Scapular Morphology and Forelimb Use during Foraging in Four Sympatric Cercopithecids

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Key Words

Colobus · *Piliocolobus* · *Cercopithecus* · *Cercocebus* · Shoulder morphology · Feeding

Abstract

Most investigations of primate scapular morphology use differences in locomotion to explain variation; less is known about how scapular geometry covaries with nonlocomotor behavior. We examined forelimb use during foraging in 4 cercopithecids ranging throughout the Ivory Coast's Tai Forest. During 5-min feeding bouts, we recorded the frequency individuals of *Piliocolobus badius*, *Colobus polykomos*, *Cercocebus atys* and *Cercopithecus diana* performed 5 forelimb behaviors involved in the acquisition and introduction of food to the oral cavity. Scapulae from these populations were examined to determine whether differences in forelimb use were reflected in features known to correspond with varying degrees of arm flexion, abduction and elevation. Our results reveal that the species differ markedly in forelimb use and that these differences are interpretable via their scapular morphology. For example, *P. badius* engages in more frequent flexion, abduction and elevation of the arm above the head relative to *C. polykomos*, and red colobus scapulae are longer craniocaudally and have larger, more cranially directed supraspinous fossae than those of closely related black-and-white colobus. Our attempt to explore how nonlocomotor behavior covaries with skeletal morphology should provide for more informed interpretations of the primate fossil record.

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Introduction

Most functional analyses of the primate scapula have relied on locomotor differences to interpret size and shape variation [Keith, 1891, 1923; Avis, 1962; Napier, 1963; Ashton and Oxnard, 1963, 1964a, b; Ashton et al., 1965, 1967; Oxnard, 1967;

Ashton et al., 1971; Roberts, 1974; Ashton et al., 1976; Fleagle, 1977a, b; Stern and Susman, 1983; Schultz, 1986; Fleagle and Meldrum, 1988; Larson, 1993, 1995; Taylor, 1997; Taylor and Slice, 2005; Wright, 2007; Young, 2008; Green, 2013; Green et al., 2015; Larson, 2015]. Even prior to the availability of quantitative field data, arguments about scapular adaptation in primates were based largely, if not exclusively, on what were perceived as the skeletal correlates of forelimb usage during locomotion, with primates sorted into locomotor groups based on such features as overall shape, size of infrapinuous and supraspinous fossae, glenoid geometry and spine orientation [Ashton and Oxnard, 1964a, b; Ashton et al., 1965; Oxnard, 1967; Roberts, 1974; Larson, 1995]. Suspensory taxa that could habitually elevate the arm above the head using scapular rotation and humeral abduction, tended to have craniocaudally long and narrow scapulae, more cranially extended supraspinous fossae, more oblique spines and shallower glenoids [Ashton and Oxnard, 1964a]. Scapulae of more quadrupedal primates were characterized by a more squared overall shape (i.e. scapular length equal to scapular width), a larger infrapinuous fossa relative to the supraspinous fossa, a more laterally oriented spine and a deeper glenoid cavity [Roberts, 1974]. Primates with scapular features ‘intermediate’ to those of bona fide brachiators, such as hylobatids, and quadrupeds, such as baboons, were labeled semibrachiators and assumed to exhibit locomotor repertoires that combined elements of quadrupedalism and brachiation. Taxa assigned to the semibrachiator category included *Alouatta*, *Ateles*, *Colobus* and *Presbytis* [Ashton and Oxnard, 1963].

Beginning in the 1960s, field studies providing data on the manner and frequency behaviors were actually performed under natural conditions revealed problems in classifications based on morphology alone, especially with regard to presumed semibrachiators and their shoulder morphology. Several authors discovered that purported semibrachiators not only did not exhibit locomotor profiles ‘intermediate’ to those of quadrupedal and suspensory taxa, but also the primates labeled semibrachiators had little in common with each other, exhibiting instead a diversity of locomotor behaviors [Ripley, 1967; Mittermeier and Fleagle, 1976; Fleagle, 1977a, b]. *Colobus* monkeys occupied the center of such discussions. At one point, all colobines were grouped together as semibrachiators based on the ‘intermediate’ scapular morphology of one taxon – *Colobus guereza* [Napier, 1961; Ashton and Oxnard, 1963, 1964a, b; Ashton et al., 1965]; however, data collected over the last 50 years have highlighted major differences in the degree to which colobines use their forelimbs during locomotion [Ripley, 1967; Rose, 1973; Mittermeier and Fleagle, 1976; Fleagle, 1977a, b, 1978; Morbeck, 1977, 1979; Rose, 1979; Gebo and Chapman, 1995; McGraw, 1996; Byron and Covert, 2004; Isler and Gruter, 2006; Wright et al., 2008]. Two points are especially relevant here. First, Asian colobines are now known to be more suspensory than any of their African counterparts, with several Asian taxa engaging in accomplished bimanual locomotion [Bleisch et al., 1993; Byron and Covert, 2004; Workman and Covert, 2005; Wright et al., 2008]. Second, of the three forms of African colobus – red colobus, black-and-white colobus and olive colobus – only one is known to regularly use its forelimbs in a suspensory manner. Studies of the 3 African colobines in the Ivory Coast’s Tai Forest reveal that while all colobines move primarily by quadrupedal walking, climbing and leaping [McGraw, 1996, 1998a], only red colobus engage in suspensory behavior. Red colobus were not observed using postures involving hanging by one or two forelimbs; however, they did occasionally use a forelimb to grasp and briefly swing from a support to propel them-

