

Sexual Dimorphism and Morphological Integration in Baboons

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Introduction

Savanna baboons are highly sexually dimorphic primates, with body mass in males reaching up to twice that of females (Plavcan and van Shaik, 1997). In addition to obvious body size differences, sexual dimorphism (SD) is particularly evident in facial features. Dimorphic traits in the baboon skull are localized particularly to the rostrum surrounding the upper canines, the supraorbital arches, and the positioning of inion (e.g., Frost et al., 2003). The ontogeny of SD in the baboon cranium has been studied extensively (e.g., Freedman, 1962; Leigh and Cheverud, 1991). Leigh and Cheverud (1991) found that although male and female baboons share a similar ontogenetic trajectory in the face, males attain their more robust phenotype by extending the growth trajectory beyond that of females (producing a “hyper-adult” morphology, i.e., via peramorphosis).

Morphological integration (MI) reflects developmental relationships within an organism manifested as the covariation of its parts (Figure 1). MI can address specific evolutionary questions by measuring the effects of known or hypothesized biological causes of association within the phenotype (Cheverud, 1982; Chernoff and Magwene, 1999). Because SD results from developmental differences in males and females, distinctive patterns of MI in males and females should mirror these variations in their respective development programs. If, as embryology suggests, female development is the default pathway for mammals, then the changes to this pathway necessary to produce a male phenotype must require changes in patterns of morphological integration.

Our study compares patterns of MI in adult male and female baboons to examine the following expectations.

