



## Hallucal grasping in *Nycticebus coucang*: further implications for the functional significance of a large peroneal process

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### ABSTRACT

Euprimate grasping feet are characterized by a suite of morphological traits, including an enlarged peroneal process on the base of the first metatarsal, which serves as the insertion site of the peroneus longus muscle. In prosimians, a large process has typically been associated with a powerful hallucal grasp via the contraction of the peroneus longus to adduct the hallux. Recent electromyography (EMG) studies have documented that peroneus longus does not contribute substantially to hallucal grasping in lemurs (Boyer et al., 2007). However, non-lemurid prosimians have a I-V opposable grasp complex that is morphologically different and phylogenetically more primitive than the I-II adductor grasp complex of the lemurs previously studied. Therefore, it is possible that peroneus longus did function during grasping in early euprimates, but lost this function in large-bodied lemurs. The present study tests the hypothesis that a large peroneal process is related to powerful grasping ability in primates displaying the more primitive I-V grasp complex. We use EMG to evaluate the recruitment of peroneus longus, other crural muscles, and adductor hallucis in static and locomotor grasping activities of the slow loris (*Nycticebus coucang*). Results show that peroneus longus is active during grasping behaviors that require the subject to actively resist inversion of the foot, and likely contributes to a hallucal grasp in these activities. Peroneus longus activity level does not differ between grasping and power grasping activities, nor does it differ between grasping and non-grasping locomotor modes. Conversely, the digital flexors and hallucal adductor are recruited at higher levels during power grasping and grasping locomotor modes. Consequently, we reject the hypothesis that an enlarged peroneal process represents an adaptation specifically to enhance the power of the I-V grasp, but accept that the muscle likely plays a role in adducting the hallux during grasping behaviors that require stabilization of the ankle, and suggest that further work is necessary to determine if this role is sufficient to drive selection for a large peroneal process.

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### Introduction

The base of the prosimian first metatarsal presents a hypertrophied peroneal process, the function of which has been contested (Walker, 1974; Conroy, 1976; Gebo, 1985, 1986, 1987, 1988, 2004; Szalay and Dagosto, 1988; Bloch and Boyer, 2002; Boyer et al., 2007; Gebo et al., 2008). This process serves as the insertion site for the tendon of the peroneus longus muscle, which has been hypothesized to adduct the hallux in addition to its commonly recognized role as an evor of the foot (Lewis, 1972; Conroy, 1976; Gebo, 1985, 1987, 1993). These actions have been

experimentally confirmed by electromyography (EMG) in two lemur species (Boyer et al., 2007).

Adduction of the hallux has been thought to play an important role in hallucal grasping by effectively pinching the substrate between the first and second digits, thus adding additional power to the grasping force generated during flexion of the digits (Cartmill, 1985; Szalay and Dagosto, 1988; Gebo, 1993; Lemelin, 1999; Boyer et al., 2007). Such speculations have led to the hypothesis that a hypertrophied peroneal process enables powerful grasping by increasing the lever arm of the peroneus longus muscle (and thereby increasing its mechanical advantage) and/or by increasing its attachment area (Walker, 1974; Szalay and Dagosto, 1988; Gebo and Dagosto, 1988). This hypothesis has, in turn, been invoked to divide species into groups of “powerful” or “non-powerful” grasping ability (Gebo, 2004).

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In contrast to this hypothesis, a recent electromyography (EMG) study has indicated that peroneus longus does not contribute significantly to grasping behaviors in lemurid prosimians (Boyer et al., 2007). Boyer et al. (2007) found peroneus longus to be relatively inactive when grasping during both static (i.e., postural) and dynamic (i.e., locomotion) activities. Accordingly, these findings call into question the plausibility of a real functional link between peroneal process size and improved hallucal grasping ability.

Boyer et al. (2007) acknowledged that lemurs possess a derived foot morphology compared to non-lemurid primates. Specifically, most lemuriformes possess what Gebo (1985) described as a I-II adductor grasp, which is characterized by (1) a continuous, oblique articular surface across the second through fifth tarsometatarsal joints, which orients the metatarsals in an arch, (2) a lateral plantar facet on the second metatarsal, which deviates laterally from vertical and is confluent with the tarsometatarsal joint, and (3) a relatively large adductor hallucis muscle with fused transverse and oblique heads. The obliquely oriented second metatarsal lateral plantar facet prevents the third metatarsal from lying in line with the second metatarsal, forcing the third metatarsal dorsally. The continuous tarsometatarsal joint allows the fourth and fifth metatarsals to shift their proximal articulations dorsally to meet the elevated third metatarsal. This arrangement of metatarsals results in an arrangement of the foot wherein the third through fifth metatarsals lie in a plane oblique to that created by the first and second metatarsals (Gebo, 1985). This oblique foot arrangement, in conjunction with a relatively larger adductor hallucis muscle, was interpreted by Gebo (1985) to be a mechanically advantageous adaptation for vertically clinging primates with large body sizes; the relatively larger adductor hallucis muscle could supply the additional force needed to generate a secure grasp around a vertical substrate.

A second, more phylogenetically primitive mechanism described by Gebo (1985) as the “I-V opposable grasp” is found in cheirogaleids, lorids, *Daubentonia*, tarsiids, and adapids. The first digit opposes the fifth digit around the substrate, with all four lateral digits contributing to force production during grasping. Species possessing the I-V grasp have feet that are characterized by (1) a discontinuous joint surface at the tarsometatarsal joints, where the ectocuneiform sits slightly more distal than the cuboid, (2) a vertically oriented lateral plantar facet on the second metatarsal, and (3) relatively more massive intrinsic musculature for flexing and opposing the first and fifth digit. The vertically oriented lateral plantar process and discontinuous tarsometatarsal joint surface allow all five digits to lie in the same horizontal plane (Gebo, 1985). This grasp is possessed largely by small-bodied primates, and has been interpreted by Gebo (1985) to be less powerful than the more derived I-II adductor grasp.

To evaluate whether or not the patterns of muscle recruitment observed by Boyer et al. (2007) reflect a general pattern of muscle use for all prosimians, or are specific for those that have the I-II grasp complex, we have undertaken a similar EMG analysis on the slow loris, *Nycticebus coucang*. Although the foot of the slow loris displays certain derived characteristics, such as a hallux that is deviated 90 degrees from digits two through five, volar pads that are expanded to increase surface contact area, and a second, clawed digit that is reduced in length (Grand, 1967; Dykyj, 1980), the slow loris retains the phylogenetically primitive I-V opposable grasp and has an enlarged peroneal process. The I-V grasp is evidenced not only by the osteological characters discussed previously, but also in the muscular contributions to, and use of, the second digit in grasping; the second digit receives the smallest of the five flexor tendons and, because of its diminutive length, rarely lies in direct opposition to the hallux during grasping activities (Grand, 1967; Dykyj, 1980).

In the present study, the hypothesized link between an enlarged peroneal process and powerful grasping ability was tested in two ways. First, involvement of peroneus longus in general grasping activities through adduction of the hallux was explored. If an enlarged peroneal process reflects the importance of peroneus longus for grasping, it should be actively recruited during all ordinary grasping activities. Second, a specific link to powerful grasping was tested; use of an enlarged peroneal process to categorize taxa into groups with “powerful” or “non-powerful” grasps requires evidence that peroneus longus is responsible for increased grasp strength during power grasping behaviors. Demonstration of increasing levels of peroneus longus EMG activity from non-grasping behaviors to ordinary grasping to powerful grasping would support such an interpretation.