Fig. 1. Red colobus (*Piliocolobus badius*) leaping in the Tai Forest. Note the abducted shoulder.

selves forward or upward, usually at the end of a leap or quadrupedal bout [McGraw, 1996, 1998a]. In other cases, leaping red colobus would occasionally land with their forelimbs elevated above the head – a behavior brought about by arm flexion or abduction [sensu Ashton and Oxnard, 1964] – and briefly suspend themselves before pulling their body up to a stable support (fig. 1). Such behaviors, labeled ‘Schwingkletter’ by Ullrich [1961], were discussed by Stern and Oxnard [1973] in their important critique of semibrachiation. Stern and Oxnard [1973, p. 47] explained that Ullrich’s term was intended to distinguish bona fide arm-swinging from behavior he observed in guerezas which occurs ‘... often between closely lying branches during which jumps the landing is made with the outstretched hands and a swing is then used to propel the animal to a branch beyond. Also, when *C. guereza caudatus* jumps to an overlying branch, the latter may be grasped with outstretched arms and the maneuver completed by a pullup’. Stern and Oxnard [1973, p. 47], citing Struhsaker [pers. commun.], also noted that ‘the red, but not black colobus, may end a jump by grabbing an overhead branch and then swinging from beneath it to its upper surface’.

These observations notwithstanding, available field data indicate that suspensory locomotion does not comprise a significant part of the positional repertoire of any African colobine. In the Tai Forest, no suspensory behavior of any kind was observed in either black-and-white colobus (*Colobus polykomos*) or olive colobus (*Procolobus verus*), and it accounted for only 3.9% of all positional activities in red colobus (*Piliocolobus badius*) [McGraw, 1996, 1998a]. Similar results were obtained in a study of sympatric red colobus and black-and-white colobus in Uganda’s Kibale National Park [Gebo and Chapman, 1995]. Still, the fact that red colobus put their forelimbs in tension during Schwingkletter – albeit infrequently – while black-and-white colobus in the same environments do not, raises the possibility that in these taxa there exist differences in scapular morphology associated with varying tendencies to flex, abduct and elevate the arm. Support for this prediction comes from recent field studies of Asian colobines documenting forelimb suspension involving arm flexion/abduction and elevation, and from comparative analyses showing that colobines have scapulae with features indicating greater shoulder mobility than cercopithecines [Wright et al., 2008; Schmidt and Krause, 2011]. Finally, given the likelihood that the

forelimbs are utilized at least as often during food acquisition (i.e. capturing food and introducing it to the oral cavity) as they are during locomotion, it is possible that differences exist in the manner and degree that monkeys use their forelimbs to obtain food from different locations. That is, the monkeys will vary in their tendency to extract food while the arm is flexed or abducted at the shoulder in order to raise the forelimb above the head. We examine these issues in 4 cercopithecoid species living in the Ivory Coast's Tai Forest for which a skeletal sample is available. We use new field data on forelimb use during foraging to test the degree to which differences in scapular morphology reflect varying tendencies for these 4 monkey species to flex/abduct and elevate the arm above the head under the general null hypothesis that species use their forelimbs in a similar fashion during foraging.

Materials and Methods

Study Site

Behavioral data were collected between December 2011 and March 2012, and May to July 2013 in the study grid of the Tai Monkey Project [McGraw et al., 2007]. The grid encompasses 1 km² of evergreen rain forest and is located near the western border of Tai National Park, approximately 25 km from the Liberian border. Primate groups in the grid are fully habituated and have been under regular observation since 1989 [Holenweg et al., 1996; Wachter et al., 1997; McGraw and Zuberbühler, 2008]. Tai National Park is part of the Upper Guinea Forest, a moist evergreen rain forest that receives an average annual rainfall of 1,830 mm during a long dry season (November to March), long wet season (April to June), short dry season (July to August) and short wet season (September to October) [McGraw, 1998a]. Tai National Park is located in the southwest corner of Côte d'Ivoire (0°15'–6°07' N, 7°25'–7°54' W) and comprises 330,000 ha of protected forest with a 20,000 ha buffer zone surrounding the boundary of the park.

