

# Are giraffes pollinators or flower predators of *Acacia nigrescens* in Kruger National Park, South Africa?

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**Abstract:** We examined the relationship between giraffes (*Giraffa camelopardalis*) and *Acacia nigrescens* in Kruger National Park, South Africa, to determine whether these tall ungulates may be providing a pollination service for the trees, or are simply flower predators. We quantified florivory and subsequent fruit set in the presence and absence of giraffes. *Acacia nigrescens* flowers are clearly a substantial dietary component for giraffes. Although *A. nigrescens* flowers contain almost three times as much condensed tannin as leaves, giraffes consume large quantities of flowers (~85% of flowers within reach), resulting in distinct browse lines on the trees. This substantial florivory is detrimental to the overall fecundity of *A. nigrescens*, with significantly reduced fruit set at heights on trees that are accessible to giraffes. Fruit set increased above the reach of giraffes, suggesting successful pollination by insects. Giraffes were effectively flower predators of *A. nigrescens* in the season we examined.

**Key Words:** florivory, *Giraffa camelopardalis*, non-flying mammal pollination, pollination ecology

## INTRODUCTION

In the savanna vegetation of Kruger National Park (KNP), *Acacia nigrescens* Oliver trees flower over a brief, 2–3-wk period towards the end of the dry season (early September). At this time they are the only flowering *Acacia* species away from riverine areas: sympatric species flower during the summer rains (van Wyk & van Wyk 1997). *Acacia nigrescens* engages in mass flowering, where all, or most, of the individual trees in a population flower at the same time. In September, the entire canopy blazes white with flowers, as all the trees begin flowering within a few days of each other (Codd 1951, du Toit 1992).

The flowers of *Acacia nigrescens* are a particularly valuable food source for giraffes (*Giraffa camelopardalis* L.). During the late dry season, browse is extremely limited and of low quality (du Toit 1992). Female giraffes in KNP spend as much as 23.5% of their September feeding time consuming *A. nigrescens* flowers (du Toit 1990a). Similar data for males are not available; however males are taller and feed higher on the trees than females (Birkett 2002, du Toit 1990b, Ginnett & Demment 1999), so may

have access to further flower resources beyond the reach of females. Additionally, *A. nigrescens* flowers constitute a substantial proportion of giraffe stomach contents at this time (Hall-Martin 1974). Although giraffes consume many *A. nigrescens* flowers, it has been suspected they may still play a significant role in pollinating this species (du Toit 1990a, 1992), a question that we set out to investigate.

In reviewing pollination by non-flying mammals, Carthew & Goldingay (1997) list three criteria that are generally sought as evidence that an animal is a pollinator. Firstly, the animal should be a regular and predominantly non-destructive flower visitor. Secondly, when visiting the flowers the animal should pick up pollen and transport it between flowering plants. Thirdly, proof is needed that successful pollination does occur as a result of visitation, and that this pollination leads to the production of seed. Giraffes fulfil some of these criteria, visiting flowering *A. nigrescens* regularly and reliably from one year to the next, but does their consumption of large quantities of flowers have a significantly detrimental effect on these trees? The objectives of this study were to quantify the role of giraffes as potential pollinators or predators of *A. nigrescens* flowers, to assess the nutritional value of *A. nigrescens* flowers compared with alternative

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available browse, and determine whether these flowers are protected from intense predation by any biochemical means. We also carried out analyses of flowering phenology and insect visitation, which are presented elsewhere (Fleming, Hofmeyr & Nicolson, unpubl. data).

## METHODS

### Study site and species

This study was conducted in the *Sclerocarya birrea* (A.Rich.) Hochst.–*Acacia nigrescens* (marula–knobthorn) savanna ecotype of KNP between Tshokwane (24°47'S, 31°52'E) and Satara (24°24'S, 31°46'E), an area approximately 50 km × 20 km. *Acacia nigrescens* is a long-lived, medium to large (15–20 m) woody tree (van Wyk & van Wyk 1997). The study area includes young plants and old, mature individuals, with high densities of *A. nigrescens* where the soil type is optimum. The soils in this vegetation type are predominantly basaltic clays (Gertenbach 1983). The mean annual rainfall is around 530 mm, of which >80% falls in the summer, between October and March. Field work was carried out during *A. nigrescens* flowering, between 2 and 19 September 2003; fruit set was followed up between 28 March and 2 April 2004.