Grasping activities were defined as those in which the hallux was observed to (1) forcefully oppose the lateral digits around a substrate, and (2) adduct to pinch the substrate between the first and second digits. Grasping behaviors were subdivided into a set of ordinary grasps involved in static positional behaviors, grasps involved in dynamic positional behaviors (i.e., locomotion), and power-grasping behaviors, which required that the grasp be maintained against a larger antagonistic force than generated by normal locomotor or static positional behaviors. Non-grasping activities were defined as those that did not require the forceful opposition or adduction of the hallux and the lateral digits (such as standing or walking across the top of a cylindrical substrate, the circumference of which was more than two or three times the circumference of a substrate that the subject could grasp with the tips of the hallucal digit just touching those of the lateral digits).

## Materials and methods

### Experimental subjects

Two adult female *Nycticebus coucang* individuals were studied. Both animals were on loan from the Duke Lemur Center and were temporarily housed in the Stony Brook University Primate Locomotion Laboratory. Body-weights for these subjects are provided in Table 1. The Animal Care and Use Committees of Stony Brook University and Duke University approved all experimental protocols.

### Focal muscles

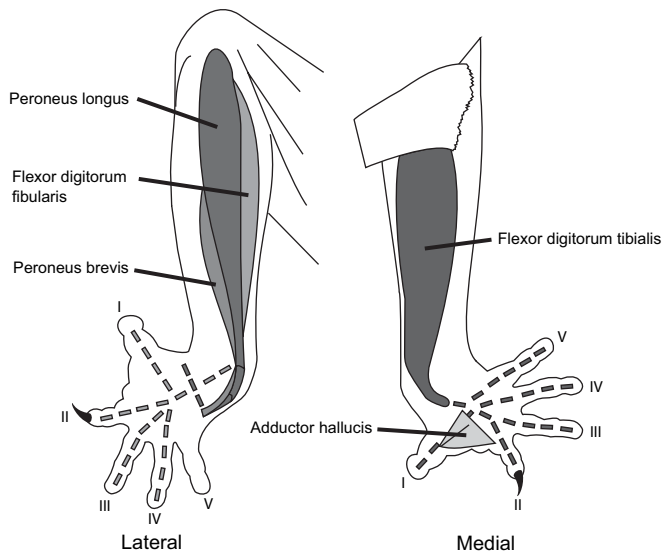
The experimental procedures of Boyer et al. (2007) were followed closely to facilitate comparison of results. These procedures are detailed here for the reader's convenience.

Because the role of peroneus longus in grasping activities was of primary interest, this known evertor of the foot was observed along with muscles used in grasping activities in other taxa: flexor digitorum tibialis, flexor digitorum fibularis, and adductor hallucis. Peroneus brevis, an evertor of the foot that does not adduct the hallux, was observed to reveal which activities require eversion (or the prevention of inversion) of the foot, with or without grasping. Figure 1 illustrates the positions of the focal muscles in the leg and foot.

**Table 1**  
Number of experiments conducted for each muscle and subject.

| Subject (Mass)     | Total | PL | PB | FDT | FDF | AH |
|--------------------|-------|----|----|-----|-----|----|
| Female 1 (0.9 kg)  | 5     | 5  | 5  | 5   | 2   | 4  |
| Female 2 (1.15 kg) | 2     | 2  | 2  | 1   | 0   | 2  |
| Total              | 7     | 7  | 7  | 6   | 2   | 6  |

PL: peroneus longus, PB: peroneus brevis, FDT: flexor digitorum tibialis, FDF: flexor digitorum fibularis, AH: adductor hallucis



**Fig. 1.** Illustration of the positions of focal muscles within the loris leg and foot, adapted from Boyer et al. (2007). Solid blocks of color represent muscle bellies; dashed lines represent tendons running within the foot.

A dissection of a slow loris leg and foot (DPC Nc1936F) was conducted in order to document and landmark the muscles of interest for the EMG experiments. We established associations between external morphological landmarks and muscles of interest to facilitate the proper placement of electrodes. We provide descriptions of the origins, insertions, and positions of the focal muscles as a quick reference to the reader, while Grand (1967) has provided a more thorough treatment.

Peroneus longus originates along the anterolateral aspect of the fibula. Its tendon runs inferiorly across the lateral malleolus and turns medially onto the sole of the foot, passing through a groove in the cuboid, and traverses the sole to insert on the peroneal process at the base of the first metatarsal. Peroneus brevis originates similarly from the anterolateral aspect of the fibula, distal to peroneus longus, and follows a similar path over the lateral malleolus. Rather than turning to enter the foot like its counterpart, peroneus brevis inserts onto the base of the fifth metatarsal.

Flexor digitorum tibialis is a two-headed muscle, and by far the largest muscle observed. The larger head originates along the posteromedial shaft and medial condyle of the femur, and from the medial shaft of the tibia; the smaller head originates from the interosseous membrane. The heads join into a single tendon, which crosses just posterior to the medial malleolus and runs distally to enter the foot, where it splits into five digital tendons. Flexor digitorum fibularis originates from the posterolateral aspect of the fibula. Its tendon passes just deep to the tendon of triceps surae to enter the sole of the foot posteriorly through a groove on the talus. Once in the foot, its tendon divides into contributions for digits one through four. The tendons of the two long digital flexors join together in the foot, sending only one fused tendon to insert on the distal phalanx of each toe.

Adductor hallucis is a two-headed muscle. The large transverse head arises from the shaft of the second metatarsal, while the smaller oblique head originates from the proximal part of the third metatarsal. Both heads insert onto the shaft of the first metatarsal and the proximal phalanx.

#### Electrode insertion and verification

Electrode construction and insertion procedures followed Stern and Larson (2001). Electrodes were threaded through a 25-gauge

hypodermic needle and inserted into the bellies of focal muscles while the subjects were under isoflurane anesthesia. Each muscle was then stimulated with a small (200–500  $\mu$ amp) sinusoidal current through the electrodes to ensure proper placement and verify the action of the muscle. Video recordings of back-stimulation of the focal muscles were taken for reference. The free ends of the electrodes were connected to a 112 g, 4-channel, FM telemetry transmitter attached to a non-restrictive harness worn by the experimental subjects. Harnesses were the same as those utilized in Boyer et al. (2007). Telemetered EMG was digitized at 2700 Hz and coupled with simultaneous video recording as detailed in Stern et al. (1977, 1980), Susman and Stern (1979), Larson and Stern (1989), Stern and Larson (2001), and Boyer et al. (2007).

#### Animal enclosure

Experimental subjects were placed in a 7.3 m  $\times$  3.7 m  $\times$  3.7 m chain link enclosure. Within this enclosure, a variety of substrates were available across which the subjects were free to move. These included two horizontally suspended poles: a larger pole 15 cm in diameter and 5.3 m long, and a smaller pole 3.1 cm in diameter and 4 m long. A similar 3.1 cm in diameter pole was secured vertically. Several 2 cm in diameter unfixed wooden dowels served as objects for the subjects to grasp. An animal trainer was present with the subjects throughout the course of the experiments to encourage the subjects to use different substrates or grasp different objects.

#### Focal behaviors

EMG activity patterns for the five muscles were analyzed for five static and three locomotor behaviors (Table 2–4). Focal behaviors follow Boyer et al. (2007).

