Debate over origin of long necks in giraffes (Giraffa camelopardalis)

Javier Martinez
Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Giraffes (G. camelopardalis) are known for their distinct long necks and there are two main hypotheses that claim to explain their evolution. One hypothesis states that giraffes developed long necks to allow them to browse high in tree canopies (Wilkinson & Ruxton, 2012). Another suggests a 'necks-for-sex' hypothesis, in which the origin is due to sexual selection in competing male giraffes (Simmons & Altwegg, 2010). Wilkinson & Ruxton (2012) examine these hypotheses by first repudiating Simmons & Altwegg's (2010) argument. Simmons & Altwegg (2010) argue that if sexual selection contributed to the evolution of giraffes, there would be differences in head mass between the sexes. Conversely, Simmons & Altwegg (2010) also state that if competition in food resources is the only reason for elongated necks, then there should be no expected difference in head mass between sexes. Mitchell et al. (2009) viewed Simmons & Altwegg's (2010) argument and examined growth patterns of male and female giraffes. Badlangana et al., (2009) also observed neck length and focuses on examining vertebral columns of giraffes to determine their evolution, in relation to the hypothesis of sexual selection. While the more commonly known and accepted argument is that giraffe necks elongated for reaching nutritional resources, the more rejected yet controversial argument of giraffe neck evolution as a result of sexual selection has enough justification to be plausible.

Mitchell et al. (2009) measured body mass (kg), total length (cm), total height (cm), foreleg length (cm), neck length (cm), neck length: foreleg length ratio (NL:FLL), head and neck mass (kg), and cervical vertebrae mass (kg) and found no significant differences between sexes. Data analyses for these measurements were made by developing log equations for each variable with respect to body mass. Mitchell et al. (2009) state that head mass was the same for both sexes, and mean head mass for males and females constituted 2.9% of the mean body and 2.5% of the mean body, respectively. Mitchell et al.'s (2009) data also show that the proportion of neck mass that was bone mass declined slightly during growth from birth to maturity from 14% to 10%. On the other hand, in females the contribution of vertebrae was more uniform, staving at 10% of neck mass both at birth and at maturity. Simmons & Altwegg (2010) analyzed all the presented information and continued to refute it.

Simmons & Altwegg (2010) argue that sexual selection does not directly predict longer necks, but more powerful ones for males. Simmons & Altwegg (2010) state that female necks can be just as long as male necks, but are ineffective for clubbing because sparring of necks combines neck length and neck size to produce momentum in the neck to club rivals. Simmons & Altwegg (2010) also state that differentiating the muscle to bone components in the neck indeed show that the mass difference is due to muscle mass and not due to bone density. For samelength skulls, male skulls were actually found to be about four times heavier than female skulls (Simmons & Altwegg 2010) and while both sexes continued to grow, males grew more by depositing 14.8 kg superficial bone over their skulls compared to females who only had 3.0 kg. Simmons & Altwegg's data

compared to Mitchell et al.'s (2009) focuses more on the weight of giraffe heads which is necessary for neck sparring, while Mitchell et al. (2009) focuses on the actual neck length and uses that to show that there is little difference bewteen the genders. Even with the given information it is still difficult to fully explain which of the hypotheses is correct.

Mitchell et al. (2009) discuss requirements that must be met in order for sexual selection to be considered a possibility. The characteristics must be: more exageratted in one sex than the other, this characteristic needs be used in dominance contests, it must have no immediate survival benefits, must hamper with survival costs, show positive allomentry, and lastly, during its phylongenetic history show growth in size that is not correlated with size growths in other parts of the body (Senter, 2007). Mitchell et al. (2009) observed these requirements and based on his results, concluded that they do not support this theory as the origin of the evolution of giraffe shape.

Simmons & Altwegg (2010) lean towards the argument of evolution of long necks being caused by sexual selection. However, they explain that there are assets and challenges to both arguments. For the hypothesis of competing browsers, Simmons & Altwegg (2010) state that there is a need to determine what maintains modern giraffes 2.5 m above possible competitors when there are costs in terms of predation rate, blood pressure and maintenance of skeletal lengthening (Warren, 1974; Mitchell et al., 2006). In additon, the main challenge of the sexual selection hypothesis is explaining why female giraffes also have long necks even if their necks are shorter than those of males. Simmons & Altwegg (2010) note that the competing browser hypothesis suggests benefits for both genders of giraffes, and a decrease in competition between sexes through foraging height partitioning is a possible benefit that remains unexplored. Simmons & Altwegg (2010) conclude that both mechanisms explained by the hypothesis have some part to play in the evolution of long necks in giraffes and the preservation of this unique trait suggests that refined measurements of costs and selection should allow them quantify the relative importance.

The more commonly known and recognized argument is that giraffes have long necks for browsing in high tress, but the more rejected, yet debatable argument of sexual selection in giraffes causing an evolution in long necks raises enough defense to be probable. As stated by reasearch done by Mitchell et al. (2009), giraffe neck length is very similar in both genders and therefore sexual selection can not be concluded as an explanation of long necks. However, Simmons & Altwegg (2010) counter Mitchell et al.'s (2009) argument by stating that it is not the neck length, but more so the head mass that allows for clubbing of necks. Simmons & Altwegg (2010) even observe a head mass of four times greater in males compared to females. Simmons & Altwegg (2010), however, also introduces reasons as to why both hypotheses may be correct or inadequate and concludes that neither hypothesis can be fully accepted. In summary, it is likely that both mechanisms played a part in the origin of long necks in giraffes and although similiarities in neck length between the genders seems to support the hypothesis of Mitchell et al. (2009), the head mass difference is what allows for Simmons & Altwegg (2010) stance on sexual selection to be questionable.

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