## fWHR in macaques

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## 11 Abstract

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13 Keywords: facial width height ratio

Word count: X

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## fWHR in macagues

16 Introduction

In many primate species, the face is used not only as a means of emotional expression 17 (Calcutt, Rubin, Pokorny & de Waal, 2017; Parr & Waller, 2006; Waller & Micheletta, 2013) 18 but as a way to communicate other socially relevant information such as fertility (Rigaill et al., 2015; Setchell et al. 2006; Dubuc et al., 2009), or health and mate fitness (Thornhill & Gangestad, 2006; Kramer & Ward, 2010; Henderson et al., 2016; Valentine et al., 2014; Little et al., 2012). Facial colouration for example has been linked to social status in male mandrills (Mandrillus sphinx) and drills (Mandrillus leucophaeus), with stronger facial 23 colouration found in higher ranking males (Setchell et al. 2008; Marty et al. 2009). In rhesus macaques, facial colouration in males is not linked to dominance status, but is 25 thought to be an indicator of mate quality (Waitt et al. 2003; Dubuc et al. 2014). It is possible however that other facial characteristics are linked to rank or assertive traits in this 27 species. For example, Borgi & Majolo (2016) found links between a measure of face width, 28 the facial Width-to-Height Ratio (fWHR) and dominance style. Across 11 macaque species, fWHR is higher in both sexes in macaque species with despotic female dominance styles, such as in rhesus macaques, compared to more socially tolerant species such as Tonkean 31 macaques. Rhesus macaques are amongst the most despotic of macaque species, with a strict female dominance hierarchy and high levels of intra-group aggression (Thierry, 2000). Borgi and Majolo's findings suggest that face width could be a signal of dominance that reduces the need for conflict amongst species for whom escalated conflict could have serious 35 consequences. Previous work in humans supports links to dominant behaviour. In human males, 37 aggressiveness and fighting ability have consistently been associated with a higher fWHR (Haselhuhn, Ormiston & Wong, 2015; Anderl et al., 2016; Trebicky et al. 2015; Zilioli et al. 2015; Goetz et al. 2013). Wider male faces are also perceived as being more aggressive (Alarajih & Ward; Lefevre & Lewis 2013; Mileva et al. 2014; Stirrat & Perrett, 2010),

suggesting that face width is a social cue to aggressive and assertive behaviour. Similar findings in brown capuchins reveal that this relationship is not unique to humans (Lefevre et al. 2014; Wilson et al., 2014). For adults of both sexes, fWHR is related to ratings of Assertiveness, and furthermore is higher amongst alpha individuals (Lefevre et al. 2014). Whether the face is a social cue of assertiveness is still under debate (Wilson et al. under review). Furthermore, it has been suggested, both in humans (Goetz et al. 2013; Welker, Goetz & Carre, 2015) and capuchins (Carré, 2014) that the relationship between face width and dominant/aggressive behaviour is driven by low social status, that is, the relationship between fWHR and aggressive behaviour is only significant amongst low-status individuals. It is possible that, given that high social status usually comes with conspecifics' social knowledge of that status, there is no need for high ranking individuals to physically advertise assertiveness. Contrastingly, for a low status individual, advertising assertive behaviour via a social cue could be beneficial to obtaining resources.

Whilst the current literature on facial morphology provides some very intriguing 55 insights into the social role of physical features, our interpretations of this data are limited by the choice of study species, which are primarily human. In the current study, we propose 57 to expand this research to a wider taxa. Given the links between fWHR and social tolerance across the Macaca genus (Borgi & Majolo, 2016), it would be interesting to explore in more detail whether this ratio is linked specifically to dominance behaviour in a despotic macaque species. In the following study we decided to explore the relationship of fWHR in rhesus macaques to two different measures of dominance, (1) hierarchical dominance measured using David's scores and (2) personality ratings of dominance, which assess overall tendencies towards assertive and aggressive behaviour, rather than social standing. As fWHR correlates positively with despotism (Borgi & Majolo, 2016), we predict that (1) higher fWHRs should be found amongst individuals with higher social status, similar to findings in capuchins (Lefevre et al., 2014); (2) fWHR should also be positively related to ratings of dominance; and (3) if the relationship between fWHR and dominance is driven by low social status, then we should find a significant relationship amongst individuals with low social status, but not high social status, as measured by David's scores.

In addition to examining the fWHR, we will explore a second metric, the facial 71 Lower-Height-Full-Height ratio (fLHFH). Whilst not well studied, this metric has previously 72 been used as part of a masculinity index in human males (Penton-voak et al., 2001). fLHFH 73 has also been associated with higher ratings of Neuroticism and lower ratings of Attentiveness in brown capuchins, traits that are both strongly related to vigilance behaviour (Wilson et al 2014; Morton et al., 2013). In capuchins, Wilson et al. (2014) proposed that 76 these traits may be conceived of as one form of social status, prosocial competence, as 77 defined by Lilienfeld et al. (2012), suggesting that facial height may also play a role in social 78 cues. Moreover, a recent study suggests that upper face height is an important component to consider when assessing face width: decreases in upper face height relative to bizygomatic width led to increased perceptions of aggressiveness compared with faces with the same width but increased upper face height (Costa, Lio, Gomez & Sirigu, 2017). Thus proportional face height may also be considered as an important component in 83 understanding facial dominance. To shed more light on the role of face height in social behaviour, we additionally aimed to examine the relationship between (1) fLHFH and ratings on six personality components, labelled Confidence, Openness, Dominance, Friendliness, Activity and Anxiety, and (2) fLHFH and David's scores. Based on previous findings in brown capuchins (Wilson et al., 2014) we predict that (4) ratings of lower Confidence or higher Anxiety were most likely to be associated with higher fLHFH ratios, and (5) we would not find a relationship between face height and David's scores. I would like to look at this, but we can't with the following data: Given the 91 links between face width and assertive behaviour, and the link to intraspecific despotism, it would be useful to explore to what extent social tolerance of different species varies with variation in fWHRs. If fWHR is dependent on social status, one would expect to find larger differences in this ratio between alpha and non-alpha individuals in despotic species over

96 socially tolerant species .

97 Methods

We report how we determined our sample size, all data exclusions (if any), all

manipulations, and all measures in the study.

100 Participants

101 Material

102 Procedure

103 Data analysis

We used R (3.4.0, R Core Team, 2017) and the R-packages devtools (1.13.3, Wickham

<sup>105</sup> & Chang, 2017), and *papaja* (0.1.0.9492, Aust & Barth, 2017) for all our analyses.

106 Results

apa\_print(m1)

108 Discussion

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