The observed static behaviors included grasps utilized during body-weight supporting positional behaviors and those utilized during non-support activities. Body-weight supporting grasps included those used during standing bouts atop a small diameter pole (“small pole standing”), and those used during quadrupedal vertical clinging (Fig. 2A). Non-support grasps were obtained by allowing subjects resting on the ground to grip a small diameter dowel (“small dowel grasping”) (Fig. 2B). Power grasps were elicited by encouraging the subject to exert extra force to maintain its grip; specifically, the subject’s foot was pulled and pushed by the experimenter in multiple directions away from the substrate during small pole standing or vertical clinging (Fig. 2C). The small size of the subjects and their inability to rapidly flee allowed this approach, which was not possible for the larger and more skittish lemurs studied by Boyer et al. (2007). Care was taken to ensure that the animal maintained a hallucal grasp at all times. To facilitate comparisons of grasping and non-grasping positional behaviors, we also observed the subjects standing atop a large diameter pole that neither required nor allowed them to grasp. An ANOVA confirmed that recordings of EMG activity of focal muscles in power grasps obtained by pushing and pulling the foot in differing directions were not statistically different ( $F = 2.58$ ,  $p > 0.05$ ).

Examined locomotor behaviors include walking across the small diameter horizontal pole (“small pole walking”) to provide a model of locomotion that requires grasping, and walking across a large diameter horizontal pole (“large pole walking”) for one that does not. Quadrupedal vertical climbing on a small diameter pole was analyzed to compare vertical locomotion to horizontal locomotion. Foot positions for all observed behaviors were documented and are illustrated in Fig. 2.

**Table 2**  
Results of Student's t-tests comparing recruitment of muscles within static activities.\*

|                  | PL                          | PB                 | FDT                | FDF                | AH    | PL                       | PB                 | FDT                | FDF      | AH   |
|------------------|-----------------------------|--------------------|--------------------|--------------------|-------|--------------------------|--------------------|--------------------|----------|------|
|                  | <b>Small Pole Standing</b>  |                    |                    |                    |       | <b>Vertical Clinging</b> |                    |                    |          |      |
| Mean % Max Burst | 8.66                        | 12.90              | 11.04              | 3.32               | 11.05 | 6.74                     | 15.67              | 7.15               | 2.05     | 2.29 |
| SD               | 4.59                        | 8.63               | 10.09              | 1.28               | 3.12  | 5.82                     | 7.56               | 2.00               | 2.14     | 1.53 |
| (N)              | (13)                        | (12)               | (10)               | (5)                | (9)   | (17)                     | (13)               | (9)                | (12)     | (8)  |
| PB               | t = 0.92                    | -                  |                    |                    |       | <b>t = 2.49</b>          | -                  |                    |          |      |
|                  |                             |                    |                    |                    |       | <b>p &lt; 0.05</b>       |                    |                    |          |      |
| FDT              | t = 0.15                    | t = 0.60           | -                  |                    |       | t = 1.75                 | t = 1.72           | -                  |          |      |
| FDF              | <b>t = 3.04</b>             | <b>t = 3.59</b>    | t = 2.12           |                    |       | <b>t = 2.27</b>          | <b>t = 4.48</b>    | <b>t = 3.90</b>    |          |      |
|                  | <b>p &lt; 0.01</b>          | <b>p &lt; 0.01</b> |                    |                    |       | <b>p &lt; 0.05</b>       | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> |          |      |
| AH               | t = 1.86                    | t = 0.31           | t = 1.03           | <b>t = 5.99</b>    |       | t = 0.97                 | <b>t = 4.74</b>    | <b>t = 4.77</b>    | t = 1.48 |      |
|                  |                             |                    |                    | <b>p &lt; 0.01</b> |       |                          | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> |          |      |
|                  | <b>Small Dowel Grasping</b> |                    |                    |                    |       | <b>Power Grasping</b>    |                    |                    |          |      |
| Mean % Max Burst | 4.83                        | 7.67               | 9.86               | 7.50               | 19.10 | 9.85                     | 19.27              | 30.51              | 9.55     | 8.13 |
| SD               | 6.94                        | 5.51               | 10.57              | 2.38               | 3.51  | 7.29                     | 7.07               | 21.22              | 3.25     | 3.31 |
| (N)              | (22)                        | (10)               | (18)               | (16)               | (6)   | (61)                     | (45)               | (52)               | (5)      | (57) |
| PB               | <b>t = 3.06</b>             |                    |                    |                    |       | <b>t = 8.19</b>          | -                  |                    |          |      |
|                  | <b>p &lt; 0.01</b>          |                    |                    |                    |       | <b>p &lt; 0.01</b>       |                    |                    |          |      |
| FDT              | <b>t = 3.36</b>             | t = 0.29           |                    |                    |       | <b>t = 6.74</b>          | t = 1.42           |                    |          |      |
|                  | <b>p &lt; 0.01</b>          |                    |                    |                    |       | <b>p &lt; 0.01</b>       |                    |                    |          |      |
| FDF              | <b>t = 3.74</b>             | t = 0.77           | t = 0.54           |                    |       | t = 0.45                 | <b>t = 3.64</b>    | <b>t = 4.40</b>    |          |      |
|                  | <b>p &lt; 0.01</b>          |                    |                    |                    |       |                          | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> |          |      |
| AH               | <b>t = 5.20</b>             | <b>t = 3.72</b>    | <b>t = 4.29</b>    | <b>t = 5.43</b>    |       | t = 0.68                 | <b>t = 9.71</b>    | <b>t = 7.64</b>    | t = 0.84 |      |
|                  | <b>p &lt; 0.01</b>          | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> |       |                          | <b>p &lt; 0.01</b> | <b>p &lt; 0.01</b> |          |      |

\* Mean EMG for each muscle is presented as a percentage of observed maximum burst. No significant (>5% of max. burst) activity was recorded for large pole standing. Numbers in bold are statistically significant. PL: peroneus longus, PB: peroneus brevis, FDT: flexor digitorum tibialis, FDF: flexor digitorum fibularis, AH: adductor hallucis, SD: standard deviation.

### Quantification of EMG

LabView version 5.01 software was used to display and store two-second sweeps of EMG signals, digitized at 2700 Hz, as unique data files. Each data file was further time-marked by a counter that began at zero and increased to 120 during each sweep, resulting in 120 marked frames per file. Focal behaviors were identified by reviewing videotape recordings that show the animal subject with superimposition of the simultaneous EMG sweeps. For static behaviors, we noted file numbers and counter values corresponding to the onset and cessation of each bout. Static behavior bouts were of varying duration, but we limited a single bout to a 20 sec maximum. For locomotor behaviors, step cycles were identified and the counter values for specific gait events (touch down, mid-support, lift-off, and mid-swing) were recorded.

The EMG interference patterns for focal behaviors were quantified by calculating the root mean square (RMS) value at intervals of 1.85 msec with a time constant of 41.58 msec using a Fortran program written by one of us (JTS). For the three locomotor behaviors, a second Fortran program read the files containing the RMS values for all sampled support and swing phases, equalized the phase durations, and calculated at 1% intervals a quartile distribution of the RMS values to create a composite mean step cycle.

A variety of factors can influence the strength of any particular EMG signal, making it difficult to compare absolute RMS EMG values across recording sessions or individuals. To facilitate such comparisons, RMS EMG values were scaled to the RMS value for the "maximum EMG burst" observed for each muscle during the recording session. The maximum burst refers to the highest level of EMG activity seen for each muscle during the entire recording session, and is not limited to focal behaviors. Use of the maximum burst as a relative scale gives an indication of how the EMG activity level during a particular behavior compares to our best estimate of the maximum the muscle is capable of, and is somewhat akin to the practice of expressing activity levels relative to a maximum voluntary contraction, as is often seen in human EMG studies. Typically, the maximum EMG bursts for the peroneal muscles were observed when the subject actively everted the ankle while the foot was fixed during

transfers between substrates. Maximum levels of activity in adductor hallucis occurred during grasping behaviors, whereas cantilevering on a vertical substrate when all of the body's weight was supported by the grasping hind feet elicited maximum bursts for the digital flexors.

