

Supplementary materials of "Large male proboscis monkeys have larger noses but smaller canines"

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1 Model

The aim of these simulations was to examine our hypothesis regarding the positive/negative correlations between body mass and canine size. Earlier work distinguished the subadult class from fully adult males based on nasal maturation as well as a fully developed body size [1]. In other words, two developmental stages likely exist among sexually mature males. Therefore, before the acquisition of harem status, subadult males reach a limit in body mass, which cannot increase without a status change. By contrast, in females, the development of body mass and canines is basically similar to that of males before the acquisition of harem status. In this study, we therefore assumed a two-stage model of male development, i.e., a first stage with primary development of body and canine size for both males and females and a second stage that only applies to males and only after the acquisition of harem status.

1.1 Primary development of body mass and canine

The body mass, m , develops under the assumption that the growth rate depends on the body mass at the time, until reaching its developmental limit K within a fixed time T , i.e.,

$$\frac{dm}{dt} = am(1 - \frac{m}{K}) \quad \forall t \in [0, T], \quad (1)$$

where $a = \text{const.}$ is the shape factor determining the sigmoidal curve of development. This is based on a previously proposed basic model for body mass development [2, 3] but with our modification to simplify the constraint of K . By contrast, the canines develop in the later stage of body mass development, and thus, we supposed that larger canines would reduce feeding efficiency, resulting in a growth rate reduction for body mass as follows:

$$\frac{dm}{dt} = (1 - cz)am(1 - \frac{m}{K}), \quad (2)$$

where cz is the reducing factor determined by the cost factor $c \in [0, 1)$ and the size of canines z and $cs < 1$ always holds. For model simplification, the canines start to develop at the time t_0 and linearly develop until $t_1 \leq T$ as follows:

$$z = \alpha(t - t_0) \quad (t_0 \leq t \leq t_1), \quad (3)$$

where $\alpha > 0$ is the growth rate of canines. Consequently, the differential equation of body mass in $t \in [0, T], T > t_1$ is

$$\frac{dm}{dt} = \begin{cases} am(1 - \frac{m}{K}) & (0 \leq t \leq t_0) \\ \{1 - c\alpha(t - t_0)\}am(1 - \frac{m}{K}) & (t_0 \leq t \leq t_1) \\ (1 - cz_1)am(1 - \frac{m}{K}) & (t_1 \leq t \leq T), \end{cases} \quad (4)$$

where $cz_1 := cz_{t=t_1} = c\alpha(t_1 - t_0)$, because proboscis monkeys likely increase their body mass until $t = T$, with the constant of the reducing factor, after terminating canine growth ($t = t_1$). Note that $0 \leq z \leq \alpha(T - t_0)$ holds; therefore,

$$\alpha \leq \frac{z}{T - t_0} \quad (5)$$

also holds.

In case of $t < t_0$, i.e., before the onset of canine eruption, the equation is a simple logistic equation; therefore, the solution is

$$m(t) = \frac{K}{1 + A_0 e^{-at}}, \quad (6)$$

where A_0 is the constant determined by the initial values of $m(0) = m_0 > 0$, as follows:

$$A_0 = \frac{K}{m_0} - 1. \quad (7)$$

Once the canines begin to develop, i.e., in the case of $t_0 \leq t \leq t_1$, the differential equations are solved as follows:

$$\frac{dm}{dt} = \{1 - c\alpha(t - t_0)\}am\frac{K - m}{K} \quad (8)$$

$$\int \frac{K}{m(K - m)} dm = a \int \{1 - c\alpha(t - t_0)\} dt \quad (9)$$

$$\int \left\{ \frac{1}{m} + \frac{1}{(K - m)} \right\} dm = a \int \{1 - c\alpha(t - t_0)\} dt \quad (10)$$

$$-\ln \left| \frac{K - m}{m} \right| = -\frac{1}{2}ac\alpha t^2 + a(1 + c\alpha t_0)t + C \quad (11)$$

$$m(t) = \frac{K}{1 + A_1 e^{\frac{1}{2}ac\alpha t^2 - a(1 + c\alpha t_0)t}}. \quad (12)$$

Then, after terminating canine development ($t = t_1$), we found that the solution is simply

$$m(t) = \frac{K}{1 + A_2 e^{-a(1-cz_1)t}}. \quad (13)$$

Note that the following equations must be satisfied:

$$m(t_0) = \frac{K}{1 + A_0 e^{-at_0}} = \frac{K}{1 + A_1 e^{\frac{1}{2}acat_0^2 - a(1+c\alpha t_0)t_0}} \quad (14)$$

$$m(t_1) = \frac{K}{1 + A_1 e^{\frac{1}{2}acat_1^2 - a(1+c\alpha t_0)t_1}} = \frac{K}{1 + A_2 e^{-a(1-cz_1)t_1}}. \quad (15)$$