We quantified forelimb use during foraging in adults of 4 taxa: *C. polykomos* (Western black-and-white or King colobus), *P. badius* (Western red colobus), *Cercocebus atys* (sooty mangabey) and *Cercopithecus diana* (Diana monkey). We were primarily interested in the behavior of the 2 colobine species; however, we included 2 other taxa – a noncolobine arboreal species (*C. diana*) and a terrestrial species (*C. atys*) – for contrast. Data were collected during 5-min focal periods with data collection commencing after an individual had been observed actively foraging for at least 1 min. No individual was sampled within 1 h of itself in order to avoid potential autocorrelation of data. During each focal period we recorded the total number of forelimb movements involved in the acquisition of food while monkeys were stationary. We excluded forelimb use involved in locomotion during feeding, restricting our sampling scheme to removal/retrieval of food from substrates and introduction of the food into the oral cavity (fig. 2). We were especially interested in the frequency that members of each species elevated their forelimb at or above the head, whether brought about by flexion and/or abduction of the arm at the shoulder [Ashton and Oxnard, 1964a; Wright et al., 2008; Schmidt and Krause, 2011]. The 5 categories of behavior were: (1) *inferior retrieval*: the forelimb extends inferior to the torso, the hand grasps an object, the elbow flexes and the food object is raised; (2) *parallel retrieval*: the forelimb extends parallel to the torso with minimal arm flexion/abduction in order to grasp the food object, the elbow flexes and brings the object toward the body; (3) *superior retrieval*: the arm is flexed or abducted and the forelimb raised above the torso so that a hand may grasp a food object, the elbow flexes and the food object is directed inferiorly; (4) *rake*: the forelimb is alternately flexed and extended, while the forearm and wrist are pronated and supinated to search the leaf litter on the ground, and (5) *manual-oral transfer*: food is introduced into the oral cavity with a flexed elbow and, frequently, flexed wrist. The number of focal periods for each species is *C. atys* n = 258, *C. diana* n = 141, *C. polykomos* n = 126 and *P. badius* n = 125. G tests of interdependence were used to compare overall forelimb movement profiles. Statistics were performed using SAS 9.3 software.

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Fig. 2. Forelimb activities used during foraging. Top row (from left to right): superior retrieval, parallel retrieval, inferior retrieval; bottom row (from left to right): rake and manual-oral transfer. See text for definitions.

Morphometric Data

Scapulae of naturally deceased adult monkeys collected in the Tai Forest were used for morphological analyses. Sample sizes for each species are *C. atys* $n = 4$, *C. diana* $n = 4$, *C. polykomos* $n = 10$ and *P. badius* $n = 10$. Digital calipers were used to create 6 indices from standard scapular landmarks: scapular shape, supraspinous fossa size, infraspinous fossa size, relative musculus teres major attachment size, relative glenoid depth and glenoid shape (fig. 3). These indices were chosen because of their relevance to shoulder mobility, particularly behaviors associated with enhanced capacity to flex, abduct and elevate the arm at or above the torso [Ashton and Oxnard, 1964a, b; Schmidt and Krause, 2011]. For example, relative to infraspinous fossa size, a larger supraspinous fossa corresponds with a larger supraspinatus muscle which functions as a forelimb elevator and aids the deltoid muscle in forelimb abduction. A more expansive and defined origin for teres major muscle on the scapula's axillary border indicates enhanced development of the m. teres major, a muscle that assists in drawing the previously elevated forelimb inferiorly and posteriorly. This action not only facilitates climbing, but is also important for frequent retrieval of items located at or above the level of the torso. A shallower, more hemispheric glenoid is associated with greater shoulder mobility compared to one that is deeper and more tear drop shaped [Roberts, 1974]. The Microsoft Windows application Surface Protractor was used to measure bar glenoid angle [Stern and Susman, 1983] and spine angle (fig. 3). We compared sample means of functional indices and angles using general linear models in SPSS.

In order to account for differences not detectable by traditional 2-dimensional indices, a MicroScribe 3DX digitizer was used to take 24 landmark points in 3 dimensions derived from Young [2008]. Data were collected on the 28 scapulae described above plus 18 additional adult *P. badius* scapulae collected from Tai Forest. These data were analyzed using (1) Procrustes analysis to control for size-related variation and (2) principal component analysis (PCA) with full tangent space projection in Morphologika2 v2.5 software [Slice, 2007].

Fig. 3. Scapula of *P. badius* in dorsal, lateral and ventral views. Landmarks and angles are as follows: B = crest of supraspinous flange; E = inferomedial corner of m. teres major attachment; F = inferolateral corner of m. teres major attachment; G = superomedial corner of m. teres major attachment; H = superolateral corner of m. teres major attachment; I = infraglenoid tubercle; K = inferior portion of glenoid; L = superior portion of glenoid; M = widest portion of glenoid on dorsal aspect; N = widest portion of glenoid on ventral aspect; O = deepest point of glenoid; U = point on dorsal surface of blade just superior to V; V = point on spine in which spine angle is perpendicular to B; Y = spine angle; Z = bar-glenoid angle. Scapular indices and angles calculated as follows: scapular shape = BF/DI , supraspinous fossa size = BU/BF , infraspinous fossa size = WF/BF , m. teres major attachment width = EF/BF , glenoid depth = O/LK , glenoid shape = MN/LK .

Results

Forelimb Foraging Behavior

Figure 4 depicts the average number of times per focal period each cercopithecoid species performed the 5 foraging behaviors. All pairwise comparisons are significant ($p < 0.01$) indicating that each species uses its forelimbs in significantly different ways and with different frequencies during foraging. Rake is the most common forelimb movement used by *C. atys*. Sooty mangabeys at Tai Forest National Park spend much of their foraging time searching the leaf litter on the ground for fallen seeds and nuts [McGraw et al., 2011]. This foraging tendency is also reflected by the greater rate of inferior retrieval practiced by sooty mangabeys compared to all other taxa. Compared to the Diana monkey, both colobines engaged in higher rates of parallel and superior retrieval, but not inferior retrieval. Both colobines bring food to their oral cavity more frequently than does either cercopithecine.