### Statistical analysis

All statistical analyses were conducted with SPSS version 16.0 (SPSS Inc., 2008), with ANOVA utilized to assess congruence of scaled RMS EMG values among experiments and subjects. No significant differences were found between experiments ( $F = 1.94$ ,  $p > 0.05$ ), or individuals ( $F = 1.29$ ,  $p > 0.05$ ). Scaled RMS EMG values were revealed by one-sample Kolmogorov–Smirnov tests to be non-normally distributed. Transforming values to their base-10 logarithms brought them into a normal distribution (confirmed by Kolmogorov–Smirnov tests with  $p > 0.05$ ).

Transformed scaled RMS EMG values were used to derive means for samples of static behaviors. In addition, for the samples of locomotor step cycles, mean transformed scaled RMS EMG values for the first half of support, second half of support, first half of swing, and second half of swing were calculated. Box-and-whisker plots and Student's t-tests were conducted to characterize and compare the activity patterns of the five muscles. In keeping with conventions used by Boyer et al. (2007), we considered RMS EMG values less than 5% of the maximum burst to be inconsequential. This provides a 95% confidence interval in which recorded values are distinguishable from electrical background noise. A muscle was considered inactive during a given bout of a focal behavior if their activity was less than 5% of the muscle's maximum burst.

## Results

### Back-stimulation

Back-stimulation of peroneus longus caused the foot to evert and the hallux to adduct. In addition, stimulation of this muscle produced dorsiflexion of the ankle. The latter, novel action for peroneus longus was determined to be consistent with lorisine

**Table 3**  
Results of Student's t-tests of muscles during different static behaviors.\*

|                          | Large Pole Standing              | Small Pole Standing | Small Dowel Grasping | Power Grasping      | Vertical Clinging  | Large Pole Standing               | Small Pole Standing | Small Dowel Grasping | Power Grasping     | Vertical Clinging |
|--------------------------|----------------------------------|---------------------|----------------------|---------------------|--------------------|-----------------------------------|---------------------|----------------------|--------------------|-------------------|
|                          | <b>Peroneus longus</b>           |                     |                      |                     |                    | <b>Peroneus brevis</b>            |                     |                      |                    |                   |
| Mean % Max Burst         | 2.47                             | 8.67                | 4.83                 | 9.85                | 6.74               | 3.35                              | 12.90               | 7.67                 | 19.27              | 15.67             |
| SD                       | 2.76                             | 4.59                | 6.94                 | 7.29                | 5.82               | 2.29                              | 8.63                | 5.51                 | 7.07               | 7.56              |
| (N)                      | (19)                             | (13)                | (22)                 | (61)                | (17)               | (15)                              | (12)                | (10)                 | (45)               | (13)              |
|                          | <b>t = 4.90</b>                  |                     |                      |                     |                    | <b>t = 4.47</b>                   |                     |                      |                    |                   |
|                          | <b>p &lt; 0.01</b>               |                     |                      |                     |                    | <b>p &lt; 0.01</b>                |                     |                      |                    |                   |
| Small Pole Standing      |                                  |                     |                      |                     |                    |                                   |                     |                      |                    |                   |
| Small Dowel Grasping     | t = 1.45                         | <b>t = 2.87</b>     | –                    |                     |                    | t = 1.98                          | t = 1.81            | –                    |                    |                   |
| Power Grasping           | <b>t = 8.05</b>                  | t = 0.08            | <b>t = 3.93</b>      | –                   |                    | <b>t = 8.53</b>                   | t = 2.15            | <b>t = 3.68</b>      | –                  |                   |
|                          | <b>p &lt; 0.01</b>               |                     | <b>p &lt; 0.01</b>   |                     |                    | <b>p &lt; 0.01</b>                |                     | <b>p &lt; 0.01</b>   |                    |                   |
| Vertical Clinging        | t = 1.71                         | t = 1.80            | <b>t = 2.31</b>      | t = 1.92            | –                  | <b>t = 4.33</b>                   | t = 0.25            | t = 1.85             | t = 1.39           | –                 |
|                          |                                  |                     | <b>p &lt; 0.05</b>   |                     |                    | <b>p &lt; 0.01</b>                |                     |                      |                    |                   |
|                          | <b>Flexor digitorum tibialis</b> |                     |                      |                     |                    | <b>Flexor digitorum fibularis</b> |                     |                      |                    |                   |
| Mean % Max Burst         | 4.48                             | 11.04               | 9.86                 | 30.51               | 7.15               | 2.19                              | 3.32                | 7.50                 | 9.55               | 2.05              |
| SD                       | 5.79                             | 10.09               | 10.57                | 21.22               | 2.00               | 3.74                              | 1.28                | 2.38                 | 3.25               | 2.14              |
| (N)                      | (19)                             | (10)                | (18)                 | (52)                | (9)                | (5)                               | (5)                 | (16)                 | (5)                | (12)              |
|                          | <b>t = 2.91</b>                  |                     |                      |                     |                    | <b>t = 1.90</b>                   |                     |                      |                    |                   |
|                          | <b>p &lt; 0.01</b>               |                     |                      |                     |                    | <b>p &lt; 0.01</b>                |                     |                      |                    |                   |
| Small Pole Standing      |                                  |                     |                      |                     |                    |                                   |                     |                      |                    |                   |
| Small Dowel Grasping     | <b>t = 2.48</b>                  | t = 0.80            | –                    |                     |                    | t = 2.57                          | <b>t = 3.42</b>     | –                    |                    |                   |
|                          | <b>p &lt; 0.05</b>               |                     |                      |                     |                    |                                   | <b>p &lt; 0.01</b>  |                      |                    |                   |
| Power Grasping           | <b>t = 8.35</b>                  | <b>t = 2.97</b>     | <b>t = 4.99</b>      | –                   |                    | <b>t = 2.78</b>                   | <b>t = 4.05</b>     | t = 1.20             | –                  |                   |
|                          | <b>p &lt; 0.01</b>               | <b>p &lt; 0.01</b>  | <b>p &lt; 0.01</b>   | –                   |                    | <b>p &lt; 0.05</b>                | <b>p &lt; 0.01</b>  |                      |                    |                   |
| Vertical Clinging        | <b>t = 3.76</b>                  | t = 0.64            | t = 0.50             | <b>t = 7.55</b>     | <b>p &lt; 0.01</b> | t = 0.84                          | <b>t = 2.37</b>     | <b>t = 3.90</b>      | <b>t = 4.29</b>    | –                 |
|                          | <b>p &lt; 0.01</b>               |                     |                      | <b>p &lt; 0.01</b>  |                    |                                   | <b>p &lt; 0.05</b>  | <b>p &lt; 0.01</b>   | <b>p &lt; 0.01</b> |                   |
| <b>Adductor hallucis</b> |                                  | Large Pole Standing |                      | Small Pole Standing |                    | Small Dowel Grasping              |                     | Power Grasping       |                    | Vertical Clinging |
| Mean % Max Burst         |                                  | 0.83                |                      | 11.05               |                    | 19.10                             |                     | 8.13                 |                    | 2.29              |
| SD                       |                                  | 1.52                |                      | 3.12                |                    | 3.51                              |                     | 3.31                 |                    | 1.53              |
| (N)                      |                                  | (14)                |                      | (9)                 |                    | (6)                               |                     | (57)                 |                    | (8)               |
|                          |                                  | <b>t = 7.94</b>     |                      | –                   |                    |                                   |                     |                      |                    |                   |
|                          |                                  | <b>p &lt; 0.01</b>  |                      |                     |                    |                                   |                     |                      |                    |                   |
| Small Pole Standing      |                                  |                     |                      | <b>t = 3.80</b>     |                    | –                                 |                     |                      |                    |                   |
| Small Dowel Grasping     |                                  | <b>t = 8.89</b>     |                      | <b>p &lt; 0.01</b>  |                    |                                   |                     |                      |                    |                   |
|                          |                                  | <b>p &lt; 0.01</b>  |                      | <b>p &lt; 0.01</b>  |                    |                                   |                     |                      |                    |                   |
| Power Grasping           |                                  | <b>t = 7.30</b>     |                      | <b>t = 2.12</b>     |                    | <b>t = 4.24</b>                   |                     |                      |                    |                   |
|                          |                                  | <b>p &lt; 0.01</b>  |                      | <b>p &lt; 0.05</b>  |                    | <b>p &lt; 0.01</b>                |                     |                      |                    |                   |
| Vertical Clinging        |                                  | <b>t = 4.39</b>     |                      | <b>t = 5.65</b>     |                    | <b>t = 7.43</b>                   |                     | <b>t = 4.48</b>      |                    | –                 |
|                          |                                  | <b>p &lt; 0.01</b>  |                      | <b>p &lt; 0.01</b>  |                    | <b>p &lt; 0.01</b>                |                     | <b>p &lt; 0.01</b>   |                    |                   |

