



Rotator cuff muscle size and the interpretation of scapular shape in primates



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ABSTRACT

Scapular shape variation among primates is widely viewed as being strongly related to locomotor differences. The relative importance of overhead forelimb elevation in the locomotor repertoire of a species, as reflected in muscular leverage for scapular rotation or in the sizes of attachment areas for muscles involved in glenohumeral elevation, has proven to be a useful organizing principle for understanding this variation. While generally successful in sorting primate scapulae into functional groups, the scapulae of some species do not entirely match predictions based on the perceived importance of forelimb elevation. A recent study has shown that scapular fossa sizes in apes are not as accurate predictors of the sizes of the muscles arising from them as has been assumed. To further explore the degree of correspondence between actual and predicted muscle size based on the perceived importance of forelimb elevation, the current study examines the relative sizes of the rotator cuff muscles in a wider sample of primate taxa using published data on muscle mass and cross-sectional area. The results do not support some of the accepted generalizations about the relative sizes of members of the rotator cuff based on measurements of the sizes of scapular fossae. For example, orthograde apes do not display enlarged supraspinatus muscles compared to pronograde monkeys. Differences in assessments of relative muscle size based on mass compared to those based on cross-sectional area suggest that poor correspondence between muscle size predicted from scapular fossa size and actual muscle size may be related to constraints on scapular form associated with muscular leverage for scapular rotation and with scapular position on the thorax.

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Introduction

In a series of papers in the 1960's and 70's, Ashton, Oxnard, and colleagues demonstrated that many aspects of scapular form in primates were more closely related to locomotor habits than to taxonomy (Ashton and Oxnard, 1964; Ashton et al., 1965a,b, 1971; 1976; Oxnard, 1963, 1967). The scapular features they examined were related to enhancements of the mechanism that brings about scapular rotation, an integral part of overhead elevation of the forelimb. They based their selection of specific scapular characteristics (Fig. 1) both on the EMG validated scapulothoracic force couple model for scapular rotation presented by Inman et al. (1944) that emphasized the importance of the cranial trapezius and caudal serratus anterior, and on their own observations of differences in the configurations of these muscles among different primate locomotor groups (Ashton and Oxnard, 1963). Their analyses were

able to explain the well-established differences among primates in the scapular index (ratio of scapular length to scapular breadth; Schultz, 1930), with the more craniocaudally broad scapulae of orthograde suspensory primates (e.g., *Pan*; Fig. 2) reflecting improved leverage for cranial trapezius and caudal serratus anterior to cause scapular rotation. Although Inman et al. (1944) also drew attention to the influence of the changing proportions of two members of the rotator cuff, supraspinatus and infraspinatus, on scapular shape, Ashton and Oxnard's (1963) own observations of minimal differences in these muscles among primate locomotor groups led them to downplay any role for the cuff muscles in shaping scapular form, and they even explored whether characteristics of dorsal scapular fossa shape might better reflect taxonomy than function (Ashton et al., 1965b).

In a landmark study, Roberts (1974) took up the suggestion by Inman et al. (1944) that the rotator cuff muscles were also an important influence on primate scapular form (see also Kimes et al., 1979; Doyle et al., 1980). He reasoned that since the supraspinatus and infraspinatus filled the areas of the dorsal scapular fossae,

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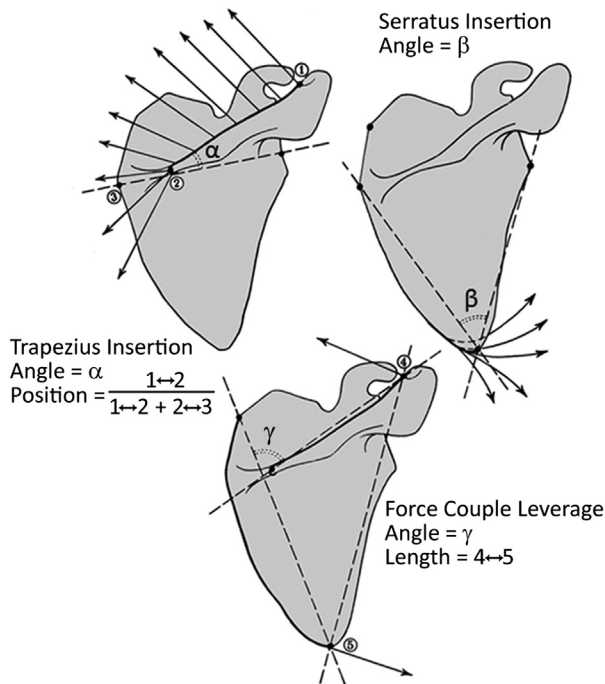


Figure 1. Features related to improved leverage for a scapulothoracic force couple mechanism involving trapezius and serratus anterior to bring about scapular rotation (Oxnard, 1963, 1967; Ashton and Oxnard, 1964; Ashton et al., 1965a,b, 1971, 1976). Adapted from Oxnard (1963).