Figure 5 depicts the relative frequencies the arboreal taxa performed each of the 3 food retrieval behaviors; that is, the frequencies reflect how often food was collected from 1 of 3 planes (superior, parallel and inferior). G tests for the food retrieval profiles of these taxa all indicate significant differences among all species combinations ($p < 0.01$ for all pairwise comparisons). The most common food acquisition behavior for all species was parallel retrieval, with this behavior ranging from 52% in *P. badius*

Fig. 4. Average number of times per focal period that each of 5 forelimb behaviors was performed by each species. All pairwise comparisons are significant ($p < 0.01$).

Fig. 5. Relative frequency that each of 3 food retrieval movements was performed by each of 3 arboreal taxa. G tests reveal that food retrieval profiles of all species are significantly different from each other. G tests for overall food retrieval profiles indicate significant differences among all species ($p < 0.01$ for all pairwise comparisons).

Fig. 6. Scapulae of 4 cercopithecoid species from Tai Forest.

to 61.9% in *C. polykomos*. Diana monkeys used inferior retrieval (31.6%) much more often than did *C. polykomos* (17.6%) and *P. badius* (14.3%). *P. badius* used superior retrieval (33.7%) more often than did *C. polykomos* (20.5%) and *C. diana* (11.2%). In other words, one third of red colobus' food is collected from above the head.

Morphometrics

Scapulae from the Tai Forest cercopithecoids are depicted in figure 6, while data and F statistics (with 3 degrees of freedom) for the scapular indices and angles are presented in table 1. With respect to overall shape, *C. atys* and *C. diana* do not differ significantly from each other. Similarly, *C. polykomos* and *P. badius* do not differ significantly from one another, but both are significantly different from the 2 cercopithecines ($p < 0.01$). The relative size of the supraspinous fossa is significantly larger in *P. badius* compared to *C. atys* ($p = 0.02$), *C. diana* ($p < 0.01$) and *C. polykomos* ($p = 0.03$). The latter 3 taxa are not significantly different from one another. All pair-

Table 1. Scapular indices and angles

Metric	F statistics/ p value	<i>C. atys</i> (n = 4)	<i>C. diana</i> (n = 4)	<i>C. polykomos</i> (n = 10)	<i>P. badius</i> (n = 10)
Scapular shape	16.80/<0.01	1.03 (0.08)	1.02 (0.04)	1.22 (0.07)	1.30 (0.13)
Supraspinous fossa size	2.83/<0.01	0.26 (0.03)	0.25 (0.01)	0.27 (0.01)	0.29 (0.01)
Infraspinous fossa size	3.62/0.03	0.73 (0.04)	0.73 (0.02)	0.77 (0.03)	0.74 (0.01)
Teres major muscle attachment size	8.48/<0.01	0.053 (0.0062)	0.035 (0.0021)	0.063 (0.013)	0.063 (0.012)
Glenoid depth	9.46/<0.01	0.17 (0.02)	0.14 (0.01)	0.14 (0.01)	0.14 (0.01)
Glenoid shape	5.64/<0.01	0.94 (0.08)	0.99 (0.07)	0.96 (0.09)	0.98 (0.17)
Bar-glenoid angle, degrees	0.28/n.s.	135.65 (3.93)	140.28 (4.80)	135.86 (4.18)	133.10 (4.86)
Spine angle, degrees	33.44/<0.01	94.41 (3.95)	93.03 (4.61)	104.85 (4.45)	112.97 (4.32)

Degrees of freedom for all F statistics are 3; n.s. = nonsignificant. Figures in parentheses indicate standard deviations.

wise comparisons of relative infraspinous fossa size are not significant except *C. atys* versus *C. polykomos* ($p = 0.05$). The relative m. teres major attachment area is significantly smaller in *C. diana* compared to *C. atys* ($p = 0.04$) and the colobines ($p < 0.01$). Relative glenoid depth is significantly greater in *C. atys* relative to *C. diana* ($p = 0.01$), *C. polykomos* ($p < 0.01$) and *P. badius* ($p < 0.01$). Relative glenoid shape differs significantly between *C. atys* and *C. diana* ($p < 0.01$). All comparisons of the bar-glenoid angle are nonsignificant. With regard to spine angle, *P. badius* is significantly greater than *C. atys* ($p < 0.01$), *C. diana* ($p < 0.01$) and *C. polykomos* ($p < 0.01$). *C. polykomos* is also significantly different from the other 3 taxa ($p < 0.01$ for all pairwise comparisons).