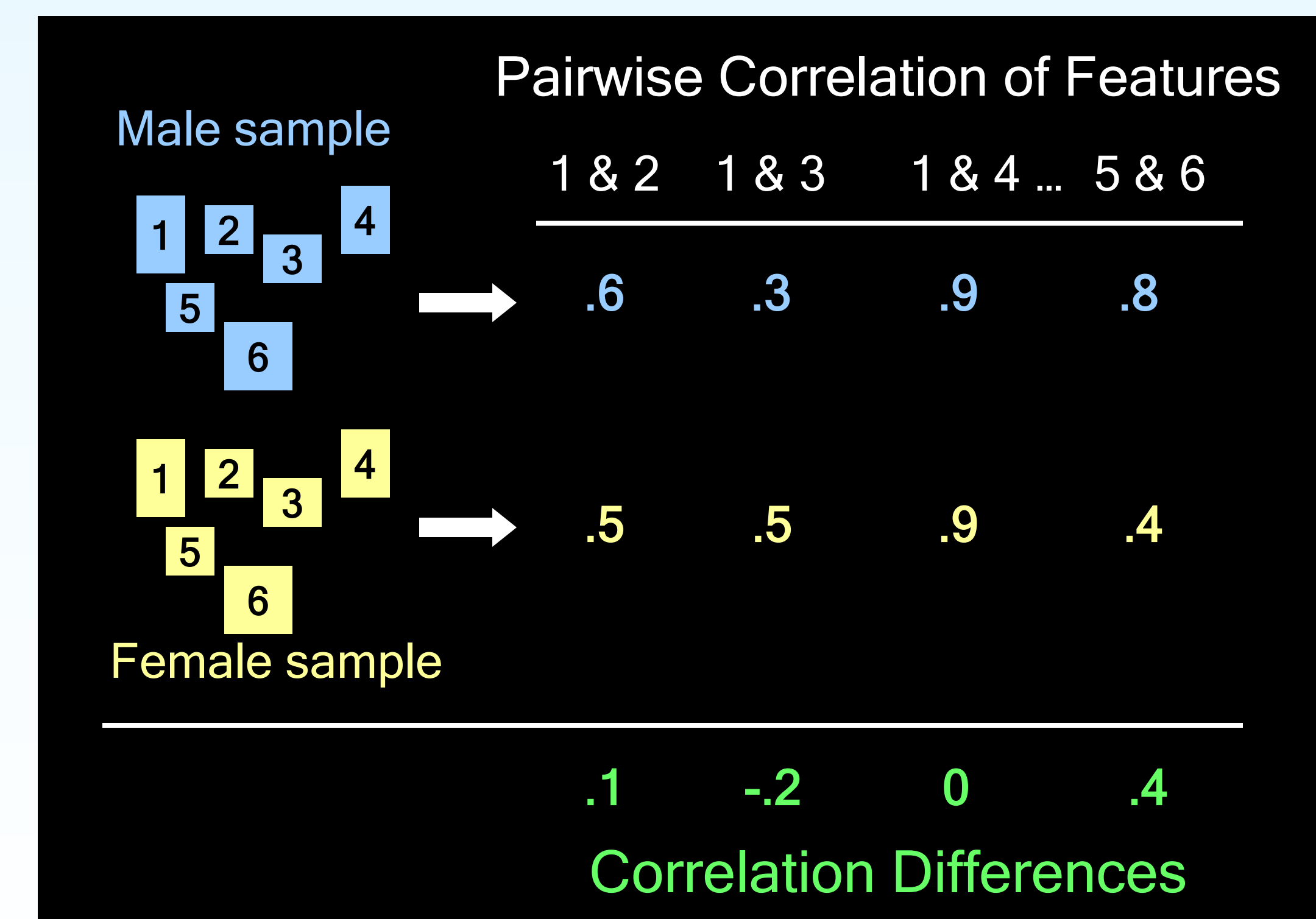


Figure 1. Schematic representation of morphological integration. Each symbol represents an average measure of a given trait within a sample.

Expectations

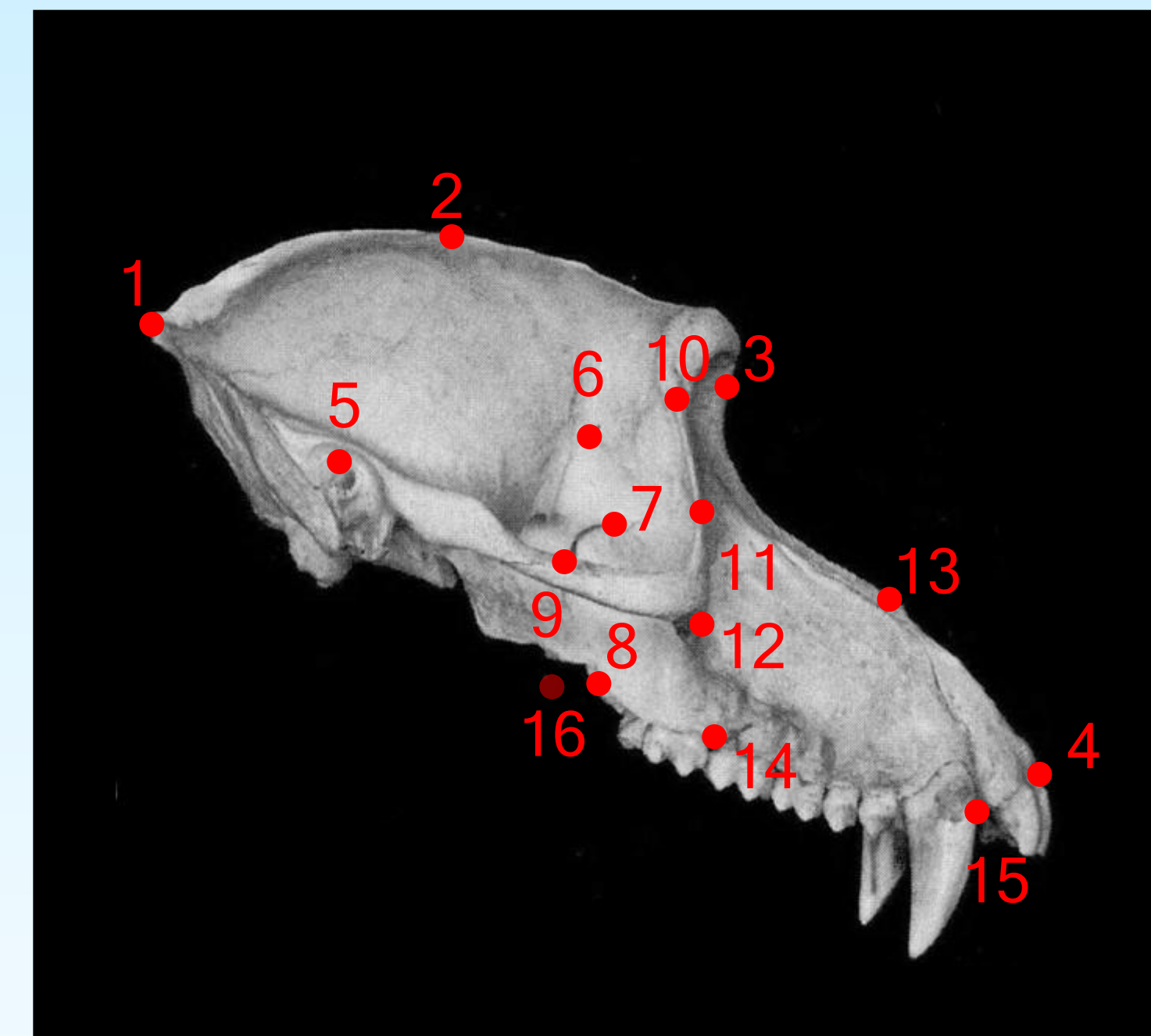
- We hypothesize that the varying developmental pathways required to produce sexually dimorphic adults will be detectable in the adult phenotype as local differences in MI.
- We expect that the strong SD in canine size, supraorbital ridging and nuchal cresting will exhibit itself in differing degrees of integration in these areas.