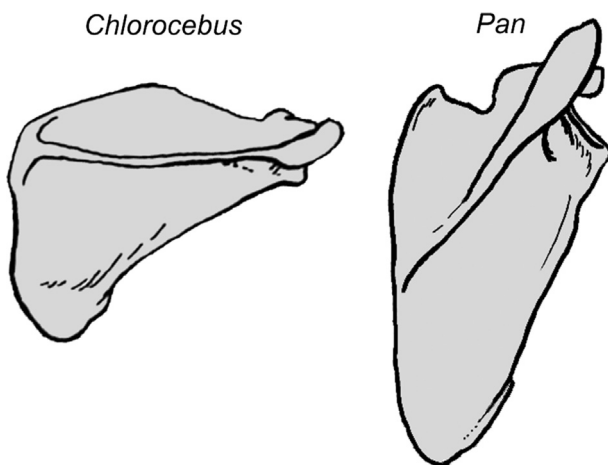


Figure 2. Contrast in scapular form between a semiterrestrial quadrupedal primate, *Chlorocebus*, and a suspensory primate, *Pan*. Scapular length is traditionally measured along the scapular spine, and breadth is the distance perpendicular to length. Therefore, the scapula of a quadrupedal monkey is described as being long and narrow, while that of a suspensory primate is short and broad. Alternatively, Hunt (1991) has characterized the scapula of suspensory primates as being mediolaterally compressed. Additional differences include a more oblique scapular spine and the existence of a more defined superior angle in suspensory primates.

differences in scapular fossa size must reflect differences in muscle size. Roberts (1974) again cited the importance of arm-raising in determining the functional importance of the rotator cuff and also noted the concomitant increased dependence on the cuff muscles for stabilization as shoulder mobility increased. Contrary to the assertion of Inman et al. (1944), however, that differences in scapular fossa size among primates were due primarily to the increasing size of the infraspinatus in species that engaged in greater use of the forelimb in overhead postures and locomotion,

Roberts (1974) reported that enlargement of both the supraspinous and infraspinous fossae in such groups was apparent when scapular fossa size was normalized to scapular spine length.

These studies have in large part formed the foundation of current views about the influence of function over phylogeny on primate scapular form. Although they were painted with a broad brush using groupings of taxa into somewhat artificial 'locomotor categories,' this functional framework has proven useful even in studies on a more detailed level (e.g., Corruccini and Ciochon, 1976; Fleagle, 1977; Fleagle and Meldrum, 1988; Larson, 1993; Fleagle and McGraw, 2002). This is not to say that there have not been unexpected or seemingly anomalous observations, particularly as morphometric techniques have improved to allow more accurate characterization of details of scapular form. For example, Taylor (1997) had limited success in using muscle function to explain scapular shape differences between lowland and mountain gorillas, in part due to the fact that the competing demands for shoulder stability versus mobility often made ambiguous biomechanical predictions regarding emphasis on particular muscles (see also Taylor and Slice, 2005). The scapula of orangutans has been especially difficult to understand within this functional framework. As the most arboreal and suspensory of the great apes (Hunt, 2004), orangutans should display a craniocaudally tall, but mediolaterally narrow scapula with an oblique scapular spine and enlarged supraspinous and infraspinous fossae. Instead, the scapula of orangutans is fairly wide mediolaterally, and though the spine is oblique, it is not markedly so (Young, 2008; Bello-Hellegouarch et al., 2013). The supraspinous fossa is unexpectedly small while the infraspinous fossa is unusually large (Schultz, 1930; Roberts, 1974; Young, 2008; Bello-Hellegouarch et al., 2013; Green, 2013). To explain why the shape of the orangutan scapula does not match predictions, some researchers have suggested that perhaps current morphometric approaches have failed to capture salient aspects of scapular fossa size in orangutans that reflect enlargement of supraspinatus (e.g., Bello-Hellegouarch et al., 2013). Alternatively, perhaps we have incorrectly emphasized orthograde manual suspension in orangutan locomotor postures and behaviors, and should instead look to pronograde suspension and horizontal bridging motions as playing more dominant roles in orangutan positional behavior (Young, 2008; Green, 2013). A third possibility is that orangutans employ different shoulder biomechanics than other apes, which has resulted in emphasis on different components of their shoulder musculature (e.g., Young, 2003).

The latter possibility was recently explored in a comparative EMG study of rotator cuff muscle function during locomotion in orangutans, chimpanzees, and gibbons (Larson and Stern, 2013). The results of this study revealed no notable differences in how supraspinatus, infraspinatus, subscapularis, and teres minor were recruited in these three taxa, thus failing to find evidence for different shoulder mechanics to account for differences in scapular form, at least in regard to the influence of the rotator cuff muscles. This study went on to compare the actual sizes of the rotator cuff muscles in orangutans, chimpanzees, and gibbons and demonstrated that contrary to impressions derived from comparative scapular fossa size, orangutans do not have an unexpectedly small supraspinatus or an unusually large infraspinatus. In fact, the authors report little correspondence between ratios of supraspinatus/infraspinatus muscle size and ratios of supraspinous/infraspinous fossa size in apes or humans. Larson and Stern (2013) suggested that analyses of scapular fossa size may be overlooking other influences on scapular shape such as the role of the scapular spine as structural reinforcement of the blade, as well as the influence of the large ventral member of the rotator cuff, the subscapularis.

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