Necks-for-sex or competing browsers? A critique of ideas on the evolution of giraffe

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Abstract
Recent years have witnessed a resurgence in tests of the evolution and origin of the great height and long neck of the giraffe Giraffa camelopardalis. The two main hypotheses are (1) long necks evolved through competition with other browsers allowing giraffe to feed above them (‘competing browsers’ hypothesis); or (2) the necks evolved for direct use in intra-sexual combat to gain access to oestrous females (‘necks-for-sex’ hypothesis). Here, we review recent developments and their relative contribution in explaining giraffe evolution. Trends from Zimbabwean giraffes show positive allometry for male necks and isometry for female necks relative to body mass, while comparative analyses of the cervical versus the total vertebral column of the giraffe, okapi and fossil giraffe suggest selection specifically on neck length rather than on overall height. Both support the necks-for-sex idea. Neither study, however, allows us to refute one of the two ideas. We suggest new approaches for quantifying the relative importance of the two hypotheses. A direct analysis of selection pressure on neck length via survival and reproduction should clarify the mechanism maintaining the trait, while we predict that short robust ossicones should have arisen concurrently with incipient neck elongation if sexual selection was the main selective driver. The main challenge for the competing browser hypothesis is to explain why giraffe have remained about 2 m taller than their tallest competitors for over 1 Myr, whereas the sexual selection hypothesis cannot provide an adaptive explanation for the long neck of female giraffe. We conclude that probably both mechanisms have contributed to the evolution and maintenance of the long neck, and their relative importance can be clarified further.

New data and tests of the origin of the elongated neck of the giraffe Giraffa camelopardalis have provided fresh insight into the origin of this trait. All attempt to test one of two main hypotheses – that of natural selection via advantages from feeding on trees above competitors (Darwin, 1871) or intra-sexual (male–male) competition via advantages found in clubbing rivals more effectively in competition for females (Simmons & Scheepers, 1996). Both mechanisms should result in longer necks and both are demonstrably advantageous to their bearers (Pratt & Anderson, 1982, 1985; Cameron & du Toit, 2007). Although both mechanisms can explain long necks in giraffes, no tests have attempted to distinguish between them as the origin or maintenance of the long neck. The two hypotheses may not be mutually exclusive, and it may not be possible to differentiate between them if both have provided selective pressures to neck lengthening. The question, therefore, should be what is the relative importance of the two mechanisms in explaining the origin and maintenance of the giraffe’s long neck?

Here, we review and clarify the main hypotheses, explore the tests that have been advanced and provide future tests for prising them apart.

Evolution of the long necks: main hypotheses

The ‘competing browsers’ idea, elucidated by later editions of Darwin (1871) proposed that the competition between browsing species for access to leaves from tall trees created an advantage for giraffe to out-reach their tallest rivals (Darwin, 1871). The individuals doing so survive food bottlenecks during dry-season dearths and live to pass on their long-necked genes to future generations. Observing giraffes browse from 5-m-tall Acacia suggests that the idea is secure with little need for further debate. However,
Simmons & Scheepers (1996) found inconsistent support from foraging studies, and recent evidence (Shorrock, 2009) also indicates that animals frequently feed at shoulder level, during winter bottlenecks (Ginnett & Demment, 1997), when their neck should assist them in gaining a feeding height advantage. The finding that giraffe feed faster at shoulder level (2.5 m for females and 3.0 m for males) in East Africa (Young & Isbell, 1991), and spend more time doing so than at higher levels (Young & Isbell 1991; Ginnett & Demment, 1997) also suggests patchy advantages from elsewhere in Africa. That giraffe are considerably taller than competing browsers and have been so for more than 1 Myr (Mitchell & Skinner, 2003) suggests other selection pressures at work on the neck. Can this be explained by competition from other extant browsers such as elephant *Loxodonta africana* and black rhino *Diceros bicornis*? Both species push over trees or destroy them while feeding, especially in times of drought (Smithers, 1983; Estes, 1991). This behaviour suggests that height *per se* is not likely to confer much advantage to a tall giraffe.

However, South African giraffe were found to browse more often above shoulder level (du Toit, 1990), partly because more browse was available there (Woolnough & du Toit, 2001) and partly due to their move into dry riverbeds in winter where leaves remained on tall trees (du Toit, 1995). Further experimental support was found in an elegant field study of feeding competition, indicating that more forage was available above 2.5 m in fenced trees at giraffe levels used by giraffe (relative to un-exclosed trees) because of the competition with shorter browsers (Cameron & du Toit, 2007). Their results support Darwin’s original hypothesis but do not distinguish between it and the sexual selection alternative (Cameron & du Toit, 2007).

