Journal of Human Evolution 82 (2015) 145–158

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Jaw-muscle architecture and mandibular morphology influence relative maximum jaw gapes in the sexually dimorphic *Macaca fascicularis*

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ARTICLE INFO

Article history:
Received 26 August 2014
Accepted 4 February 2015
Available online 7 April 2015

Keywords:
Crab-eating macaques
Fossil primates
Craniofacial morphology
Physiologic cross-sectional area
Functional morphology

ABSTRACT

Maximum jaw gape is a performance variable related to feeding and non-feeding oral behaviors, such as canine gape displays, and is influenced by several factors including jaw-muscle fiber architecture, muscle position on the skull, and jaw morphology. Maximum gape, jaw length, and canine height are strongly correlated across catarrhine primates, but relationships between gape and other aspects of masticatory apparatus morphology are less clear. We examine the effects of jaw-adductor fiber architecture, jaw-muscle leverage, and jaw form on gape in an intraspecific sample of sexually dimorphic crab-eating macaques (*Macaca fascicularis*). As *M. fascicularis* males have relatively larger maximum gapes than females, we predict that males will have muscle and jaw morphologies that facilitate large gape, but these morphologies may come at some expense to bite force.

Male crab-eating macaques have relatively longer jaw-muscle fibers, masseters with decreased leverage, and temporomandibular joint morphologies that facilitate the production of wide gapes. Because relative canine height is correlated with maximum gape in catarrhines, and males have relatively longer canines than females, these results support the hypothesis that male *M. fascicularis* have experienced selection to increase maximum gape. The sexes do not differ in relative masseter physiologic cross-sectional area (PCSA), but males compensate for a potential trade-off between muscle excursion versus muscle force with increased temporalis weight and PCSA. This musculoskeletal configuration is likely functionally significant for behaviors involving aggressive canine biting and displays in male *M. fascicularis* and provides additional evidence supporting the multifactorial nature of the catarrhine masticatory apparatus. Our results have implications for the evolution of craniofacial morphology in catarrhine primates and reinforce the importance of evaluating additional factors other than feeding behavior and diet in analyses of masticatory apparatus form, function, and evolution.

Introduction

Maximum jaw gape is a performance measure (*sensu* Arnold, 1983) that has been functionally linked to ingestion, mastication, and display behaviors across mammals (Arendsen de Wolf-Exalto, 1951; Herring, 1972, 1975; Greaves, 1974, 1995; Herring and Herring, 1974; Hylander, 1979a; Lucas, 1981, 1982; Jablonski, 1993a; Dumont and Herrel, 2003; Vinyard et al., 2003; Williams et al., 2009; Santana et al., 2010; Hylander, 2013). A large gape facilitates the exploitation of food items that may otherwise remain inaccessible to individuals or taxa with smaller gapes (Hylander, 1979a; Bourke et al., 2008; Norconk et al., 2009). Maximum jaw opening ability is also a critical component of canine displays (or 'yawning') in some primates (Herring and Herring, 1974; Smith, 1984; Jablonski, 1993a). Canine displays occur in multiple contexts, but in Old World monkeys these behaviors are often interpreted as aggressive threats or other social displays. A wide jaw gape also facilitates canine biting and slashing during aggressive encounters with conspecifics or predators (Altmann, 1967; Kummer, 1968; Hadidan, 1980; Troisi et al., 1990; Plavcan and van Schaik, 1992;

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http://dx.doi.org/10.1016/j.jhevol.2015.02.006
0047-2484/

Plavcan, 2001; Hylander, 2013). Male primates engage in agonistic canine display behaviors with other males to compete for access to mates while females generally compete for access to resources (Plavcan, 2011). In crab-eating macaques and mangabeys these display behaviors occur more frequently in males than in females, and in older individuals compared to subadults (Deputte, 1994). Canine size, along with timing of canine eruption, wear, and breakage, are significantly correlated with male reproductive success in sexually dimorphic mandrills (Leigh et al., 2008). Collectively, these data suggest that maximum jaw gape, which facilitates maximum canine clearance beyond the occlusal plane (Herring and Herring, 1974; Lucas, 1981; Hylander, 2013) and arguably signals social rank, may also be correlated with male fitness in sexually dimorphic Old World monkeys.

Building on previous work for primates (e.g., Lucas, 1981) and other mammals (e.g., Herring and Herring, 1974), Hylander (2013) recently demonstrated that maximum jaw gape varies within and among catarrhine species as a function of canine height. Thus, in catarrhines exhibiting marked canine sexual dimorphism, males have both relatively more projecting canines and are capable of achieving relatively larger maximum gapes compared to conspecific females. The ability of primates and other mammals to produce relatively large gapes has been correlated with relative muscle fiber length, jaw-adductor position on the skull (i.e., leverage), and aspects of jaw form (Herring and Herring, 1974; Dechow and Carlson, 1990; Wall, 1999; Vinyard et al., 2003; Taylor et al., 2009; Hylander, 2013).