Results of the PCA are presented in figure 7. The first 2 principal components explain 38.1% of the total variance and readily separate the 4 taxa. PC1 comprises 25.6% of the overall variance and predominantly discriminates *P. badius* from the other 3 taxa. The variation associated with PC1 primarily relates to craniocaudal length, dorsoventral width and supraspinous fossa size and shape. Positive PC1 values indicate a squarer overall shape with a smaller, less cranially extending supraspinous fossa, while negative PC1 values correspond with a taller, narrower shape and a larger and more cranially extending supraspinous fossa flange. PC2 explains 12.5% of the overall variance and distinguishes *C. diana*, *C. atys* and *C. polykomos* from one another. The variation summarized by PC2 largely encompasses m. teres major attachment size and coracoid process orientation. Positive PC2 values correspond with a larger (i.e. more superiorly extending and ventrally projecting) m. teres major attachment and a coracoid process projecting more anteroinferiorly. Negative PC2 values are associated with a shorter, broader m. teres major attachment and more superiorly projecting coracoid process.

C. atys is associated with extreme positive PC1 values and mean PC2 values indicating the most square-like shape of all the taxa, a shallow scapular notch and a short, broad m. teres major attachment. *C. diana* is likewise characterized by positive PC1 values and is associated with a flatter, squarer overall shape and a short, broad m. teres major attachment. A more superiorly projecting coracoid process associated with negative PC2 values separates *C. diana* from *C. atys*. *C. polykomos* is associated with mean to positive PC1 values and positive PC2 values. *C. polykomos* PC1 values

Fig. 7. PCA of adult *C. atys*, *C. diana*, *C. polykomos* and *P. badius* scapulae with wireframes of principal component axes.

lie between those of *P. badius* and *C. atys* translating to an overall shape and supraspinous fossa size that are intermediate to the aforementioned taxa. Positive PC2 values differentiate *C. polykomos* from *C. diana* and correspond with a longer, narrower m. teres major attachment and a more inferiorly projecting coracoid process. *P. badius* is associated with negative PC1 values and virtually the entire spectrum of PC2 values. In general, *P. badius* scapulae have a craniocaudally longer, narrower overall shape, more cranially extending supraspinous fossa, and more pronounced anterior curvature.

Discussion

The manner and frequency that monkeys – especially colobines – use their forelimbs in a suspensory fashion, the term(s) describing such a behavior, and the influence suspensory activities have on monkey scapular form have been discussed and debated for over 50 years. Arguments about whether colobines employ some form of

bimanual progression have swung back and forth: the term semibrachiation was created [Napier, 1961], applied to several taxa including colobines [Ashton et al., 1964a, b], critiqued and discredited [Stern and Oxnard, 1973; Mittermeier and Fleagle, 1976], and recently resurrected [Byron and Covert, 2006; Wright et al., 2008]. With the benefit of actual locomotor field data, it has been established that several Asian colobines, particularly *Pygathrix* spp., regularly engage in bimanual locomotion and forelimb suspensory postures [Wright et al., 2008]. Similar bimanual locomotion involving alternating hand-holds is unknown among African colobines, but there is now ample evidence that some African colobus are more apt than others to use their forelimbs in flexed/abducted, elevated positions during locomotion (e.g. leaping) and, especially, during foraging. This point was emphasized by Napier who noted that ‘arm-swinging locomotion constitutes a spectrum of activity ranging from the locomotion of essentially quadrupedal Primates which use the hands freely to slow or arrest their progress when jumping gaps in the forest canopy (semibrachiators), to the fully specialized bimanues which are solely dependent on their hands for rapid and effective arboreal locomotion (brachiators)’ [Napier, 1963, pp. 186–187]. We are not recommending that the semibrachiation label be reapplied to any African colobine, but we agree with Napier’s position that there are monkeys who engage their forelimbs in activities which, while not brachiation per se, do involve elevation of the forelimb above the head which is brought about by flexion and/or abduction of the arm at the shoulder. Such behaviors may include a brief suspensory period, and several scapular correlates of forelimb elevation align some African colobines more with suspensory apes than with more quadrupedal cercopithecids, just as Ashton et al. [1965] contended. The case is even stronger among Asian colobines: in their study of *Pygathrix* spp. and *Nomascus leucogenys*, Wright et al. [2008, p. 1476] concluded that ‘red-shanked and gray-shanked doucs at the EPRC are capable of adopting suspensory forelimb postures similar to those exhibited by lesser apes. The behaviors are reflected in morphological features of the forelimb...’ Given the evidence for suspensory locomotion in at least some colobines, the primary purpose of our project was to examine the extent that scapular features associated with arm flexion/abduction and elevation were associated with differences in forelimb use during foraging.

The high frequencies of raking behavior and inferior retrieval in sooty mangabeys are a consequence of a foraging strategy aimed at locating and collecting foods from the leaf litter on the forest floor [McGraw, 1998a; Fleagle and McGraw, 2002; McGraw et al., 2011]. Diana monkeys engage in the fewest forelimb movements during foraging, most likely due to their tendency to continually move through feeding patches while scanning for ripe fruit and insects [McGraw, 1998b; Kane et al., 2013]. Diana monkeys often feed either while moving or from quadrupedal standing positions, and they frequently retrieve food located above them by standing on their hindlimbs and grasping a support with one forelimb while the other is used to procure food (fig. 8). This latter behavior, described by McGraw [1998b] after Hunt et al. [1996] as ‘stand-forelimb suspend’, accounts for nearly 20% of all Diana monkey foraging postures and explains their modest frequencies of superior retrieval compared to the other 2 arboreal taxa. In sum, most Diana monkey food is acquired from parallel and inferior planes and when food is located above them, Diana monkeys frequently stand on 2 legs to acquire it.