This so-called ‘necks-for-sex’ idea (Senter, 2007) suggested that long, powerful necks were sexually selected as clubs, allowing males with large powerful necks to beat rivals for access to oestrous females. Females don’t fight, and so they are predicted to have less powerful necks. Feeding competition predicts equally long necks if both sexes benefit from feeding above other browsers. Clubbing involves males standing flank to flank and head to head, and smashing the back of the head into their opponents ribs and legs by whipping the neck back and then their rival. Fatalities are not uncommon (Simmons & Scheepers, 1996). Female mate choice may also play a role if females prefer males with larger necks.

Several lines of evidence support the sexual selection idea: (1) males with larger necks win most contests for access to oestrous females (Pratt & Anderson 1982, 1985); (2) oestrous females show preference for large-necked males or darker, older males (Pratt & Anderson, 1985; Brand, 2007); (3) dominance contests involve prominent displays of the long neck by male giraffe during erect walking (Dagg & Foster, 1976; Estes, 1991; Brand, 2007); (4) sexually selected traits are condition-dependent and costly (Darwin, 1871; Kodric-Brown & Brown, 1984; Andersson, 1994), for which there is some support from sex-biased mortality and physiological costs. Morphologically (5) sexually selected traits are usually positively allometric (Clutton-Brock, Albon, Harvey, 1980; Petrie, 1992; Kodric-Brown, Sibly, Brown, 2006), relative to body size, a trait confirmed for giraffe necks and heads (Simmons & Scheepers, 1996); and (6) the fossil record should show a departure from typical ratios of neck vertebrae to remaining vertebrae lengths, for extant giraffe relative to ancestral giraffids, as confirmed by Badiangana, Adams, Manger, (2009).

**Testing between hypotheses: directly observed selection pressure**

The best evidence for either hypothesis would be directly observed fitness benefits. The observation that larger-necked male giraffes win contests more often than smaller-necked giraffes and are preferred by oestrous females (Pratt & Anderson 1982, 1985) provides direct evidence indicating that sexual selection on neck size is occurring. Paternity tests are required to confirm that these mating advantages lead to higher reproductive success. We are unaware of similar direct evidence for the feeding competition hypothesis (i.e. taller giraffe survive food bottlenecks). Estimating sex-specific selection on neck characteristics in individually recognizable giraffes would be a powerful tool for quantifying the selection pressure acting on the two sexes, and for measuring short-term evolutionary change. This has been done for other species (e.g. Roulin et al., 2010), and a study of giraffe could largely settle the question regarding what maintains the long neck. The feeding competition hypothesis predicts positive selection on both sexes, whereas the sexual selection hypothesis predicts neutral selection on females and positive selection on males. Differential food resource allocation between male and female giraffe has been well studied (Young & Isbell, 1991; Ginnett & Demment, 1997), but its role in reducing food competition between the sexes remains unexplored; this too may influence natural selection on neck length.

**Necks: size matters**

Under sexual selection, males should have proportionally larger necks and heads than females, whereas the competing browsers idea predicts similar relationships for both sexes, assuming no inter-sexual competition. Sexually selected traits are more often positively allometric than naturally selected ones among mammals (Kodric-Brown et al., 2006), but not universally so (Bonduriansky, 2007; Cuervo & Moller, 2009). Thus, positive allometry is more likely for male giraffe under sexual selection than for females and this was verified for 77 Namibian giraffe (Simmons & Scheepers, 1996). This hypothesis has been re-assessed recently using a Zimbabwean sample (Mitchell, van Sittert, Skinner, 2009, *n* = 17 males and 21 females). The allometric relationship is given by

\[ T = aM^k \]  

where *T* is the trait of interest (the neck mass or the head mass in this case), *M* is the body mass (excluding the neck
and head mass to make $T$ independent of $M$ and $a$ is a constant. The exponent $k$ determines whether the relationship between $T$ and the body mass is isometric ($k \approx 1$), positively allometric ($k > 1$) or negatively allometric ($k < 1$). The Zimbabwean studies fitted linear regression models after taking the logarithm on both sides of equation (1). We re-analysed the Namibian data using non-linear regression models implemented in the function nls in program R 2.9.0 (R Development Core Team, 2009). The critical question is whether $k$ differs between the sexes, and this approach allows us to test this statistically. We modified equation (1) to include sex ($s$: 0 = male, 1 = female):

$$T = (a + bs)M^{(k + cs)}$$

Equation (2)Parameters $b$ and $c$ estimate sex differences in the constant and in the exponent, respectively. Differences between the Namibian and Zimbabwean data could be tested formally in a similar way. Therefore, we requested the original data from Mitchell and colleagues but our request was refused (G. Mitchell, pers. comm.).