Some morphological features that facilitate a relatively wide jaw gape, however, do so at the expense of relative bite force production. For example, adult male catarrhines might be predicted to have relatively long jaw-adductor muscle fibers, more caudally positioned jaw muscles, and/or relatively long mandibles to increase relative maximum gape (e.g., Herring and Herring, 1974; Lucas, 1982; Smith, 1984; Vinyard et al., 2003; Taylor et al., 2009; Hylander, 2013). A potential trade-off in bite force follows (Gans and Bock, 1965; Gans, 1982; Van Eijden et al., 1997) because for two muscles of comparable volume, increasing jaw-muscle fiber length will improve muscle stretch and excursion, but at some expense to muscle physiologic cross-sectional area (PCSA), which determines the muscle's intrinsic force-generating capacity (Powell et al., 1984). Additionally, caudally positioned jaw muscles and longer jaws would be expected to decrease muscle leverage. Given these potential trade-offs, if selection has acted on behaviors emphasizing relatively wide maximum jaw gapes in male catarrhines, then selection for these behaviors may come at some expense to male masticatory features that facilitate muscle and bite forces (Hylander, 2013). In fact, Dechow and Carlson (1990) previously showed that in the highly dimorphic Rhesus macaque (*Macaca mulatta*), females have greater mechanical advantage of the masseter for both incisor and molar biting compared to males. This mechanical advantage in females was due to their shorter load arm (i.e., more posteriorly placed molars) relative to masseter moment arm lengths. With improved leverage, females could convert a greater percentage of masseter muscle force to bite force compared to males, particularly at the molars. Similarly, Hylander (2013) hypothesized that in early hominins, reduced canine size and maximum jaw gape facilitated increased mechanical efficiency of the masticatory apparatus.

The interplay among competing functional demands is a fundamental challenge for organisms when navigating their complex environments. These interactions are difficult to identify in fossils where we essentially lack a physiological and behavioral record. Thus, paleontological studies often turn to living species to better understand the functional and adaptive significance of the morphological configurations we observe across the evolutionary history of primates, including our own evolution. Here we look specifically at the non-masticatory use of the feeding apparatus in studying the morphological correlates of maximum jaw gapes to better understand the factors that influence intra- and interspecific variation in masticatory form. We extend previous work (e.g., Herring and Herring, 1974; Lucas, 1981, 1982; Dechow and Carlson, 1990; Hylander, 2013) to explore the musculoskeletal correlates of jaw gape in the sexually dimorphic crab-eating macaque (*Macaca fascicularis*), with the explicit intention of testing Hylander's (2013) hypothesis. Linear maximum gape is sexually dimorphic in *M. fascicularis*, with male gapes reaching 112% of jaw length while female maximum gapes are only ~80% of their jaw length (Hylander, 2013). Given that large gape likely contributes to canine display behaviors, we hypothesize that as selection acted to increase relative male canine length in Old World monkeys, a functional consequence of displaying elongated canines was an increase in relative maximum jaw gape (Hylander, 2013). Based on this hypothesis, we explore musculoskeletal mechanisms for achieving relatively wide maximum gapes and the concomitant costs to relative muscle and bite forces in crab-eating macaques.

We acknowledge that this analysis of one species may not fully characterize the evolutionary pattern observed for all Old World monkeys, as multiple morphological solutions to the challenges of increasing gape may readily exist across primates (Bock, 1959; Vinyard et al., 2003). That said, there are advantages to examining these potential tradeoffs in a single species. First, macaques, including *M. fascicularis*, have long served as model species for experimental and comparative approaches to understanding masticatory apparatus form, function, and evolution in primates (e.g., Hylander, 1979a,b; Bouvier and Hylander, 1981; Hylander and Crompton, 1986; Hylander et al., 1987, 1992; Hylander and Johnson, 1989, 1994; Dechow and Carlson, 1990; Hiiemae et al., 1995; Wall, 1999; Ross et al., 2005, 2010). Thus, by identifying which of the predicted musculoskeletal changes underlie the capacity for relatively wide mouth opening in male *M. fascicularis*, we extend this previous work to better understand how the macaque masticatory apparatus has evolved to meet multiple and often competing demands, including those linked to both feeding and non-feeding behaviors involving the masticatory apparatus. Moreover, addressing these relationships in a single species enables us to control for the interspecific variation in feeding and social behaviors that would be present in a broader comparative analysis. From this perspective, intraspecific variation serves as an important baseline for interpreting the functional and adaptive significance of interspecific patterns in both living and fossil primate species.

Predictions linked to facilitating increased jaw gape and diminished muscle and bite force

To determine potential musculoskeletal features that facilitate relatively wide jaw gapes in male *M. fascicularis*, we draw on biomechanical theory and previous studies to generate a series of predictions regarding internal muscle architecture, muscle position and leverage, and skull morphology. We frame these predictions in terms of the expected musculoskeletal attributes that maximize jaw gape in males and the attendant costs to males in terms of their capacity to generate muscle and bite forces. Most predictions are not mutually exclusive.

<u>Prediction 1a. Males have relatively longer and less pinnate muscle fibers.</u> Muscle architecture refers to the internal orientation of muscle fibers relative to the force-generating axis of the muscle (Lieber, 2010). Two architectural variables underlying muscle function are 1) fiber length (Lf), which is proportional to maximum muscle excursion and contraction velocity (Bodine et al., 1982), and 2) physiologic cross-sectional area (PCSA), which