Materials and Methods

Sample. The study sample consists of 47 adult, wild-caught individuals from the American Museum of Natural History, New York and the National Museum of Natural History, Washington D.C. This total number includes males (N=28) and females (N=19) of three subspecies of *Papio hamadryas*: *P. h. cynocephalus*, *P. h. anubis*, and *P. h. ursinus*. Three-dimensional coordinate locations were collected for 16 landmarks from the midline and right side of the neurocranium, face, and palate (Figure 2) using a 3Space™ digitizer (Aldridge and Richtsmeier, 1999). Linear distances were calculated from the coordinate data and used in this study of MI.

Figure 2. Landmarks used in this analysis: **1)** lambda, **2)** bregma, **3)** nasion, **4)** intradentale, **5)** external auditory meatus, **6)** pterion, **7)** superior pterygopalatine fissure, **8)** maxillary tuberosity, **9)** superior zygo-temporal suture, **10)** zygo-frontal suture at orbital rim, **11)** superior zygo-maxillary suture, **12)** inferior zygo-maxillary suture, **13)** nasale, **14)** external alveolar border between M²-M³, **15)** external premaxillary-maxillary suture, **16)** vomer-sphenoid junction (hidden from view).

Measuring morphological integration. MIBoot© (Cole and Lele, 2002) was used to statistically compare the patterns of morphological integration in males and females. Differences in the correlation matrices of linear distance measurements for males and females were calculated. If MI is the same in males and females (the null hypothesis), the differences in correlations will be equal to zero. A non-parametric bootstrapping algorithm (10,000 bootstraps) was used to calculate confidence intervals for each correlation difference to determine the statistical significance of differences in MI patterns local to particular anatomical features (Cole and Lele, 2002).



Results

- Overall, the pattern and magnitude of integration in males and females are very similar (Figure 3). The highest levels of MI in both sexes represent the relationship of landmarks located on the premaxilla to the rest of the skull.

