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Natural History Miscellany

Winning by a Neck: Tall Giraffes Avoid Competing with Shorter Browsers

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ABSTRACT: With their vertically elongated body form, giraffes generally feed above the level of other browsers within the savanna browsing guild, despite having access to foliage at lower levels. They ingest more leaf mass per bite when foraging high in the tree, perhaps because smaller, more selective browsers deplete shoots at lower levels or because trees differentially allocate resources to promote shoot growth in the upper canopy. We erected exclosures around individual *Acacia nigrescens* trees in the greater Kruger ecosystem, South Africa. After a complete growing season, we found no differences in leaf biomass per shoot across height zones in exclosed trees but significant differences in control trees. We conclude that giraffes preferentially browse at high levels in the canopy to avoid competition with smaller browsers. Our findings are analogous with those from studies of grazing guilds and demonstrate that resource partitioning can be driven by competition when smaller foragers displace larger foragers from shared resources. This provides the first experimental support for the classic evolutionary hypothesis that vertical elongation of the giraffe body is an outcome of competition within the browsing ungulate guild.

Keywords: natural selection, African ungulates, guilds, resource partitioning.

The evolution of the giraffe's elongated neck is widely considered a classic example of evolutionary biology based on foraging competition (e.g., Darwin 1871). This competition hypothesis had been implicitly accepted because it seemed so obvious (e.g., Dagg and Foster 1976; Pellew

1984; Harvey and Pagel 1991), until Simmons and Scheepers (1996) questioned the evidence for it and suggested that alternative explanations, such as sexual selection, could be equally plausible. The problem was that no study had been designed to explicitly test whether giraffes achieve a foraging advantage by foraging above the reach of smaller browsers.

African savanna ungulates may be functionally divided into grazing and browsing guilds, of which the latter has only recently become the subject of resource partitioning studies (reviewed in du Toit 2003). Conversely, the grazing guild has been the subject of extensive research on ecological separation (Gwynne and Bell 1968; Bell 1970, 1971; McNaughton and Georgiadis 1986; Illius and Gordon 1987; Murray and Illius 2000), and it is parsimonious to examine whether overarching principles elucidated for grazers may also apply to browsers. For example, the Jarman-Bell principle was primarily developed for grazing ecosystems and has been fundamental to our understanding of resource partitioning within ungulate assemblages (Bell 1971, 1986; Geist 1974; Jarman 1974; Demment and van Soest 1985). Essentially, the principle states that an increase in body size is associated with an increase in dietary tolerance, due to lower mass-specific metabolic requirements and increased absolute gut capacity. The ecological result is that the smallest ungulate species feed selectively on the highest-quality plant parts available. To meet their greater intake requirements, the larger-bodied species are forced to eat larger quantities of more abundant but lower-quality food, which they can tolerate, although they would prefer higher-quality food.

Our understanding of the principle is predominantly based on the African grazing guild. In this system, the larger species (buffalo *Syncerus caffer*, zebra *Equus burchelli*, wildebeest *Connochaetes taurinus*) consume less leaf and more stem than the smaller-bodied species (Grant's and Thomson's gazelles, *Gazella granti* and *Gazella thomsonii*), which results in a grazing succession, as described for the Serengeti Plains of East Africa (Gwynne and Bell 1968; Bell 1970, 1971). It was initially hypothesized that the larger species facilitated the grazing opportunities of

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the smaller species (Bell 1970, 1971), but long-term data did not support the facilitation hypothesis (Sinclair and Norton-Griffiths 1982). Rather, the smaller grazers are more specialized feeders, using their narrower muzzles to deplete individual grass tufts of the highest-quality parts and thereby reducing the overall quality of the sward for the larger generalist grazers (Illius and Gordon 1987, 1992; Murray and Illius 2000). Consequently, there are strong empirical and theoretical grounds to suggest that the succession is maintained by competition from the smaller grazers, not facilitation by the larger ones.

Like grazers, browsers exhibit size-structured resource partitioning (du Toit 1990; Dekker et al. 1996). Steenboks (*Raphicerus campestris*) and impalas (*Aepyceros melampus*) forage low in the tree (mainly <1 m), kudus (*Tragelaphus strepsiceros*) forage higher (<2 m), and giraffes, which could forage throughout the canopy, generally forage above the level of the other browsers (mainly 2–4 m; Pellew 1983, 1984; du Toit 1990; Ginnett and Demment 1997; see appendix in the online edition of the *American Naturalist*). Giraffes gain a nutritional advantage by foraging above the height of the other species, as they receive more biomass per bite higher in the canopy (Woolnough and du Toit 2001). This suggests that the depletion of higher-quality plant parts by smaller browsers drives giraffes to forage higher in the canopy, thereby supporting the competition hypothesis, paralleling results from the grazing guild (Illius and Gordon 1987; Murray and Illius 2000). However, it is also possible that the tendency of trees to allocate less leaf biomass to shoots low in the canopy may explain this variation even in the absence of competition (Woolnough and du Toit 2001).