Consequently, the basic models for body mass are

$$m(t, t_0, t_1, K, a, c, \alpha, A_0, T) = \begin{cases} \frac{K}{1 + A_0 e^{-at}} & (0 \leq t \leq t_0) \\ \frac{K}{1 + A_0 e^{\frac{1}{2}acat_0^2 + \frac{1}{2}acat^2 - at(1+c\alpha t_0)}} & (t_0 \leq t \leq t_1) \\ \frac{K}{1 + A_0 e^{\frac{1}{2}acat_0^2 - \frac{1}{2}acat_1^2 - at + ac\alpha t_1 t - ac\alpha t_0 t}} & (t_1 \leq t \leq T), \end{cases} \quad (16)$$

and those for canine size are

$$z(t, t_0, t_1, \alpha, T) = \begin{cases} 0 & (0 \leq t \leq t_0) \\ \alpha(t - t_0) & (t_0 \leq t \leq t_1) \\ \alpha(t_1 - t_0) & (t_1 \leq t \leq T). \end{cases} \quad (17)$$

1.2 Rank-dependent secondary development of body mass and nose

Our previous study suggested that males who acquire harem alpha status develop their noses as a badge of status in coordination with body mass [4]. In this study, we supposed that alpha status males can dominate both copulation opportunities and *foraging resources* because harem groups with larger males better defend resources from all-male groups generally consisting of smaller males [5]. Therefore, such alpha status males would possibly continue their body mass growth after completing their primary developmental process, whereas males who fail to acquire harem status terminate body mass growth. Then, the differential equations of the body mass in the secondary development for harem males are equivalent with equation (4), i.e.,

$$\frac{dm}{dt} = (1 - cz_1)am(1 - \frac{m}{K}) \quad (t \geq T), \quad (18)$$

whereas those for non-harem males are

$$\frac{dm}{dt} = (1 - cz_1)\{a - \frac{t - T}{t_2 - T}a\}m(1 - \frac{m}{K}) \quad (t \geq T), \quad (19)$$

where, t_2 is the termination time of the body mass growth. This equation is solved in the same manner as equations (8) - (12), namely

$$m(t, t_0, t_1, K, a, c, \alpha, A_0, T, t_2) = \frac{K}{1 + A_3 e^{\frac{1}{2}\beta t^2 - \beta t_2 t}} \quad (20)$$

$$A_3 = A_0 e^{\frac{a c \alpha (t_0^2 - t_1^2)}{2} - a T + a c \alpha T (t_1 - t_0) - \beta T (\frac{1}{2} T^2 - t_2 T)}, \quad (21)$$

where $\beta := \frac{a(1 - c \alpha t_1 + c \alpha t_0)}{t_2 - T}$. Based on our findings of allometric development of ornaments and body size in free-ranging specimens [2, 3], we supposed that nose size is primary determined by body mass.

2 Simulations

2.1 Overview of aims

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 as follows.

2.2 Parameter proposals

First, the time parameter was normalized at the males primary maturation time T , i.e., $T := 1$. Therefore, our time parameters t_0 , t_1 and t_2 , are the time relative to the male maturation time, T . By definition, $0 \leq t_0 \leq t_1 \leq T = 1 \leq t_2$ holds. Additionally, the maximum canine size z was also normalized to 1 for the case in which the monkey maximally develops its canines during the periods between t_0 and $T = 1$. Following equation (3), $\alpha = \frac{1}{1 - t_0}$.

Next, we supposed that the primary maturation age of males ($t = T = 1$) at which males reach sexual maturity at approximately 8 years old [6], although male nose enlargement does not typically start until that time [1]. In *Cercopithecus* [7] and proboscis monkeys [8], canine development starts at approximately 4 years old and continues until 8 years old. The onset time of canine development was therefore set at 4 years old in our model, or half the subadult maturation time, i.e., $t_0 = \frac{1}{2}$. By contrast, females mature earlier than males. We supposed that the female maturation age was 6 years [6]; i.e., we used $T = \frac{6}{8}$ in the model for female development. The time of onset of canine growth is likely similar in both sexes, but females likely terminate canine growth earlier, corresponding to their earlier physical maturation. Therefore, we supposed that female canines develop from approximately 4 years old until 6 years old, representing a shorter than observed in males (i.e., $t_0 = \frac{1}{2}$ for females). Records for body mass were used for the parameters in the simulations. Proboscis monkey neonatal body mass was reported as 0.45kg [8], and the maximum body mass among our specimens was 25.5

kg for males and 14.5 kg for females. Therefore, we set $m(0) = 0.45$, $K_{male} = 25.5$, and $K_{female} = 14.5$. Additionally, we used the body mass record at approximately 4 years old, or the onset time of canine eruption, which was approximately 6.5 kg ($N = 3$, records in Japan Monkey Centre). Therefore, we used $m(\frac{1}{2}) = 6.5$ in the simulations for both males and females. Finally, we assumed that body mass development would terminate immediately after the maturation time T was reached; therefore, we used $t_2 = T + 0.1 = 1.1$ for males and $t_2 = T + 0.1 = 0.85$ for females.

