The nose is mightier than the tooth: larger male proboscis monkeys have smaller canines

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The uniquely enlarged noses of male proboscis monkeys (*Nasalis larvatus*) are prominent adornments, and a sexually selected male masculine trait, as recently revealed by the significant correlations among nose, body, and testis sizes and the clear association between nose size and the number of females in a male's harem. However, till date, the analyses of other common male traits, i.e., canines, are lacking. Whereas male nose size had a positive correlation with body size, we unexpectedly found a negative correlation between body and canine sizes. Similar relationship between nose and body size was observed in females, whereas only a weak correlation was noted between canine and body size. We explain this by an interaction between sexual and natural selection. Larger noses in males may interfere with the use of canines, thereby reducing their effectiveness as weapons. However, longer canines are opposed by natural selection because they impose a larger gape upon its bearer and reduce foraging efficiency, particularly in folivores. The difference between the sexes regarding the regression intercept for body size vs. canine size was significant, although the difference of the slopes was insignificant, consistent with the hypothesis that the nose interferes with the effectiveness of canines as weapons in males but not in females. Moreover, a mathematical simulation supported our prediction. This unique case of decoupling of body and canine size reveals that large canines carry an ecological cost. It also raises interesting questions regarding the developmental mechanism that produces a negative correlation among adult body, nose size, and canine size.

Introduction

Darwinian evolutionary theory explains male-specific characteristics as a consequence of sexual selection [1]. Large canines in some mammals, including primates, represent a typical example of a weapon used in contests with conspecific male rivals [2]. By contrast, ornaments independently evolve for a function in combat, reflecting their function as a partner attraction signal (ultimately determined by female choice). However, some male-specific traits are neither weapons nor ornaments, and they serve as a badge of male social status, advertising competitive potential with respect to other males [1, 3], particularly as observed for social rank-dependent masculine traits in some primate species [4]. Proboscis monkeys (*Nasalis larvatus*) represent a typical sexually dimorphic primate with male-specific enlarged noses that are prominent adornments, which have been linked with their sexually competitive social system of one-male groups. Recently, we reported significant positive correlations among nose, body, and testis size as well as a clear association between nose size and both nasalized acoustic signals and the number of females in one-

male groups; this supports the hypothesis that larger noses audiovisually advertise a male's fighting ability with conspecifics [5], and thus serve as status badges rather than ornaments.

Till date, an analysis of another common sexually selected male trait, i.e., canine size, is lacking. Sexually dimorphic male traits (e.g., body mass, nose, testis, and canines) develop after sexual maturation, primarily in response to endocrine changes in the levels of androgens such as testosterone. Comparisons of these male traits would enable us to study the relationships among weapons, badges, ornaments, and testes. In this study, we compared canine size among previously investigated wild proboscis monkeys [5]. Notably, proboscis monkey one-male groups (and all-male groups) aggregate on a regular basis at their sleeping sites (suggestive of a "multilevel social system" [6]), and female dispersal among the groups is typical [7], creating the potential for both female choice and male-male competition for females. Therefore, male canines are expected to serve as important weapons for mate competition or defense, especially because canine size generally reflects the strength of intra-sexual selection more directly than body size [2, 8].

Material and methods

Between July 2011 and December 2016, we captured 18 free-ranging adult male proboscis monkeys in the Lower Kinabatangan Floodplain, Sabah, Borneo, Malaysia (5°18′N to 5°42′N and 117°54′E to 18°33′E), as described in detail in the methods and ethical statement of Stark *et al.*[9]. In this study, we added the data for maxillary canine length to those on body mass and nose size (length × width) for the same males obtained by Koda *et al.* [5] as well as data for female canine length, body mass, and nose size. The maxillary canine was selected because of its larger size and greater importance in behavioral displays and weaponry [10]. A linear model was used to establish whether body mass was related to other physical properties such as nose and canine size. To obtain a linear dimension comparable to the canine dimension, body mass and nose size were cube root- and square root-transformed, respectively, to generate response and explanatory variables. The variance inflation factors were 1.00 for both nose size and body mass, indicating that collinearity among independent factors would not affect the results [11]. We examined a set of models with all possible combinations of the explanatory variables and ranked them according to the corrected version of the Akaike information criterion (AIC) for small sample sizes, called AICc [12]. Following guidelines published for wildlife research, we selected models with ΔAICc ≤ 2, where ΔAICc = AICc − minimum AICc within the candidate model set [12]. Analysis of covariance served to compare the slopes and intercepts of regression lines between the sexes. These analyses were performed using

R ver. 3.3.2 [13].

Our motivation for the model simulation was to clarify the mechanism by which the termination time of canine development t_1 determines the final results of body mass and canine size. We simulated the growth pattern based on several deterministic parameters, considering the developmental evidence for proboscis monkeys. Additionally, we tried to apply the model for both males and females within the same developmental frameworks, considering the sex differences of the developmental parameters. More details of the mathematical models and parameter proposals are described in the Supplementary Information or code repositories (https://github.com/hkoda/nasalis_canine_bodymass_model).