\* Bolded values are significant at 0.05.



**Table 4**  
Comparison of muscle recruitment during large and small pole walking.\*

| Gait Phase       | Muscle | Large Pole Walking |       | Small Pole Walking |       | t           | p                |
|------------------|--------|--------------------|-------|--------------------|-------|-------------|------------------|
|                  |        | % Max Burst        | SD    | % Max Burst        | SD    |             |                  |
| 1st half support | PL     | 14.66              | 9.95  | 17.21              | 7.51  | 1.41        | ns               |
|                  | PB     | 16.36              | 9.26  | 12.99              | 3.58  | 1.33        | ns               |
|                  | FDT    | 11.62              | 12.65 | 19.16              | 11.07 | <b>2.93</b> | <b>&lt; 0.01</b> |
|                  | FDF    | 4.32               | 4.59  | 3.61               | 2.29  | 0.59        | ns               |
|                  | AH     | 10.03              | 5.21  | 21.93              | 6.54  | <b>5.67</b> | <b>&lt; 0.01</b> |
| 2nd half support | PL     | 7.02               | 5.73  | 7.36               | 5.45  | 0.59        | ns               |
|                  | PB     | 5.47               | 4.42  | 6.48               | 4.22  | 1.41        | ns               |
|                  | FDT    | 8.14               | 9.09  | 5.91               | 2.95  | 0.79        | ns               |
|                  | FDF    | 0.67               | 0.77  | 1.85               | 2.08  | 1.01        | ns               |
|                  | AH     | 1.79               | 2.80  | 8.06               | 5.96  | <b>5.07</b> | <b>&lt; 0.01</b> |
| 1st half swing   | PL     | 2.19               | 2.46  | 1.16               | 0.89  | 1.11        | ns               |
|                  | PB     | 3.43               | 2.84  | 2.45               | 3.95  | 0.39        | ns               |
|                  | FDT    | 5.31               | 5.30  | 3.62               | 4.10  | 0.69        | ns               |
|                  | FDF    | 0.58               | 0.90  | 0.73               | 1.32  | 0.02        | ns               |
|                  | AH     | 0.59               | 0.42  | 1.04               | 0.94  | 0.86        | ns               |
| 2nd half swing   | PL     | 8.47               | 5.87  | 5.32               | 5.76  | 0.27        | ns               |
|                  | PB     | 17.94              | 8.24  | 13.87              | 5.89  | 1.02        | ns               |
|                  | FDT    | 9.16               | 13.25 | 5.07               | 5.71  | 0.46        | ns               |
|                  | FDF    | 2.46               | 2.99  | 1.33               | 1.05  | 0.07        | ns               |
|                  | AH     | 2.78               | 2.99  | 2.62               | 3.75  | 2.05        | ns               |

Means and standard deviations are untransformed. PL: peroneus longus, PB: peroneus brevis, FDT: flexor digitorum tibialis, FDF: flexor digitorum fibularis, AH: adductor hallucis, ns: not significant.

\* Mean EMG scores are presented as a percentage of the maximum burst activity for each gait phase. Gray shaded areas indicated EMG values <5% of maximum burst.

anatomy—the tendon of peroneus longus is not restrained behind the lateral malleolus as it is in other primates; rather, it passes directly over the lateral surface of the malleolus. Adduction of the hallux pulls the tip of this digit into contact with the tip of the shortened second digit. This pattern of adduction was also produced by the intrinsic hallucal adductor, which produced no action other than pure adduction of the hallux. In both instances, the experimenters manually abducted the first digit before stimulation to ensure adduction was taking place. Peroneus brevis only caused eversion of the foot. Flexor digitorum tibialis produced flexion of the metatarsophalangeal and the proximal and distal interphalangeal joints of all toes. Flexor digitorum fibularis produced flexion of these same joints in digits I–IV only. Both digital flexors flexed the hallux at the metatarsophalangeal and interphalangeal joints, and produced a small amount of plantarflexion at the talocrural joint. Stimulation of flexor digitorum tibialis also produced pronounced inversion and adduction of the foot.

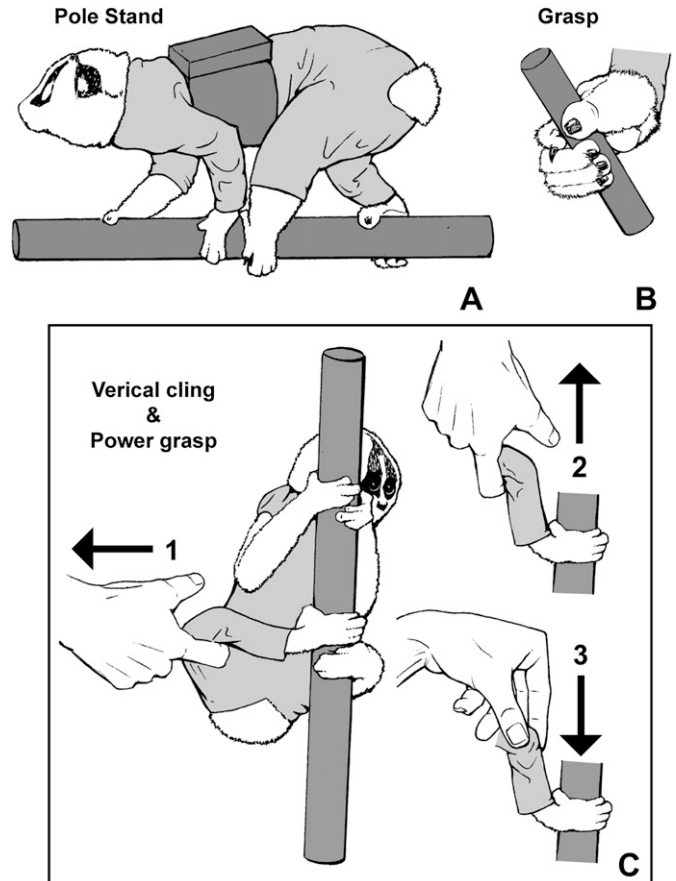
#### Static grasping behaviors

##### Small dowel grasping

All muscles, except peroneus longus, displayed a low level of meaningful (>5% of observed maximum burst) activity during small dowel grasping that occurred outside a context of body-weight support. Adductor hallucis showed a statistically significantly higher level of activity than any of the other focal muscles. This relatively high level of recruitment suggested that this non-supporting grasp relies on force produced by adduction of the hallux. Peroneus longus, however, is not recruited in this activity.