Results from Namibia were similar to that originally reported (Simmons & Scheepers, 1996): neck mass showed a positive allometric relationship to body mass in males [Fig. 1; $k = 1.34$, 95% confidence interval (CI): 1.16–1.51] and an isometric relationship in females (Fig. 1; $k = 0.90$, CI: 0.69–1.10). This difference was significant (parameter $c$ in equation (2) significantly different from zero, $P = 0.007$). Slopes derived previously using RMA regression for males ($k = 1.35$) and females ($k = 0.97$) were similar (Simmons & Scheepers, 1996). Mitchell et al. (2009) reported $k = 1.13$ for males and $k = 1.06$ for females in their smaller Zimbabwean sample. While Mitchell et al. (2009) interpreted their results as evidence for positive allometry in both sexes, they reported neither confidence intervals or significance levels for $k$ nor differences between the sexes. The $k = 1.06$ reported for Zimbabwean females (Mitchell et al., 2009) appears to reveal isometry, not positive allometry, because it lies close to 1.00 and within confidence limits from the Namibian dataset; thus the two populations probably do not differ significantly. Mitchell et al. (2009) appear to have misinterpreted this result, and their data therefore support the idea that female neck mass is directly related to body size, a pattern not usually seen in sexually selected traits.

Mitchell et al. (2009) also measured neck length and found no apparent difference in dimensions between males and females (significance levels were unreported) or in neck length regressed against body mass for males and females. However, sexual selection does not directly predict allometrically longer necks but more powerful ones for males. Female’s necks could be equally long but ineffective as clubs because clubbing combines neck length and neck size (related to muscle mass) to generate momentum in the head for clubbing rivals (Simmons & Scheepers, 1996; Simmons, 2008). Differentiating the muscle to bone components in the neck (Mitchell et al., 2009) indeed shows that the mass difference is due to muscle mass and not due to bone density. While Dagg & Foster (1976) indicate that necks of females are about 35 cm shorter, data presented on neck length by Mitchell et al. (2009) indicated that ‘females were 18.3 cm shorter, but with necks 4.6 cm longer and forelegs 2.6 cm longer than males of the same mass’. This suggests some discrepancy in their measurements but again original data were unavailable. The critical point is that males need only a long neck to reach high-level leaves (natural selection hypothesis), a massive and ever increasing one to do so. For sexual selection, this is required and predicted for males and not for females. Thus, both Zimbabwean and Namibian data support the sexual selection idea on male necks. Furthermore, the neck mass of male but not female giraffe in the Namibian sample continued to increase with age, as expected for a trait that enhances intra-sexual combat. Growth in relation to age of Zimbabwean giraffes was not given.

Sexual selection of size and shape in ungulates is, of course, not limited to giraffe and it may well explain the dimorphism of many species, including a larger body size and the growth of male characters such as horns and antlers (e.g. Bergeron et al., 2008). These in turn can be reliable indicators of mating success or individual fitness-related traits (Malo et al., 2005; Vanpe et al., 2007).

**Heads as clubs**

If sexual selection contributed to the evolution of giraffes’ large necks for clubbing opponents, we expect significant differences between the sexes in head mass. Conversely, if feeding competition was the sole selective force, no differences would be expected. Re-evaluating the Namibian data (Simmons & Scheepers, 1996) using the allometric methods described above indicated that males had significantly
A larger heart and the highest known blood pressure in any animal (Warren, 1974; Mitchell et al., 2006). Under the sexual selection hypothesis, costs are expected to accompany sexually selected traits because they are condition-dependent (Andersson, 1994). While traits such as long tails or long necks may attract predators (e.g. Petrie, 1992), the individual doing so benefits from increased mating access. Available evidence on predation is scanty for giraffe, but males in a wild South African population suffered 1.8-fold higher predation levels than females (Pienaar 1969), and the 108 giraffe killed (2% of the population) over 2 years indicated that giraffe were the third most preferred prey for lions Panthera leo. If giraffe live to an average of 25–28 years (Dagg & Foster, 1976), their annual adult mortality (~1/longevity) should be less than ~4% suggesting that lion predation adds greatly to mortality. This may arise from the behaviour of males persistently following oestrous females or from physiological costs. Adult males have longer (Dagg & Foster 1976) and proportionately larger necks than females (this study), and have larger skeletons that require more protein and calcium-rich browse (Mitchell & Skinner, 1993). Thus, males may lose condition quickly if food becomes limiting, and this may lead to increased mortality. It is critical, however, to determine the neck size of those males suffering the highest predation, and whether males in good condition grow the largest necks.