Our 2-dimensional analysis reveals that when corrected for size, *C. diana* exhibits a shallower glenoid and a smaller m. teres major attachment than does *C. atys*.

Fig. 8. Adult female Diana monkey in Tai Forest retrieving food from above while standing on its hindlimbs.

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Fig. 9. Adult female red colobus resting in Tai Forest abducts its arm at the shoulder while its infant nurses. We argue that red colobus have more mobile shoulders than do black-and-white colobus and that this mobility is reflected in differences in their respective scapulae.

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These results are corroborated by the PCA which shows that *C. diana* scapulae exhibit smaller *m. teres major* attachments. In addition, the PCA reveals differences between *C. diana* and *C. atys* scapulae not captured by our 2-dimensional indices: *C. diana* has narrower inferior angles and a more superiorly positioned coracoid process relative to the glenoid cavity. While the functional significance of some features is not yet clear (e.g. coracoid process orientation), morphological distinctions between the 2 taxa are generally consistent with differing degrees of arboreality: *C. diana* is almost exclusively arboreal, while *C. atys* is largely terrestrial [McGraw, 1998a, b]. Others have noted that scapulae of terrestrial quadrupeds typically have a mediolaterally/dorsoventrally wide blade, a more laterally oriented spine, absence of pronounced supraspinous fossa flange, and a deeper glenoid relative to scapulae of arboreal primates [Roberts, 1974; Larson, 1995]. Our 2-dimensional indices and PCA results support this functional distinction.

Like *C. diana*, the colobines in this study are arboreal foragers; however, forelimb use profiles of *P. badius* and *C. polykomos* differ significantly from that of the Diana monkey. Both colobines use superior and parallel retrieval more frequently

than does *C. diana*, a difference likely attributable to the colobines' reliance on more ubiquitously distributed foods in contrast to those sought by *C. diana* [McGraw, 1998b]. Many foods preferred by Tai colobines, such as leaves and large seed pods, can be obtained and/or processed from seated positions. Indeed, *P. badius* and *C. polykomos* feed and forage from seated positions more than 97% of the time, a practice we believe explains why the 2 colobines are able to gather so much of their food using parallel or superior retrieval and which accounts for such modest frequencies of inferior retrieval. Despite the shared tendency to forage from seated positions, there are significant differences between the colobine species in overall food retrieval profiles. *P. badius* utilizes superior retrieval more often (33.7%) than does *C. polykomos* (20.5%). Though we only quantified movement of the forelimb directly involved in food procurement, we suspect that the more frequent superior retrieval exhibited by *P. badius* may be associated with more pronounced shoulder mobility (fig. 9) and that this is reflected in their scapular morphology. *P. badius* at Tai Forest forages more often in tree crown peripheries than does *C. polykomos* [McGraw and Sciulli, 2011], so a more mobile shoulder that expands the foraging radius would obviously be adaptive.

Consistent with the differences in forelimb use profiles, colobine scapulae display features indicative of greater arm flexion, abduction and elevation compared to cercopithecines. Such features include a more cranially extended supraspinous fossa and a more oblique scapular spine (fig. 6). These results are in accordance with those of Schmidt and Krause [2011] who determined that, relative to body size, the scapulae of the Colobinae and Hominidae were the most dorsoventrally narrow (short) of the 16 primate families sampled. According to these authors, this shape 'allows for a dorsal position but combined with a more laterally facing glenoid' [Schmidt and Krause, 2011, p. 99]. If such a configuration facilitates greater shoulder mobility – as the analyses of these authors would suggest – then it helps explain why the Tai Forest colobines engage in more frequent arm elevation than do either cercopithecine. Furthermore, a more expansive, ventrally projecting m. teres major attachment in the colobines is consistent with differences in their foraging behavior compared to the cercopithecines. The m. teres major is responsible for drawing an elevated forelimb downward and backward just after the superior retrieval of food items and during their manual delivery to the oral cavity. Significantly, these trends discriminating colobines from cercopithecines are also evident to a lesser degree when comparing *C. polykomos* and *P. badius*. As the foraging behavior would suggest, our 2-dimensional indices and PCA found that the *P. badius* scapulae exhibit the greatest extremes of these features, indicating a more flexible shoulder.

We recognize our behavioral data set is modest, and we are in no position to determine how much scapular morphology is attributable to locomotion versus posture; however, understanding that nonlocomotor behaviors, such as the foraging movements highlighted here, covary with scapular features associated with significant arm flexion, abduction, elevation and occasionally suspension provides for more informed interpretations of the behavioral repertoires associated with different scapulae, including those of fossil taxa [Birchette, 1982; Anapol, 1983; MacLatchy et al., 2000; Senut et al., 2004]. We also recognize the role of phylogeny in constraining morphology; however, the clear separation in the PCA of the two most closely related taxa, *C. polykomos* and *P. badius*, strongly suggests that our analyses primarily reflect functionally significant differences. We therefore conclude that forelimb movements

during foraging are reflected in differences in scapular morphology and that red colobus monkeys, known to occasionally use their forelimbs in suspensory locomotion, also abduct, flex and elevate their arms above their head more often during foraging than do black-and-white colobus in the same habitat.