Results and discussion

The best-fitting model included both male nose and canine size. Whereas nose size was positively correlated with body mass, the model with canine size was unexpectedly negative (Fig. 1), although the fit of the model including only canine size was almost as good (i.e., ΔAICc < 2.0: Table 1). Conversely, for females, the best-fitting model only included nose size, which had a positive effect on body mass. The second-best model was the null model (Table 1). The difference in the regression slopes and intercepts for body size vs. nose size between the sexes was not significant (slope: $t = -1.41$, $P = 0.17$; $t = 0.28$; intercept: $P = 0.78$). However, the difference in the regression intercept for body size vs. canine size was significant ($t = 8.28$, $P < 0.0001$), although the slopes were not different ($t = -0.33$, $P = 0.74$). Previous results illustrated that secondary sexual male traits reflect both pre- and post-copulatory competition; specifically, larger noses serve as both “female attraction” and “badge of status,” and simultaneously, larger testes reflect sperm competition [5]. Body size also contributes to both male-male competition and female attraction.

These results can be interpreted in two ways. The minimal interpretation is that canine size does not contribute to the fighting ability of harem-holding males, unlike the findings in other primate species forming harem societies [2]. Battles featuring fatal physical attacks using canines are commonly observed in typical harem species such as hanuman langurs (*Semnopithecus entellus*) [14] or howler monkeys (*Alouatta seniculus*) [15]. Nonetheless, the benefit of a larger body size in proboscis monkey males is clear. Indeed, branch shaking is commonly used to keep groups apart [6], and in chases without physical contact, males repeatedly exhibit such displays accompanied by leaps between trees (IM. pers obs). Additionally, among proboscis monkey males, nose size, which is highly correlated with body size, determines the formant frequencies of loud vocalizations,

which may decide contests without any direct physical competition, or at least direct biting [5, 7, 16]. Thus, a larger body, which contributes to male athleticism, would allow more effective displays of fighting ability, whereas nose size is the best indicator of fighting ability because it is easier to assess via vocalization opposed to visual examination. Consequently, males might invest their physiological resources to develop nose, body, and testis size more than canine weapons, in line with the trade-off phenomenon recently reported in other harem primates e.g., [17].

Contrarily, whereas females do not compete through sound as do males, they unexpectedly exhibited the same nose size/body size correlation, suggesting that female nose size is linked to the effect on males. Female noses are probably sufficiently small to avoid interfering with their activity, and thus, selection toward sex-differentiated expression does not occur.

However, the significantly negative correlation between male canine and body size supports an alternative interpretation; namely, it suggests an ecological cost of large canines, as suggested for the taxonomic variation in canine size observed across primate lineages [18, 19]. The prominent nose may interfere with effective canine bites, thereby reducing their effectiveness as weapons. Moreover, given their reduced effectiveness, natural selection may actually favor smaller canines because larger canines increase gape, which reduces bite force and thus mastication efficiency [18]. This foraging cost may be especially severe in large-sized folivores, such as proboscis monkeys and gorillas [19]. Thus, a negative correlation might evolve in the rate of post-adolescent growth of the size of the body frame and that of canines. We therefore predict that in proboscis monkeys, body-size dependent displays are more effective at greater distances than the facial displays commonly observed in most other primates [20].

Contrary to the significant negative slope for the male canine size-body size correlation, we only found a weak correlation for the female slope. Although the difference of the slopes between the sexes was not significant, possibly because of the limited sample size, the significant sex difference in the intercept for body size vs. canine size suggests that canine size has a different relationship with body mass between males and females. The difference in the sex-differentiated pattern between noses and canines would confirm the hypothesis that large canines interfere with effective biting in males, making them less effective as weapons and thus leading to negative selection on canine size in the largest males.

Concerning the mechanism underlying the trade-off among body mass, nose size, and canine size, we predict that canine growth would actually exhibit a negative correlation with testosterone levels, opposite to the common and ancestral situation [17]. To

test this “costly canine hypothesis”, we conducted preliminary mathematical simulations considering body mass development with a growth constrained by canine size (for a model description, see Supplementary Information). Echoing our empirical findings, the negative relationship between body and canine size was observed only in males when we assumed a large cost of canine development (Fig. 2). Future detailed studies focusing on the behavior and development system of proboscis monkeys are therefore required.

Acknowledgements

We thank the Sabah Biodiversity Centre and the Sabah Wildlife Department for granting permission to carry out this research, our research assistants for support in the field, and the Japan Monkey Centre (Dr. N. Kimura) for providing the information used in our mathematical simulations. We appreciate Prof. I. Tsuda to support verifying the mathematical simulations. The authors would like to thank Enago for the English language review. This study was partially funded by Japan Science and Technology Agency Core Research for Evolutional Science and Technology 17941861 (#JPMJCR17A4), Ministry of Education, Culture, Sports, Science and Technology Grant-in-aid for Scientific Research on Innovative Areas #4903 (Evolinguistic), 17H06380, and Yayasan Sime Darby (to BG). This paper is dedicated to the memory of Dr. Diana Angeles Ramirez Saldivar.