Based on the aforementioned parameters, we simulated body mass at the time at which monkeys fully develop. For this purpose, we attempted to simulate/evaluate $m(2)$, or body mass at approximately 16 years old, using the various combinations of cost parameters and canine termination times, i.e., $c \in (0, 1)$ and $t_1 \in (0.5, T)$

3 Results of simulations

Figure 1 shows the simulated results of developmental growth curves for harem alpha status males, non-alpha status males, and females with various cost and termination time parameters. Our simulations revealed that higher costs caused by canine development negatively influenced body mass growth in males. Male body mass also varied depending on the termination time of canines, i.e., canine size, whereas female body mass was relatively independent of canine size. In the case of no or weak costs attributable to canine development, body mass for both sexes was independent of the canine growth termination time, but under the assumption of a large cost for canine development, canine size had a clear negative influence on body mass, particularly in males (see Figure 2).

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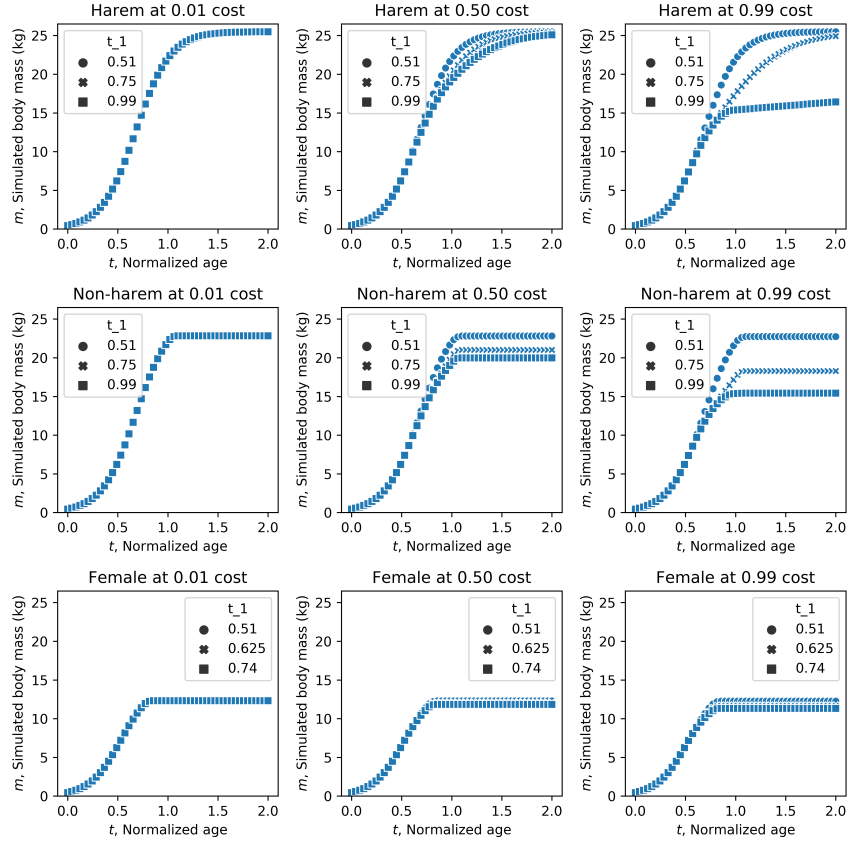


Figure 1: Developmental growth curves for females, non-harem males, and males. The cost parameters ranged between 0.01(almost no cost), 0.5(moderate), and 0.99 (strong cost). The terminations of canine development were set at each of 0.51 (immediate termination), 0.75 (middle), and 0.99 (maximum canine growth).

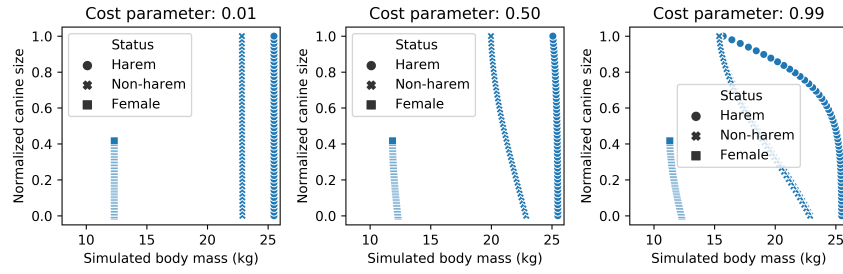


Figure 2: The relationships of normalized canine size and body mass at the final developmental stages, for simulated harem alpha status males, non-alpha status males, and females. The left panel is the simulation of weak cost parameter ($c = 0.01$), middle is that of moderate ($c = 0.5$), and right is of strong ($c = 0.99$). In case of strong cost parameter, the negative correlations between body mass and canine size were observed for both statuses of males, but not or weak in females, which are consistent with our observations.