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References

- Anapol F (1983). Scapula of *Apidium phiomense*: a small anthropoid from the Oligocene of Egypt. *Folia Primatologica* 40: 11–31.
- Ashton EH, Oxnard CE (1963). The musculature of the primate shoulder. *Transactions of the Zoological Society of London* 29: 553–650.
- Ashton EH, Oxnard CE (1964a). Functional adaptations in the primate shoulder girdle. *Journal of Zoology* 142: 49–66.
- Ashton EH, Oxnard CE (1964b). Locomotor patterns in primates. *Proceedings of the Zoological Society of London* 142: 1–28.
- Ashton EH, Flinn RM, Oxnard C, Spence TF (1971). The functional and classificatory significance of combined metrical features of the primate shoulder girdle. *Journal of Zoology* 163: 319–350.
- Ashton EH, Flinn RM, Oxnard CE, Spence TF (1976). The adaptive and classificatory significance of certain quantitative features of the forelimb in primates. *Journal of Zoology* 179: 515–556.
- Ashton EH, Healy MJR, Oxnard CE, Spence TF (1965). The combination of locomotor features of the primate shoulder girdle by canonical analysis. *Journal of Zoology* 147: 406–429.
- Ashton EH, Oxnard C, Spence TF (1967). Scapular shape and primate classification. *Proceedings of the Zoological Society of London* 145: 125–142.
- Avis V (1962). Brachiation: the crucial role for man's ancestry. *Southwestern Journal of Anthropology* 18: 119–148.
- Birchette M (1982). *The Postcranial Skeleton of Paracolobus chemeroni*. PhD dissertation, Harvard University.
- Bleisch W, Cheng A-S, Ren X-D, Xie J-H (1993). Preliminary results from a field study of wild Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*). *Folia Primatologica* 60: 72–82.
- Byron CD, Covert HH (2004). Unexpected locomotor behavior brachiation by an Old World monkey (*Pygathrix nemaeus*) from Vietnam. *Journal of Zoology* 263: 101–106.
- Fleagle JG (1977a). Locomotor behavior and muscular anatomy of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *American Journal of Physical Anthropology* 46: 297–308.
- Fleagle JG (1977b). Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yearbook of Physical Anthropology* 20: 440–453.
- Fleagle JG (1978). Locomotion, posture, and habitat utilization in two sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). In *The Ecology of Arboreal Folivores* (Montgomery GG, ed.), pp 243–251. Washington, Smithsonian Press.
- Fleagle JG, McGraw WS (2002). Skeletal and dental morphology of African papionins: unmasking a cryptic clade. *Journal of Human Evolution* 42: 267–292.
- Fleagle JG, Meldrum DJ (1988). Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *American Journal of Primatology* 16: 227–249.
- Gebo DL, Chapman CA (1995). Positional behavior in five sympatric Old World monkeys. *American Journal of Physical Anthropology* 97: 49–76.

- Green DJ (2013). Ontogeny of the hominoid scapula: the influence of locomotion on morphology. *American Journal of Physical Anthropology* 152: 239–260.
- Green DJ, Serrins JD, Seitelman B, Martiny AR, Gunz P (2015). Geometric morphometrics of hominoid infrapinnous fossa shape. *Anatomical Record* 298: 180–194.
- Holenweg AK, Noe R, Schabel M (1996). Waser's gas model applied to associations between red colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Folia Primatologica* 67: 125–136.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D (1996). Standardized descriptions of primate and postural modes. *Primates* 37: 363–387.
- Isler K, Gruter CC (2006). Arboreal locomotion in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). *Folia Primatologica* 77: 195–211.
- Kane EE, Bitty EA, Daegling D, McGraw WS (2013). A preliminary investigation of forelimb use among cercopithecoid primates in Côte d'Ivoire's Tai Forest. *American Journal of Physical Anthropology* 150(suppl 56): 162.
- Keith A (1891). Anatomical notes on Malay apes. *Journal of the Royal Asiatic Society* 23: 77–89.
- Keith A (1923). Man's posture: its evolution and disorders. *British Medical Journal* i: 451–454, 499–502, 545–548, 587–590, 624–626, 669–672.
- Larson SG (1993). Functional morphology of the shoulder in primates. In *Postcranial Adaptation in Non-human Primates* (Gebo DL, ed.), pp 45–69. DeKalb, Northern Illinois University Press.
- Larson SG (1995). New characters for the functional interpretation of primate scapulae and proximal humeri. *American Journal of Physical Anthropology* 98: 13–35.
- Larson SG (2015). Rotator cuff size and the interpretation of scapular shape in primates. *Journal of Human Evolution* 80: 96–106.
- MacLatchy L, Gebo D, Kityo R, Pilbeam D (2000). Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *Journal of Human Evolution* 39: 159–183.
- McGraw WS (1996). Cercopithecoid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 190: 507–522.
- McGraw WS (1998a). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 105: 493–510.
- McGraw WS (1998b). Posture and support use of Old World monkeys (Cercopithecidae): the influence of foraging strategies, activity patterns and the spatial distribution of preferred food items. *American Journal of Primatology* 46: 229–250.
- McGraw WS, Sciulli PW (2011). Posture, ischial tuberosities and tree zone use in West African cercopithecids. In *Primate Locomotion: Linking Field and Laboratory Research* (D'Août K, Vereecke EE, eds.), pp 215–245. New York, Springer.
- McGraw WS, Zuberbühler K (2008). Socioecology, predation and cognition in a West African monkey community. *Evolutionary Anthropology* 17: 254–266.
- McGraw WS, Vick A, Daegling DJ (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 144: 140–153.
- McGraw WS, Zuberbühler K, Noe R (eds.) (2007). *Monkeys of the Tai Forest: An African Primate Community*. Cambridge, Cambridge University Press.
- Mittermeier RA, Fleagle JG (1976). The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. *American Journal of Physical Anthropology* 45: 235–256.
- Morbeck ME (1977). Positional behavior, selective use of habitat substrate and associated non-positional behavior in free-ranging *Colobus guereza*. *Primates* 18: 35–58.
- Morbeck ME (1979). Forelimb use and positional adaptation in *Colobus guereza*: integration of behavioral, ecological, and anatomical data. In *Environment, Behavior and Morphology: Dynamic Interactions in Primates* (Morbeck ME, Preuschoft H, Gomberg N, eds.), pp 95–117. New York, Fischer.
- Napier JR (1961). Prehensility and opposability in the hands of primates. *Symposia of the Zoological Society of London* 5: 115–132.
- Napier JR (1963). Brachiation and brachiators. The Primates. *Symposia of the Zoological Society of London* 10: 183–194.
- Oxnard CE (1967). The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. *American Journal of Physical Anthropology* 26: 219–240.
- Ripley S (1967). The leaping of langurs: a problem in the study of locomotor adaptation. *American Journal of Physical Anthropology* 26: 149–170.
- Roberts D (1974). Structure and function of the primate scapula. In *Primate Locomotion* (Jenkins FA Jr, ed.), pp 171–200. New York, Academic Press.
- Rose MD (1973). Quadrupedalism in primates. *Primates* 14: 337–357.

