F_O and F_I) (Liem et al. 2001):

Eq. 3: $$V_O = \frac{V_I \bullet L_O}{L_I}$$

Eq. 4: $$F_O = \frac{F_I \bullet L_I}{L_O}$$

Many adaptations allow animals to exploit this relationship to increase the efficiency of their individual methods of locomotion. For example, ungulates walk on the tips of their digits, giving them a distinctive advantage for running, because the lengthened out-lever distance of their limbs increases maximum velocity. Most primates, having plantigrade feet, have a higher lever ratio and are slower runners than ungulates. Humans and other animals are sometimes able to achieve a higher velocity while running simply by raising up on their toes to lower the lever ratio of their legs (Liem et al. 2001).

Longer limbs are another characteristic of fast running animals, but an increase in length is typically not uniform throughout the leg. Many fast running animals, horses for example, rely upon unguligrade locomotion combined with a drastically elongated zeugopodium and autopodium (Liem et al. 2001). The distal portion of the limb is often proportionally longer than the proximal region, because the shank and forearm house bones and tendons but not nearly as much of the cumbersome muscle mass that is characteristic of the thigh and brachium. By minimizing the bulk of a lengthened limb, an animal can achieve increased velocity without greatly increasing its kinetic energy (KE) demand:

Eq. 5: $$KE = 1/2 \bullet \text{Limb Mass} \bullet (\text{Velocity})^2$$

Our study of *Scalopus aquaticus* demonstrated that its forelimbs had evolved in such a way that these velocity-enhancing mechanisms are virtually absent. Although the manus of *S. aquaticus* was found to be disproportionately lengthened, it did not resemble the characteristic elongation of the ungulate zeugopodium for several reasons. The lengthened manus of the eastern mole did not correlate with a similar elongation of the pes. Also, the manus displayed its greatest development by width rather than by its length. Indeed, *Scalopus aquaticus* has a prepollex, a radial sesamoid element lateral to the thumb, that gives the manus the appearance of having six digits (Sánchez-Villagra and Menke 2005; Prochel 2006). Some researchers have proposed that this element is a burrowing adaptation, providing the hand with increased stability and width (Yalden 1966). The lengthened out-lever arm of the mole appears to be a coincidence of the evolution of its broadened manus, rather than an adaptation for velocity. Equations 3 and 5 indicate that any gain in forelimb velocity resulting from a slightly lengthened out-lever arm would be diminished by the increased mass of the substantial eastern mole manus.

The humerus of the eastern mole is highly developed for muscle attachment. In his study of shoulder anatomy of the family Talpidae, Campbell found that the humerus of the true moles (subfamilies Talpinae and Scalopinae, including *S. aquaticus*) was the most prominently developed (1939). The enlargement of the medial epicondyle and the teres tubercle, on which both the teres major and latissimus dorsi insert, has caused the two protrusions to nearly merge, drastically reducing the medial surface of the humerus (Campbell 1939). Similarly, the lateral surface has been diminished by the encroachment of the greater tuberosity and the lateral epicondylar spine (Campbell 1939). Of all the members of Talpidae, *Scalopus aquaticus* has the most highly developed humerus with a width to length ratio of .448 (Campbell 1939) to better accommodate the attachment of its extensive shoulder musculature.

The lever ratio analysis of the four prominent muscles that contribute to forelimb adduction also signified that *S. aquaticus* relies upon force more than velocity for burrowing. The mean lever ratio of these four muscle groups ranged from 0.23 to 0.34, with an overall average of 0.29. This is a relatively high figure based on comparative lever ratio values characteristic of limbs of the armadillo (~0.25) and of ungulates (~0.10) (Liem et al. 2001). These values suggest that *Scalopus aquaticus*'s forelimbs are well adapted to generate considerable force at the expense of rapid velocity.

Vector analysis of the forces contributing to forelimb adduction was coincident with our assumptions about this fossorial species' actions, further supporting our biomechanical model. The latissimus dorsi and teres major muscles both inserted on the humerus at positions dorsal to the position of the humeral head, therefore dorsal to the fulcrum. The opposite is true of the subscapularis and pectoral complex insertion points. The mean total forelimb force in the horizontal plane that the specimens could produce was 0.4851N in a posterior direction, while the mean total force in the vertical plane was merely 0.0022N in the ventral direction.

The 220-fold difference between the horizontal and vertical force vectors demonstrates that *Scalopus aquaticus*' shoulder musculature has evolved in such a way that the maximum tetanic tension from the ventral and dorsal muscles nearly cancel out in the vertical axis, as would be expected from an animal that uses its forelimbs to burrow with a horizontal line of action. These force values indicate that the muscle contraction would move the forelimb posteriorly at a mere 0.32° angle below the horizontal. The near-horizontal line of action greatly contributes to the integrity of this model of force transduction. Moreover, this slight deviation might be further accounted for if the actions of miniscule stabilizer muscles (such as the supraspinatus and infraspinatus muscles) were taken into account.

To more easily contemplate the maximum tetanic force produced by a forelimb of *Scalopus aquaticus*, it has been scaled based on mean body mass to represent this value in human standards. According to recent data, the average American male weighs 190lb (86kg) (McDowell et al., 2005). If the eastern mole were scaled up to this size, it would be able to move one forelimb with a force of 370.6N. Comparatively, this would closely resemble a 190lb person doing lat pull-downs on an exercise machine using a 172lb load, lifting nearly his own weight strictly using straight-arm forelimb adduction.

This model of force transduction provided a thorough description of the locomotion of *Scalopus aquaticus*'s forelimbs during burrowing. Major sources of force reduction along the path of transduction included the lever mechanics (although the eastern mole's lever ratio tends to maximize force relative to many other species) and the muscles' angles of insertion onto the humerus. However, the relative reduction in force that occurs is small when considering the force-velocity continuum. *Scalopus aquaticus* seems to have evolved with a hypertrophied musculoskeletal system that powerfully enhances the force of forelimb adduction to the detriment of its potential for increased velocity.

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