##### Horizontal pole standing

Mean scaled RMS EMG for all focal muscles while standing in a quadrupedal posture on the large diameter pole were negligible (<5% of maximum burst). Muscle activity increased significantly for all muscles (except for flexor digitorum fibularis) when the animals stood on a small diameter pole (Table 2, Fig. 3).



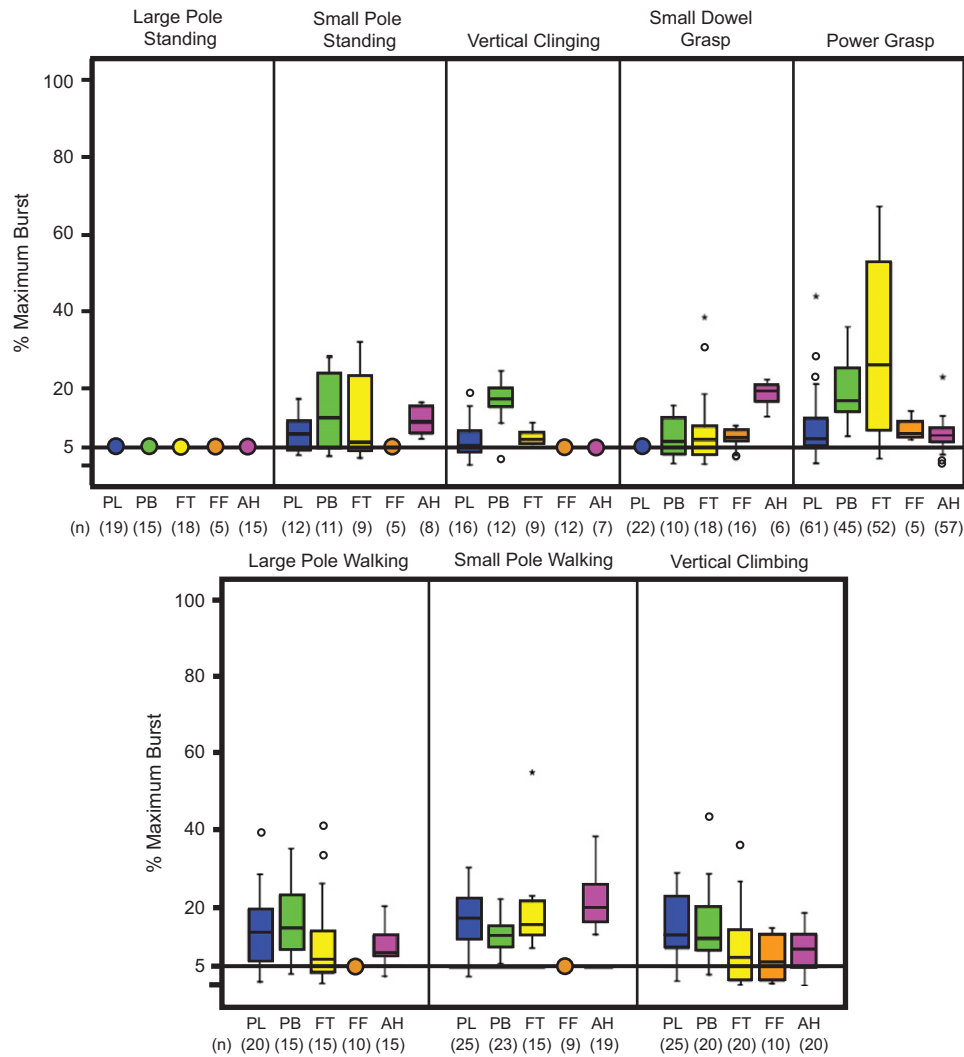
**Fig. 2.** Illustration of a loris wearing jumpsuit and transmitter in various focal behaviors. A: Small pole stand/walk. The subject fired adductor hallucis and flexor digitorum tibialis at higher levels in these situations than in similar postures on a substrate that was too large to grasp. However, peroneal muscles showed no increase in activity. B: Small dowel grasp. The subject showed activity in adductor hallucis and flexor digitorum tibialis while holding onto a dowel such as depicted. C: Vertical cling/climb and power grasp. While the animal was clinging statically to the vertical pole, we elicited power grasps by pulling and pushing the foot in different orientations (i.e., 1: pulling the foot away from the substrate, 2: pulling the foot parallel to the substrate upwards, and 3: pushing the knee parallel to the substrate downwards). During such power grasps all muscles, but especially flexor digitorum tibialis, showed increased activity as compared to B.

##### Vertical clinging

Focal muscles showed at most low-level activity during vertical clinging to a small diameter pole (Fig. 3). Peroneus longus was active at a low level, while both flexor digitorum fibularis and the hallucal adductor were essentially silent during this behavior. Peroneus brevis was the most active muscle, which suggested an important role in resisting inversion to keep the substrate firmly fixed in the subject's grasp, maintained by flexor digitorum tibialis (Table 2).

##### Power grasping

All muscles showed a significant amount of EMG activity during power grasping, with flexor digitorum tibialis exhibiting a significantly greater level of activity than all other muscles except peroneus brevis (Table 2). Peroneus longus exhibited a level of activity significantly higher than in small dowel grasping, but equivalent to that observed during small pole standing and vertical clinging (Table 3). The hallucal adductor displayed a level of activity significantly lower than during small dowel grasping and small pole standing, yet significantly higher than that observed during vertical clinging (Table 3). Flexor digitorum tibialis and flexor



**Fig. 3.** Boxplots illustrating the mean, 25th, and 75th percentiles for observed EMG activity. Boxes represent 50% of all data points, with the median depicted as a horizontal bar through the middle. Whiskers mark the range boundary for all data, excluding outliers, which are depicted as circles. Muscles are abbreviated as follows: PL (peroneus longus), PB (peroneus brevis), FT (flexor digitorum tibialis), FF (flexor digitorum fibularis), and AH (adductor hallucis). The number of recordings for each muscle and activity are provided in parentheses. For locomotor activities, only the first half of the support phase is illustrated here. Observed EMG values have been scaled to a percentage of maximum burst, represented by the y-axis. Boxes are pictured here only if the mean EMG for the activity was >5% of the maximum burst.

digitorum fibularis were recruited at higher levels during power grasping than any other focal behavior (Table 3).