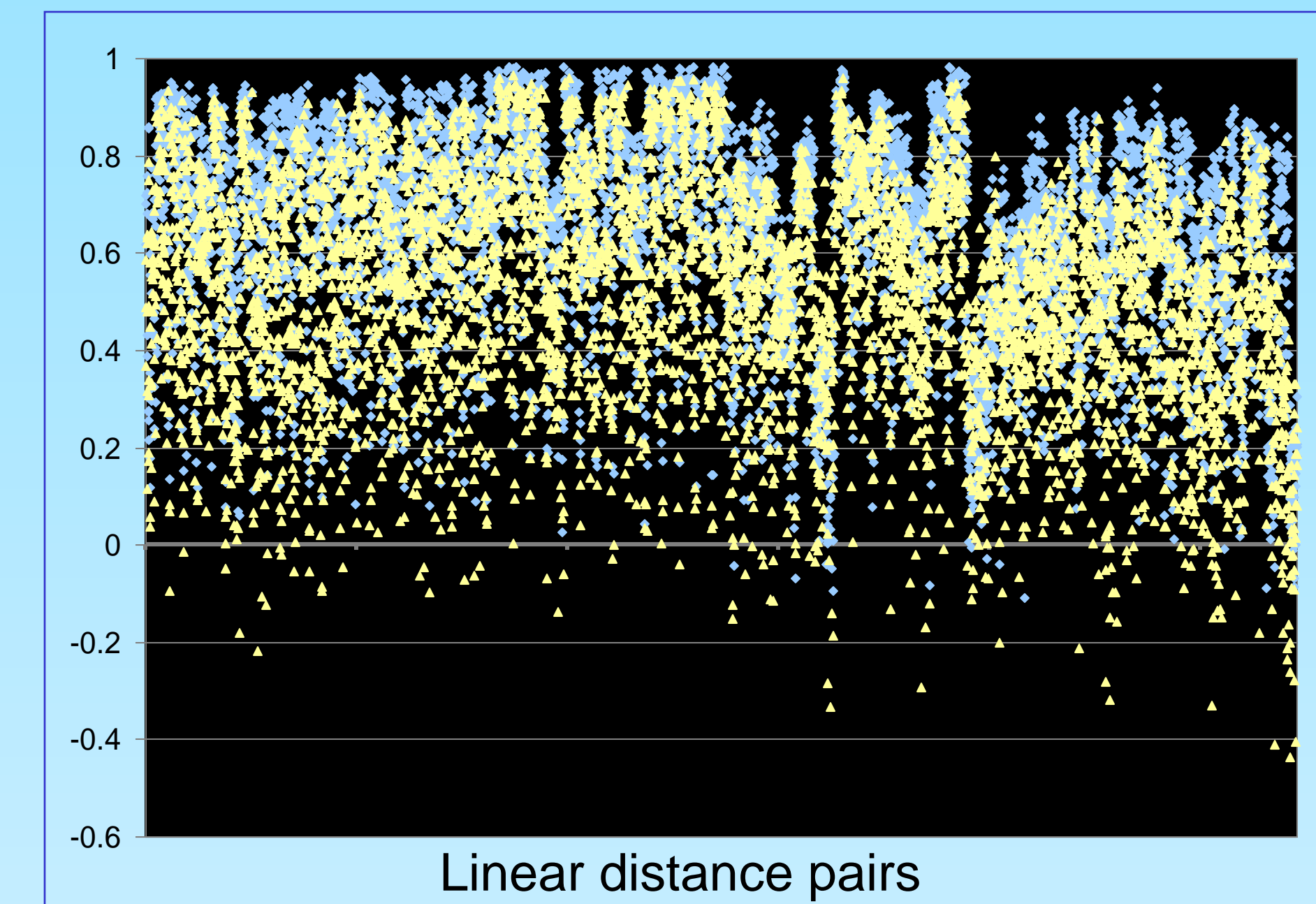


Figure 3. Correlation values for 5,460 linear distance pairs calculated for males (blue diamonds) and females (yellow triangles).

- Despite these similarities, our analysis shows a localized pattern of significantly increased MI in the skulls of male baboons compared to females. The biggest increases in MI among males describe height and breadth dimensions of the maxilla and zygoma correlated with length and height of the neurocranium (Figures 4, 5).