- Rose MD (1979). Positional behavior of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In *Environment, Behavior and Morphology: Dynamic Interactions in Primates* (Morbeck ME, Preuschoft H, Gomberg N, eds.), pp 75–93. New York, Fischer.
- Schmidt M, Krause C (2011). Scapula movements and their contribution to three-dimensional forelimb excursions in quadrupedal primates. In *Primate Locomotion: Linking Field and Laboratory Research* (D'Août K, Vereecke EE, eds.), pp 83–107. New York, Springer.
- Schultz M (1986). The forelimb of the colobinae. In *Comparative Primate Biology Vol 1: Systematics, Evolution and Anatomy* (Swindler D, Erwin J, eds.), pp 559–670. New York, Liss.
- Senut B, Nakatsukasa M, Kunimatsu Y, Nakano Y, Takano T, Tsujikawa H, Shimizu D, Kagaya M, Ishida H (2004). Preliminary analysis of *Nacholapithecus* scapula and clavicle from Nachola, Kenya. *Primates* 45: 97–104.
- Slice D (2007). Geometric morphometrics. *Annual Review of Anthropology* 26: 261–281.
- Stern JT, Oxnard CE (1973). Primate locomotion: some links with evolution and morphology. *Primateologia* 4: 1–93.
- Stern JT, Susman RL (1983). The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology* 60: 279–317.
- Taylor AB (1997). Scapula form and biomechanics in gorillas. *Journal of Human Evolution* 33: 529–553.
- Taylor AB, Slice DE (2005). A geometric morphometric assessment of the relationship between scapular variation and locomotion in African apes. In *Modern Morphometrics in Physical Anthropology* (Slice DE, ed.), pp 299–318. New York, Kluwer Academic/Plenum Press.
- Ullrich W (1961). Zur Biologie und Soziologie der Colobusaffen (*Colobus guereza caudatus* Thomas 1885). *Zoologischer Garten Leipzig* 25: 305–368.
- Wachter B, Schabel M, Noe R (1997). Diet overlap and polyspecific associations of red colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Ethology* 103: 514–526.
- Workman C, Covert HH (2005). Learning the ropes: the ontogeny of locomotion in red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh langurs (*Trachypithecus hatinhensis*). I. Positional behavior. *American Journal of Physical Anthropology* 128: 371–380.
- Wright KA (2007). The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. *American Journal of Primatology* 69: 736–756.
- Wright KA, Stevens NJ, Covert HH, Nadler T (2008). Comparisons of suspensory behaviors among *Pygathrix cinerea*, *P. nemaeus*, and *Nomascus leucogenys* in Cuc Phuong National Park, Vietnam. *International Journal of Primatology* 29: 1467–1480.
- Wu B-Q (1993). Patterns of spatial dispersion, locomotion and foraging in three groups of the Yunnan snub-nosed langur (*Rhinopithecus bieti*). *Folia Primatologica* 60: 63–71.
- Young NM (2008). A comparison of the ontogeny of shape variation in the anthropoid scapula: functional and phylogenetic signal. *American Journal of Physical Anthropology* 136: 247–264.