#### Locomotor behaviors

##### Horizontal pole walking

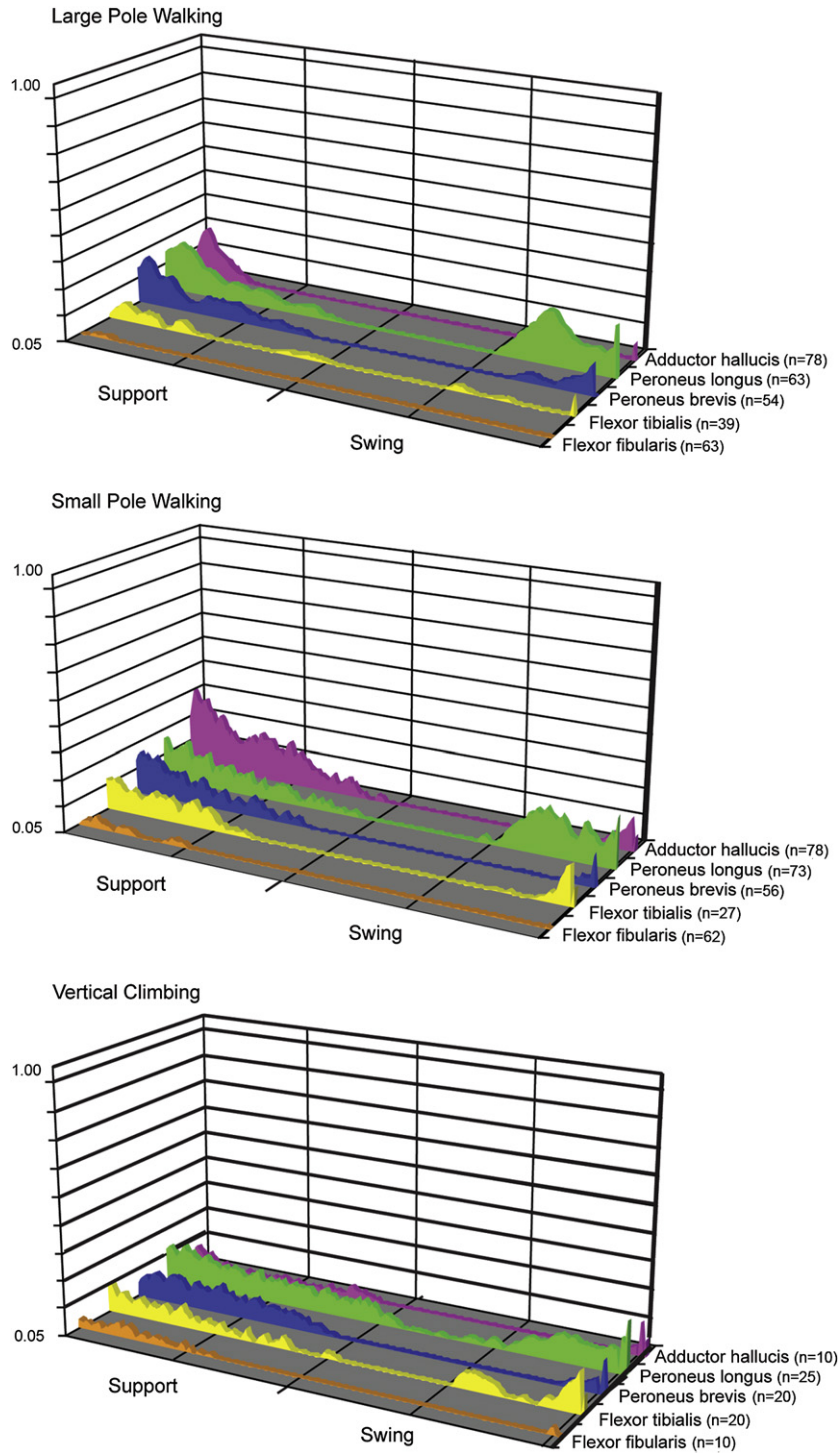
Walking on a large diameter pole yielded a moderate level of activity in both of the peroneal muscles, and a small amount of activity from flexor digitorum tibialis and adductor hallucis. We view as very important the fact that when the subjects traversed a small diameter pole, no significant change in peroneal activity occurred (Table 4, Fig. 4), whereas significant increases in activity were seen in both the flexor digitorum tibialis and the intrinsic hallucal adductor. As illustrated in Fig. 4, the activity in adductor hallucis during small pole walking was not only of higher amplitude, but also of longer duration.

##### Vertical climbing

Like vertical clinging, vertical climbing failed to elicit strong grasping muscle activity. The highest levels of activity were seen in the peroneal muscles (Figs. 3 and 4).

#### Discussion and conclusions

Numerous anatomical studies have inferred that peroneus longus serves as an important hallucal grasping muscle in prosimian primates because it attaches to a hypertrophied peroneal process on the first metatarsal in these taxa. Consequently, this trait has been used to categorize taxa into powerfully and non-powerfully grasping groups (Gebo, 1985, 2004; Szalay and Dagosto, 1988; Gebo and Dagosto, 1988). However, as was the case with the study of peroneus longus function in lemurs (Boyer et al., 2007), the present results contradict the view that peroneus longus, and by extension an enlarged peroneal process, is related to powerful grasping ability. While back-stimulation of peroneus longus does produce adduction of the hallux (along with ankle eversion and dorsiflexion), and though the muscle almost certainly contributes some amount of force to a hallucal grasp, it appears that peroneus longus is neither recruited specifically for this purpose, nor does it contribute increasing amounts of force to grasps of greater strengths. Rather, activity in peroneus longus during grasping activities is inseparable from its role as an evertor of the foot, and our data indicate that grasp strength is enhanced by increased



**Fig. 4.** Graph of EMG activity for all muscles during a full step cycle of large and small pole walking and vertical climbing. Step cycles are broken into 200 equal parts, depicted by the x-axis. Observed EMG values have been scaled to a percentage of maximum burst, represented by the y-axis. The scaled EMG values for each type of horizontal pole walking depicted here represent an average of all steps recorded in that activity.

recruitment of other cheiridial muscles, specifically adductor hallucis and flexor digitorum tibialis. These findings are supported by several lines of evidence and refute the idea that an enlarged peroneal process is an adaptation specific to enhanced grasping strength.

First, peroneus longus recruitment parallels that of peroneus brevis, which is a pure ankle evertor. During static grasping activities in which peroneus longus is recruited (power grasping,

small pole standing, vertical clinging), there was often even greater amplitude activity in peroneus brevis (Fig. 3, Table 3). The two muscles also showed a similar pattern of recruitment during walking along the horizontal poles and climbing the vertical pole (Fig. 4). In addition, the maximum bursts for the two muscles frequently occurred simultaneously, and were associated with active eversion of the ankle as the subject would shift its weight laterally over the supporting foot. This parallel recruitment of



peroneus longus and brevis indicates that the two are acting in concert, either to actively evert the ankle or to help stabilize it by resisting an inverting force.

Examination of foot postures during the different focal behaviors suggests that in most cases this parallel recruitment of the peroneal muscles is related to resisting inversion, and to bringing the foot into position for touch-down during swing phase. During static grasping behaviors, the subjects' feet were inverted to maintain a hallual grasp (Fig. 2); in these situations, the weight of the body tended to push this already inverted foot into greater inversion around the substrate, and the activity of the peroneal muscles resisted this tendency, helping to stabilize the foot. Similarly, during horizontal locomotion, the subjects' feet were slightly abducted and rested on the lateral sides of the cylindrical substrates (Fig. 2). As body-weight moved over the supporting limb, the tendency for the foot to be forced into greater inversion was resisted by the combined action of the peroneal muscles. The feet were also in an inverted posture during vertical clinging and climbing (Fig. 2), and again, action of the peroneal muscles helped prevent further inversion.