Phylogenetic evidence

The earliest obvious fossil ancestor of the giraffe Giraffacaroti x punjabensis had skeletally short legs and neck (Colbert, 1933; Badlangana et al., 2009), and occurred in India some 12–15 Mya (Mitchell & Skinner, 2003). The giraffid Paleotragus primaevus, similar in size to the okapi Okapia johnstoni, showed long legs but an unelongated neck and arose about 12–15 Mya (Mitchell & Skinner, 2003) and went extinct about 9 Mya. Among subsequent ancestors, the medium-sized Paleotragus germaini and the large Samotherium sp. exhibited elongated necks relative to their total vertebral column (Badlangana et al., 2009). Paleotragus germaini was apparently the first species to show elongation of modern giraffe proportions as reconstructed from fossil cervical vertebrae (Badlangana et al., 2009). Samotherium species that followed were also long necked but much larger and dominated from about 9–5 Mya. Thus, giraffid necks elongated during a period when the climate was cooling, grasslands were expanding and rainfall was declining (Mitchell & Skinner, 2003).

Under the competing browser hypothesis, legs should have elongated at the same pace as necks (selection was on reaching higher levels), whereas the sexual selection hypothesis predicts that neck length increased disproportionately (as a runaway process). At present, the fossil record is too patchy to support one hypothesis over the other. However, the closely related okapi has a leg : neck ratio of c. 1:0.44 (Simmons & Scheepers, 1996) compared with the giraffe’s 1:1.13 (female) and 1:1.08 (male) (Mitchell et al., 2009). In other words, necks have grown more than twofold longer in
giraffe relative to okapi. Given that okapi are similar in proportion to the ancestral *G. punjabiensis*, (Colbert, 1938; Savage & Long, 1986), ancestral giraffe have shown a disproportionate lengthening of the neck and palaeontology needs to inform us what precipitated and accompanied the change from 1:0.44. Badlangana et al. (2009) determined the increased length of the seven cervical vertebrae relative to the overall vertebral column length. The neck vertebrae of the okapi comprise 35% of the total vertebral column, while that of the giraffe comprise 54%. Ancestral *Paleotragus* species or *Samotherium* could not be resolved in the same manner, but graphing the relative change in neck to the total vertebral column would indicate when, and how fast, the elongation occurred in the giraffe’s closest ancestors.

**Long necks as a pre-requisite for necking?**

Some authors argue that ‘necking’ cannot have been the origin of elongation because a long neck is required at the incipient stages (Mitchell et al., 2009). The evolution of a morphological trait comprises two parts: (1) the incipient growth (origin) of the trait and (2) its present-day maintenance. Clarification of the incipient origin is often only possible with a precise fossil record, showing forms before and after the presumed event. Present-day maintenance is easier to evaluate because intra-sexual competition, female mate choice, predators and competition for resources can be measured directly and the selective pressures quantified. This point was clarified in Simmons & Scheepers, (1996) when they stated that long necks may be an exaptation (Gould & Vrba, 1982) – a trait arising from other selection pressures and now ‘hijacked’ for other purposes. So the tipping point does not have to be the same as the selection pressures that either drove the neck ever longer or maintain it present day. More arid climates and advancing grasslands during the mid-to late Miocene (Mitchell & Skinner, 2003; Badlangana et al., 2009) appear to have coincided with this change. Simultaneously, the ancestral Palaeotraginae moved into Africa where new habitats such as open treed savannas existed (Mitchell & Skinner, 2003). These slightly elongate animals may have adapted to their new environment by growing taller to feed off tall trees. Equally plausible is an isometric change in body proportions with an increasing body size (e.g. due to a cooler climate) that increased the neck length beyond a point that disallowed head-butting or wrestling. This would signal the beginning of a sexually selected lengthening as one of the ancestral giraffids (e.g. *Giraffkeryx* or *Paleotragus primaevus*) switched exclusively to head clubbing.