We investigated whether the difference in leaf biomass available to giraffes at different heights in the canopy can be ascribed to the feeding actions of smaller browsers or differential resource allocation within the tree. Fences excluding smaller browsers were built and maintained for a growing season at a savanna site in South Africa with an intact guild of indigenous browsing ungulates.

Methods

Availability of browse was studied using *Acacia nigrescens*, a staple browse plant of giraffes in southern Africa (du Toit et al. 1990), from November 2001 to July 2003 in the Lion Sands Game Reserve in the Sabi Sand Wildtuin, part of the greater Kruger ecosystem (240°46'S, 310°52'E). The area has a seasonal rainfall pattern, with a distinct wet and dry season, and vegetation dominated by *Sclerocarya birrea/A. nigrescens* savanna on a basaltic plain. There is high browsing pressure in the area, with giraffes, kudus, impalas, and steenboks all present.

We constructed fences around individual *A. nigrescens*

trees in November 2001. Nine enclosure plots were created by selecting trees that were taller than 4 m and had branches throughout their height range. We constructed fences 2.2 m in height, 1 m from the outside canopy branches. Therefore, we excluded all small browsers and partially excluded larger browsers, except giraffes, who could freely forage at heights above 2.2 m. The fences were monitored and repaired whenever damaged, for example, by elephants (*Loxodonta africana*). Each excluded tree was paired with the nearest unfenced (control) tree within 10 m that met the same selection criteria (at least 4 m tall with branches at all potential foraging heights).

Experimental and control trees were sampled before fencing and again in the early dry season (July 2003) after two complete growing seasons. We defined three levels for sampling available browse: 1 m (available to steenboks, impalas, kudus, and giraffes), 2.5 m (available for kudus and giraffes), and 4 m (available only to giraffes). At each height level, we recorded the presence of recent browsing of shoot ends on a presence/absence basis for 10 randomly selected shoots around the canopy. This provided a proportional index of browsing intensity up and down the canopy (du Toit et al. 1990). For sampling forage availability, we used a previously defined giraffe browse unit (GBU). The GBU is equivalent to the average twig pruned or leaf stripped by a giraffe in a single bite, which for *A. nigrescens* is 144 mm long (Woolnough and du Toit 2001). The GBU thus incorporates the smaller bites of steenboks, impalas, and kudus and provides a measure of biomass return per bite, reflecting both foliage depletion and foraging efficiency. At each tree, five GBUs were clipped from around the canopy at each of the height levels, for a total of 15 GBUs per tree. These GBUs represented the twig and leaf material available to browsers at the time of sampling. Collected samples were stripped of leaves, and the leaf and twig material was placed in a labeled paper bag for drying. Samples were air dried in the field and later oven dried at 60°C until mass was constant. For each GBU sampled, leaf dry mass, twig dry mass, and twig proximal diameter were recorded. We calculated the difference in leaf biomass from prefencing to postfencing two growing seasons later. Two experimental trees were excluded from the final analysis because of elephant damage.

To conduct statistical analysis, we log transformed data to conform to a normal distribution where necessary. Paired analyses were initially used, but the loss of two trees to elephant damage reduced significance levels for these analyses. The results for these analyses were, however, qualitatively the same. All statistical analyses were conducted using Statistica.

Results

Before fencing, our results confirm the findings of previous research. There was a significant difference in forage availability at the different heights, with less browse per GBU low in the tree and more at heights available only to giraffes (ANOVA, $F = 9.20$, $df = 2, 51$, $P < .0005$). There was no significant difference between control and treatment trees at any height. The patterns for recent foraging were more ambiguous, with no significant difference in foraging with tree height and no difference between control and treatment trees.

There was a significant difference from pre- to post-fencing between control and excluded trees at 1 m (paired t -test, $t = 2.62$, $P = .03$). At 2.5 m, the pattern looked similar (fig. 2) but was not significant (paired t -test, $t = 1.30$, $P = .24$), and there was no difference at 4 m (paired t -test, $t = 0.07$, $P = .95$; fig. 1). In addition, there was a significant difference in forage availability at 1 m between excluded and control trees ($t = 3.60$, $P < .005$) but not at 2.5 m ($t = 1.48$, $P = .16$) or 4 m ($t = 0.10$, $P = .92$). After fencing, there was still a significant difference in forage availability by height for the control (un-

fenced) trees, with less forage available at 1 and 2.5 m and significantly more at 4 m (ANOVA, $F = 5.54$, $df = 2, 22$, $P < .01$; fig. 2). However, there was no significant difference in forage availability for the excluded trees (ANOVA, $F = 0.01$, $df = 2, 22$, $P = .98$).