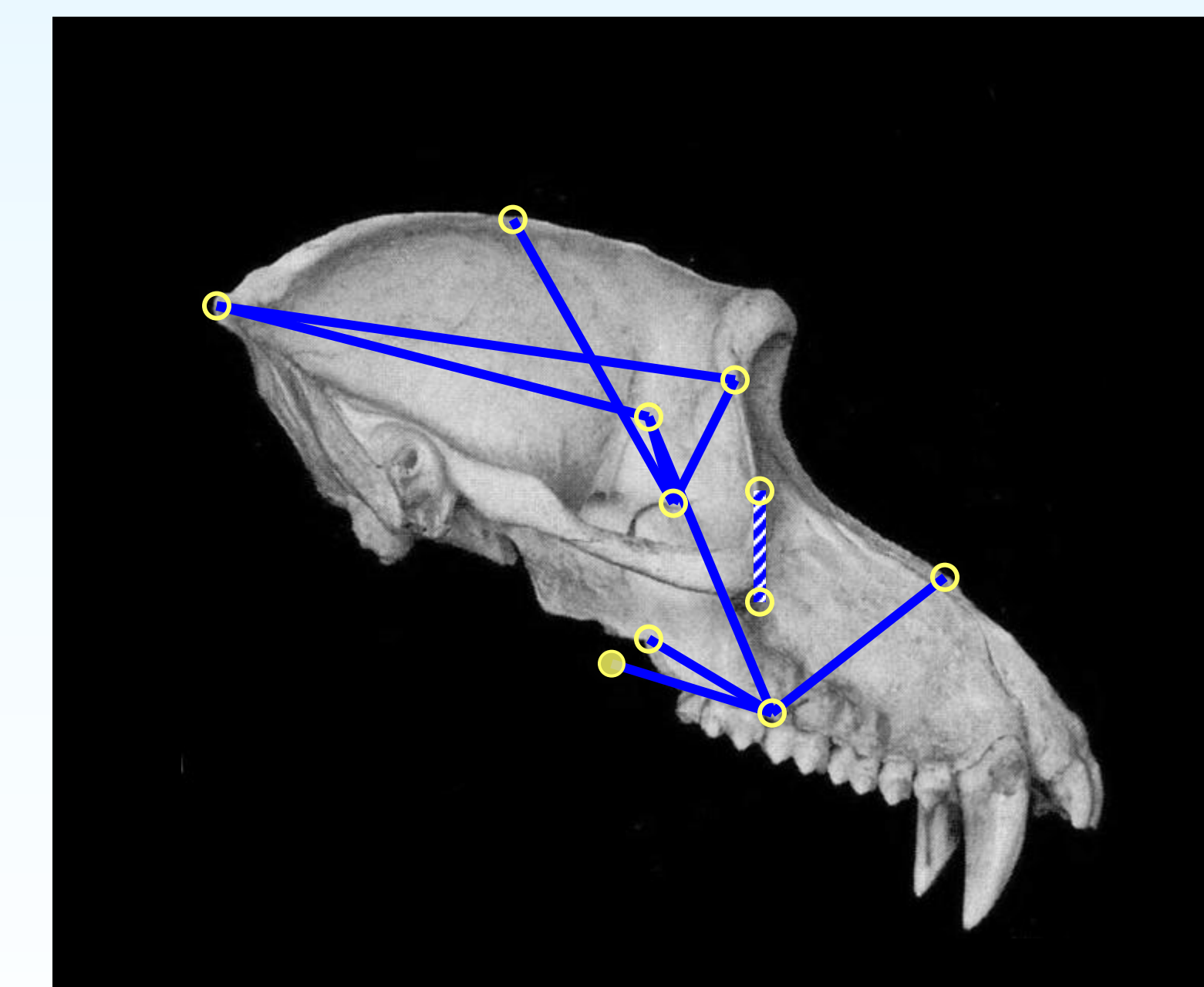


Figure 4. Localized areas of significantly increased MI in males. All linear distances represented in blue are highly correlated with the striped blue linear distance. These correlations were very low (i.e., zero) in females.