Furthermore, the horns and ossicones used for combat in several early ancestors were neither forward-facing (implying head-butting) nor antlered (implying head wrestling: Caro et al., 2003), but were positioned laterally on the skull to point almost perpendicular from it. This occurred in the earliest known ancestor *Canthumeryx sirtensis* (Churcher, 1976) and was repeated by the four-horned *Giraffkeryx*, with rather laterally orientated and backward-pointing ossicones (Colbert, 1933). Neither exhibited elongated necks of the proportion seen in giraffe. This positioning implies that both species fought with sideways movements of the head, possibly while standing side by side. This is precisely the precursor one would predict for the longer swinging arcs evident in the extant giraffe but without their elongated necks. Further support comes from unpublished data suggesting that okapi males also exhibit side-to-side head swinging as well as typical head butting (S. Shurter, pers. comm.), implying that this is a deep-seated behavioural trait common to giraffids.

**Future tests – ossicones and necks evolving in unison**

We propose that the two main hypotheses can be distinguished by assessing the phylogenetic development of short stout ossicones in conjunction with neck elongation. Traditionally, head wrestling is undertaken by ungulates with antlers (e.g. Cervidae) or twisted and ribbed horns (e.g. Antilopinae) that lock on contact, while head butting is practised by species with massive curved horns (e.g. Caprinae) or frontal bosses (e.g. Bovinae) (Geist 1966, Clutton-Brock, 1982; Estes, 1991; Caro et al., 2003). By contrast, stout ossicones are used by male giraffe to concentrate the force of a swinging head to sometimes splinter bones of opposing males (Innis, 1958; Simmons & Scheepers, 1996). Thus, if the origin of neck elongation occurred because of competition over females rather than browse, the incipient neck elongation should be accompanied by a change in horn morphology from large antlers to small, stout ossicones. The giraffe fossil record should indicate at what stage the small sideways pointing horns of the ancestral giraffids (e.g. *Canthumeryx sirtensis* Churcher, 1976) evolved to the short blunt ossicones we see on the extinct long-necked *Samotherium* and all subsequent giraffids (Colbert, 1933; Mitchell & Skinner 2003; Badlangana et al., 2009). Simultaneously, we should see a change in the relative length of the neck and forelegs. The sexual selection hypothesis predicts that the appearance of ossicones is most likely to coincide with the time that the neck becomes slightly too long for wrestling or butting, and this in turn should lie at the start of an allometric departure from isometric neck length to foreleg length ratios. Neck elongation should also coincide with sexual dimorphism in the skulls of ancestral giraffids. Natural selection predicts that the neck and leg elongation should co-occur, but it makes no predictions concerning skull dimorphism.

**Main challenges for both hypotheses remain**

Our review of evolutionary hypotheses explaining the giraffe’s long neck shows that both main hypotheses have merits and challenges. For the competing browsers hypothesis, we need to determine what maintains modern giraffe c. 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). An animal approximately half the size of the present-day giraffe (i.e.~2.5–3.0 m high) would be sufficient to out-compete other foliviore. The main challenge for the sexual selection hypothesis is to explain why female giraffes also have long necks, even though their necks are shorter than those of males. Genetic correlation between the sexes is one reason for male-like characters (Darwin, 1871, Fisher, 1930, Lande 1987, but see Stankovich & Caro, 2009), and the small ossicones of female giraffe are more likely to arise from such correlations than female–female competition. If, however, there are costs to having a long neck and no benefits to females, genetic correlations between female and male neck length may break down and result in more pronounced dimorphism. Estimates of the genetic correlation between female and male neck characteristics are required together with precise estimates of the physiological costs to determine whether the long female neck is a by-product of selection on males. The competing browser hypothesis proposes benefits for both sexes, and a reduction in competition between the sexes through foraging height partitioning is a possible advantage that remains unexplored. In the absence of direct selection on neck length under sexual selection, it may be sufficient to propose that the shorter necks of females (and the lack of growth after 8 years: Simmons & Scheepers, 1996) is one way of reducing physiological and heart-to-head costs.

We conclude that both mechanisms may play a role in the origin and maintenance of this unique trait and suggest that refined measurements of costs and selection pressure together with a fresh look at the fossil record should allow us to quantify their relative importance.

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