Our recently browsed shoot data confirmed that we had successfully excluded foragers at low foraging heights; no shoots were foraged on excluded trees at 1 m (fig. 2). Because fences were 2.2 m high, we reduced but did not eliminate foraging at 2.5 m.

Discussion

Our study confirms that there are differences in browsing intensity with foraging height in an intact browsing guild and that browsing pressure across feeding heights is associated with the available leaf biomass per bite for browsers (Woolnough and du Toit 2001). Consequently, giraffes gain a foraging advantage by browsing above the reach of smaller browsers. We additionally show that variation in leaf biomass per shoot across browsing heights diminishes significantly if the smaller browsers are experimentally ex-

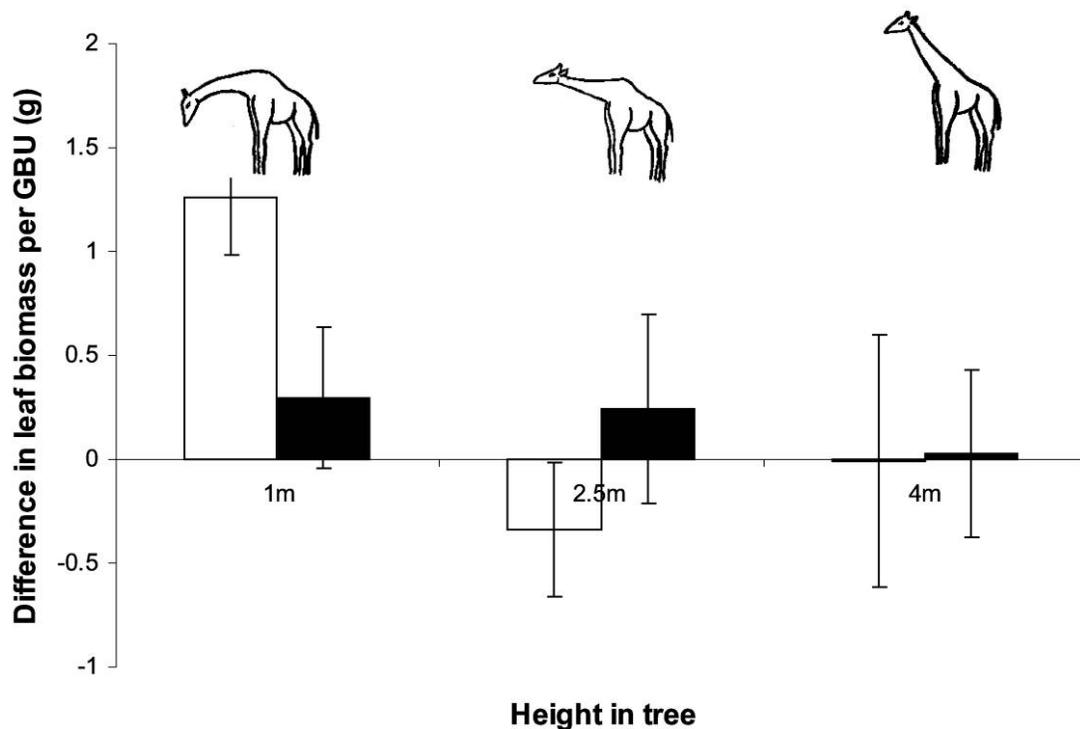


Figure 1: Difference in leaf biomass per giraffe browse unit (GBU) between prefencing and two growing seasons after the erection of enclosures around experimental trees. Open bars are excluded trees; filled bars are control trees. Schematic giraffes indicate the posture of an adult female when browsing at each height.