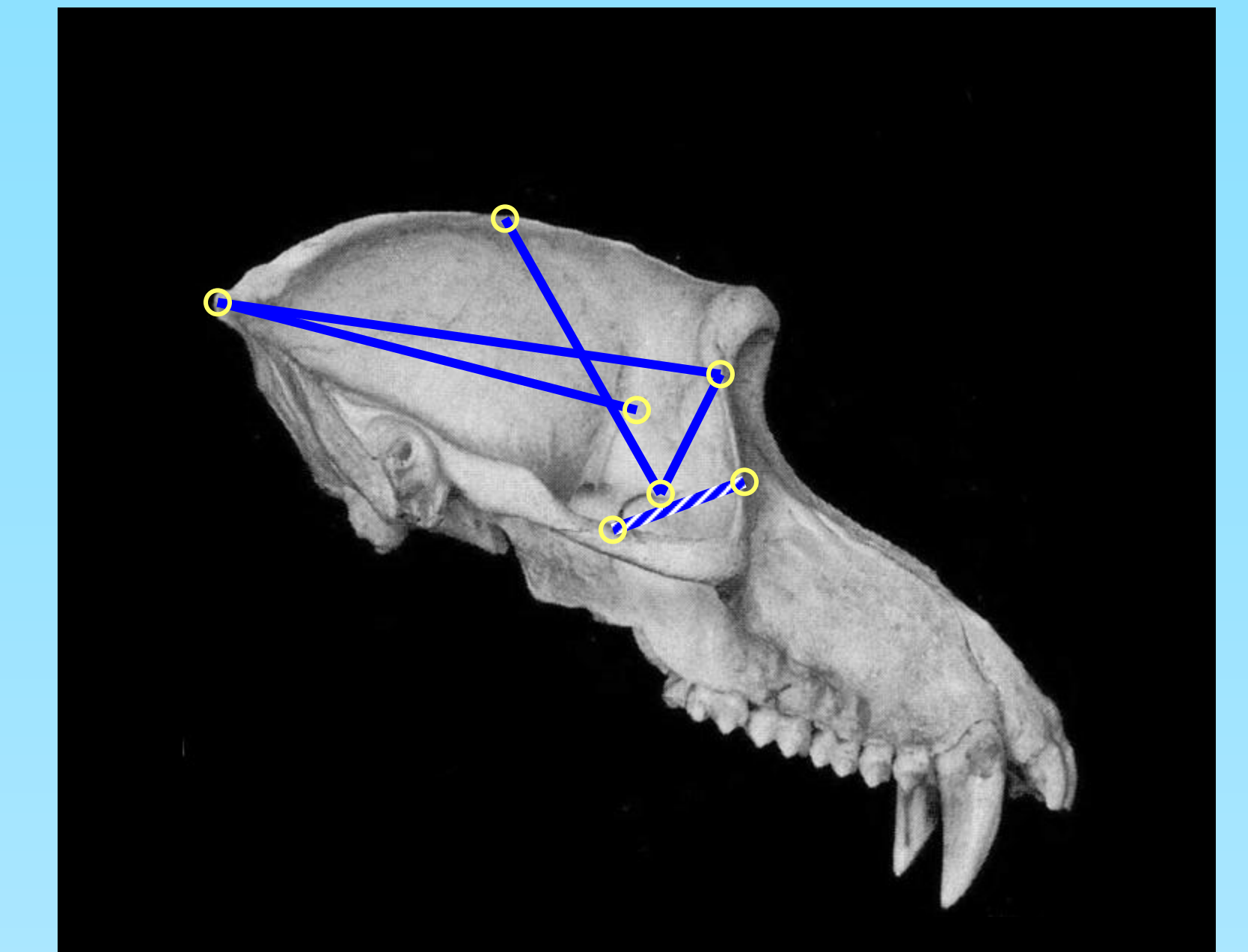


Figure 5. Localized areas of significantly increased MI in males. All linear distances represented in blue are highly correlated with the striped blue linear distance. These correlations were very low (i.e., zero) in females.

Discussion and Conclusions

The baboon skull shows a high degree of MI overall in both sexes, as would be expected from our knowledge of the integrated nature of skull growth and function. Despite this overall similarity, however, there are also statistically significant localized differences in integration. Seven percent of linear distance pairs were significantly more integrated in males than in females. Our results suggest that development of the robust zygo-maxillary complex in males is highly integrated with the form of the neurocranium and posterior aspect of the palate. This result may reflect a direct and necessary relationship between malar/maxillary robusticity and the robusticity of nuchal musculature in males.

We did not find evidence, however, for significant differences in the degree of MI in the rostrum, suggesting that males acquire their robust muzzle without obvious adjustments in integration local to this area of the skull. Instead, the significant changes in MI appear to occur in the hafting of the palate and midface to the neurocranium. These results suggest that changes in MI are not required to produce the dimorphic facial features. Rather, changes in morphological integration, that we assume represent developmental relationships, are required to combine these features into a functioning whole. This is seen most clearly in correlations between measures of the midface and neurocranium and also local to the most posterior aspect of the palate: the site of hafting of the face onto the skull.

References available from authors upon request.

ACKNOWLEDGEMENTS

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