Second, the amplitude of peroneus longus activity in grasps against gravity, such as during clinging or climbing on a vertical small pole, was not elevated relative to the corresponding behaviors on the large horizontal pole (large pole stand/walk) (Fig. 3).

Finally, and perhaps most importantly, peroneus longus did not display increased activity during behaviors that entailed greater grasping effort as indicated by elevated activity in adductor hallucis and/or the digital flexors, such as small dowel grasping (elevated adductor hallucis activity) or power grasping (elevated digital flexor activity) (Fig. 3, Table 3). Similarly, there was no significant elevation in peroneus longus activity during small pole walking as compared to large pole walking, while there was an increase in activity in both adductor hallucis and flexor digitorum tibialis (Figs. 3 and 4, Table 4).

In general, these results agree well with the patterns of EMG activity reported previously for lemurid grasping (Boyer et al., 2007). As was the case in the present study, activity in peroneus longus paralleled that of peroneus brevis, was highest during periods of resisting inversion and preparing the foot for touch-down, and did not show elevated activity during power grasping and small pole walking, while adductor hallucis and flexor digitorum tibialis did exhibit this pattern. Both studies report the flexor digitorum tibialis to be the most actively recruited muscle during power grasping. This may indicate that forceful adduction of the hallux is less important than forceful flexion to the maintenance of a powerful grasp in the behaviors observed in these studies. Adduction of the hallux beyond a position of opposition to the lateral digits may compromise the force of the grasp. The fact that both studies indicate that the power of a hallual grasp depends markedly on the recruitment of the digital flexors and not peroneus longus, regardless of whether or not a I-II or I-V grasp is utilized, underscores the need to revise previous models of character evolution that rely on an enlarged peroneal process as evidence of powerful grasping ability, and suggests that future explorations into the evolution of pedal grasping should focus on the ability of the digits to flex sufficiently around the substrate. Recent studies have already taken this approach, placing more significance on the possession of a nailed, divergent hallux as an indicator of grasping ability than the presence of a hypertrophied peroneal process (Hamrick, 2001; Sargis, 2001, 2002; Bloch and Boyer, 2002; Sargis et al., 2005, 2007).

Both the present study and Boyer et al. (2007) note a differential use of the two digital flexor muscles. Flexor digitorum tibialis – the larger of the two muscles – is recruited more frequently and at a higher level during grasping activities in all taxa examined. This

further supports the notion that these muscles, despite sharing insertion tendons, do not share the same function (O'Donovan et al., 1982; Trank and Smith, 1996; Courtine et al., 2005; Boyer et al., 2007, but see Gebo, 1993).

The observation by Boyer et al. (2007) of low levels of activity for all focal muscles during vertical climbing in lemurids also parallels our results, and reinforces their challenge to the hypothesis that the increased size of the adductor musculature in the I-II grasp is an adaptation to vertical clinging at large body sizes (Gebo, 1985). The lack of expected muscle activity further suggests that additional research is needed into the forces acting on the fore- and hindlimbs of small-bodied primates during vertical locomotion; the distribution of body-weight between limbs during this activity is unknown and likely affects the required strength of the manual and pedal grasps.

Despite general similarity between the results of this study and those of Boyer et al. (2007), the muscle recruitment patterns reported by Boyer et al. (2007) for I-II grasping in lemurs do differ from those reported here for I-V grasping in lorises in two notable ways. First, during small dowel grasping, lorises rely largely on the hallual adductor to maintain this grasp, while lemurs exhibit little to no activity in this muscle, recruiting the two digital flexors instead. This is contrary to the recruitment pattern predicted by the relative size of the musculature and configuration of the bony grasping complex advocated by Gebo (1985). Because lemurs utilize a I-II grasp, they were expected to use the hallual adductor to “pinch” the dowel more so than the lorises (Gebo, 1985). That they did not suggests that while a morphological dichotomy exists within the prosimian pes, it is not necessarily related to grasping. We suggest that referring to the different pedal morphologies as “grasp types” is inaccurate, but acknowledge that our findings here may relate to a need to adduct the osteologically hyper-abducted hallux of the loris to pull it into opposition with the other digits; lemurids exhibit a lower degree of osteological abduction and may not need to physically adduct the hallux to pull it into a more optimal position to grasp the dowel. This hypothesis could be tested by examining recruitment patterns in other strepsirrhines exhibiting a I-V grasp, but lacking the extreme physiologic abduction of the loris hallux (e.g., galagos).

The second difference involves the recruitment of peroneus longus and brevis during small pole standing and power grasping. While in the present study, both peroneal muscles are active during these behaviors, they remain notably silent in Boyer et al.'s (2007) lemurid subjects. Indeed, recruitment of the peroneal muscles in the lemurid subjects was limited to locomotor behaviors. It is possible that the more frequent EMG activity of the lorises' peroneal muscles may be related to the ability of peroneus longus to dorsiflex as well as evert the foot (although dorsiflexion was not observed for peroneus brevis during back-stimulation in this study, the tendon of this muscle also passes over the lateral surface of the fibula and any dorsiflexion it produces may be slight). Dorsiflexion may be important for stabilization of the ankle while standing on or clinging to small diameter substrates, but would not have been detected in the lemur study since no dorsiflexors were included. Alternatively, the more frequent use of the peroneal muscles may be related to the type of grasp utilized by the lorises. The I-II adductor grasp of the lemurids studied by Boyer et al. (2007) featured an oblique orientation of the third through fifth metatarsals relative to the first and second metatarsals. In contrast, all metatarsals in the I-V opposable grasp of lorises lie in the same plane. It is possible that the rearrangement of the tarsometatarsal joint into a continuous, obliquely oriented structure in a I-II adductor grasp provides better osteological support for the foot in inverted positions, and thereby reduces the need for muscular effort in stabilizing the ankle. If this indeed is the case, then in such

situations it is plausible that the contribution of peroneus longus to maintaining a I-V hallual grasp may be substantial enough to drive selection for an enlarged peroneal process. This in turn may relieve the hallual adductor of the need to fire at high levels. This speculation, however, is beyond the scope of the current study.

As was the case with lemurids (Boyer et al., 2007), the present study has demonstrated that peroneus longus is not a major contributor to grasp strength through hallual adduction in subjects with a I-V opposable grasp. We conclude, therefore, that an enlarged peroneal process is not directly associated with powerful grasping ability. Of course, our data do not allow us to rule out the possibility that the large peroneal tubercle of lorises serves to increase the mechanical advantage of peroneus longus to adduct the hallux as a means of assisting the hallual adductor during strenuous grasping behaviors in which peroneus longus is already active as an ankle evertor. A detailed study of the energetics associated with the recruitment of these muscles may shed light on a possible benefit of such an arrangement as a potential mechanism of selection for a large peroneal tubercle.

If an enlarged peroneal process is not directly related to grasping, then what, if any, functional purpose may this trait serve? An alternative hypothesis put forth by Szalay and Dagosto (1988) suggested that the large peroneal process buttresses the entocuneiform-first metatarsal joint from unusually large strains generated during landing after a leap. This hypothesis seems to be garnering some support from recent studies that have found a weak correlation between the “robustness,” or size of the process and leaping frequency (Gebo et al., 2008; Jacobs et al., 2008, in press). While this correlation most likely does not fully explain the presence of the hypertrophied peroneal process (lorises possess such a peroneal process and do not leap), these results offer a plausible alternative direction for researchers interested in the role of the peroneal process in primate evolution that may be better developed through the study of landing forces on the hallual tarsometatarsal joint and biomechanical modeling of stresses on the first metatarsal.

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