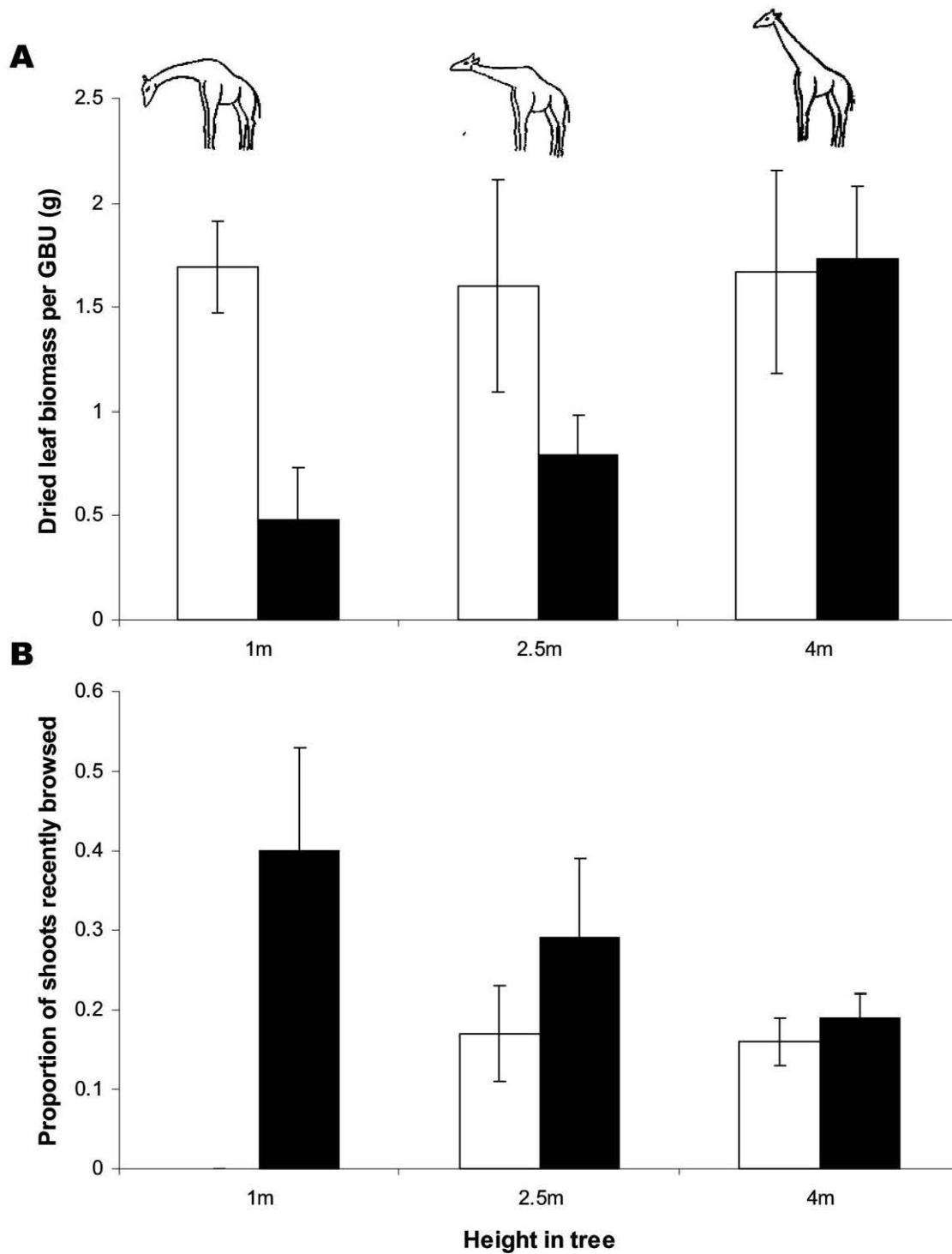


Figure 2: Leaf biomass per giraffe browsing unit (*GBU*; *A*) and the proportion of shoots that had been recently browsed (*B*) at different heights in the tree canopy two growing seasons after erection of exclosures around experimental trees. Open bars are excluded trees; filled bars are control trees. In *B*, the missing bar at 1 m for excluded trees represents 0, as no shoots were browsed. Schematic giraffes indicate the posture of an adult female when browsing at each height.

cluded. Consequently, the pattern of variation in leaf biomass per GBU across feeding heights must be due to depletion of leaf biomass by selective browsing at low canopy levels, supporting the hypothesis that giraffe feeding efficiency is reduced at low heights as an outcome of competition with smaller guild members.

The smallest browsers, impalas and steenboks, are both highly selective feeders, usually plucking individual leaves from woody plants and showing a preference for young and soft shoots early in the growing season (Cooper and Owen-Smith 1986; du Toit 1993). At levels accessible to steenboks and impalas, therefore, the overall food quality and leaf biomass per GBU are both depleted by selective feeding that removes individual leaves from lignified twigs. Similar selectivity for higher intake per bite is shown by kudu compared with impalas (de Garine-Wichatitsky et al. 2004). The higher intake requirement of giraffes means they are forced to browse above the heights accessible to smaller browsers. We conclude that the mechanical effects of giraffe browsing cannot facilitate the feeding of smaller browsers. Instead, our findings are consistent with the hypothesis that competition drives feeding height stratification in a process analogous with that proposed for the grazing succession (Illius and Gordon 1987; Murray and Illius 2000).

Despite popular acceptance that giraffes have long necks because of foraging competition during their evolution, no previous studies have experimentally investigated foraging competition between giraffes and smaller browsers. Simmons and Scheepers (1996) argued that there was little evidence that giraffes forage high in the canopy because of competition and suggested sexual selection as an alternate hypothesis. However, Woolnough and du Toit (2001) showed that giraffes achieve a bite-size advantage by feeding higher in the tree, and now we show that this is explained by the avoidance of competition with smaller browsers. While not resolving the controversy, our study provides the first experimental evidence that the giraffe's extremely elongated body form is naturally selected in response to competition from smaller browsing species.

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