Author contributions

IM, BG, CV and HK conceptualized the initial idea, IM, DJS, DARS, SKSSN performed the wild morphology sampling, AT BG arranged the sampling in the wild, IM, HK performed and interpreted the statistical analyses and mathematical simulation, IM, CV, HK drafted the manuscript. All authors contributed to the final version of the manuscript.

Competing interests

The authors declare that they have no competing interests.

Table and figure legends

Table 1 Summary of model selection. Linear models were used to investigate whether body mass was related to other body traits such as nose and canine size (only the models with ΔAICc ≤ 2 are shown).

Figure 1 Relationships of nose size (left) and canine size and (right) with body mass.

Figure 2 Relationships of normalized canine size with body mass in the mathematical simulation. We observed a negative correlation between body mass and canine size for both male statuses, but no correlation was noted for females, consistent with our observations in free-ranging specimens (see Supplementary Information for details of the simulation).

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Table 1. Summary of model selection. Linear models were used to investigate whether body mass was related to other body traits such as nose and canine size (only the models with ΔAICc $\leq$ 2 are shown).

Intercept	Nose size	Canine size	df	Log-likelihood	AICc	Δ-AICc	AICc weight
Male							
42.3	0.11	-0.01	4	25.0	-39.0	0	0.41
33.0		-0.01	3	23.2	-38.7	0.34	0.34
Female							
1.387	0.2724		3	12.3	-14.6	0	0.77

Figure 1. Relationships of nose size (left) and canine size and (right) with body mass.

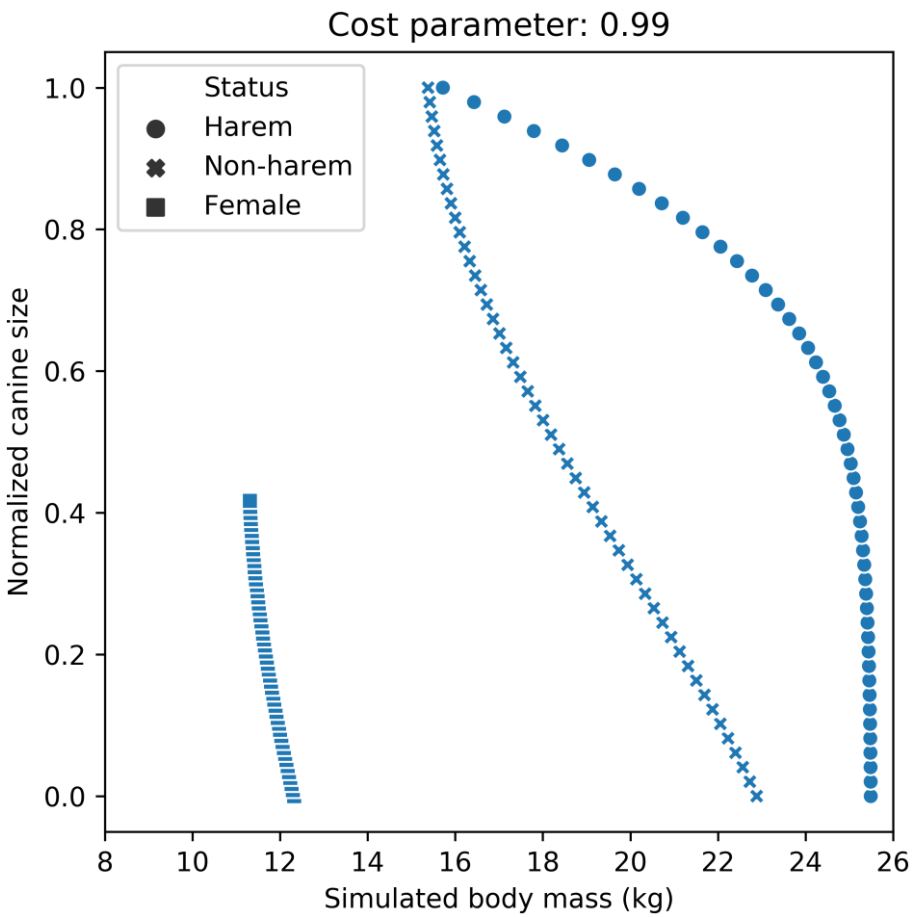

Figure 2. Relationships of normalized canine size with body mass in the mathematical simulation. We observed a negative correlation between body mass and canine size for both male statuses, but no correlation was noted for females, consistent with our observations in free-ranging specimens (see Supplementary Information for details of the simulation).