### Browse patterns and giraffe foraging behaviour

To confirm that giraffes were feeding on *A. nigrescens* flowers, the heights they were feeding at, and to assess their species fidelity when browsing, giraffe foraging behaviour was recorded opportunistically. In total, 63 sightings of giraffe feeding were recorded (28 adult males, 20 adult females and 15 juveniles or sub-adults). Sightings were spread over the entire study area (> 100 km<sup>2</sup>), over 3 wk, with minimum likelihood that the same individuals were repeatedly encountered. For each observation, we recorded the initial plant species browsed, and any others moved to within the first 5 min.

A distinct browse line was evident for *A. nigrescens* trees in the presence of giraffes. To quantify this browse line, the abundance of flowers and leaves was rated during September 2003 for flowering *A. nigrescens* trees as indicated below, in areas accessible to giraffes (61 trees outside tourist camps in KNP) and in areas where giraffes were excluded (22 trees inside Satara and Skukuza tourist camps in KNP or outside the park). It was impossible to set up a properly controlled enclosure trial for this experiment, since elephants will destroy such structures. In an attempt to reduce confounding factors, we sampled trees from as many locations within the study area as possible. Furthermore, we recorded variables over

the complete height of each tree, effectively recording two independent factors for this natural experiment: accessibility to giraffes as well as height on tree. Trees analysed were at least 1 m taller than giraffes, had branches within giraffe browsing range, and were within a suitable distance from the road for access (< 50 m, depending on visibility); every attempt was made to match tree height and shape between the two treatments. Each tree was divided into five height classes, based on 'person heights' (PH), the approximate height of one of us (~1.7 m) standing next to the base of the tree. The fifth height class included everything > 4 PH. We had no a priori expectation of heights at which giraffe browsing was most prominent and so data for each height class was recorded (although later pooled and averaged).

In September, a quantitative estimate of relative density of flowers and leaves within each height class was recorded on a scale from 0 (none present: bare twigs) to 5 (maximum observed abundance for the volume of twigs). Fruit set was recorded in April using the same subjective scale. For 42 trees (20 giraffe accessible, 22 inaccessible to giraffes), GPS or map data enabled positive identification of the individual tree 7 mo later, enabling calculation of the ratio of seed set to flowering at the different heights (not calculable for heights where no flowering was recorded, '0'). Another 48 trees were also examined for pods to increase the sample size of fruiting analysis. Differences in leaf, flower and pod distributions were compared for trees exposed to giraffes and those from which giraffes were excluded at PH2 and PH3 (within giraffe browse range), and PH4 and above (above giraffe browse range). Data within giraffe browse range were compared with giraffe accessibility (giraffes excluded '0' and accessible to giraffes '1') and the values above giraffe browse range (as a covariate predictor of an individual tree's leaf/flower/fruit abundance) as independent factors by multiple regression analysis.

### Browse quality

From behavioural observations (du Toit 1988), we know that adult female giraffes in KNP spend 79% of their feeding time in September browsing from six plant species (Table 1). Six samples each of *A. nigrescens* flowers, *A. nigrescens* leaves and the leaves of the five alternative browse species were collected at sites scattered throughout the study area (selected by observing where giraffe were feeding, where possible). Samples were cut from within the giraffe browsing range (~1.7 m to ~5.1 m) and comprised approximately equal amounts by volume from each of up to five individual trees at each site (depending on the number of trees available). Wet mass of leaves and flowers was determined on the day of collection (to 0.01 g, Mettler Toledo, Switzerland) after

**Table 1.** Feeding time for adult female giraffes in Kruger National Park during September (unpublished data from du Toit 1988) and the results of browse quality analyses. Quantities presented are in percent wet mass (% WM) or percent dry mass (% DM), except for condensed tannin (CT), which is the proportion of the maximum CT concentration found. Values are mean  $\pm$  1 SD for  $n = 6$  samples. Multiple regression analysis was carried out comparing nutritional value with feeding time (dependent variable) for each tree species. Levels of statistical significance are represented as follows: ns = not significant, \* =  $P < 0.05$ , \*\*\* =  $P < 0.001$ .

| Plant species (plant part)   | % of feeding time | Water (% WM)              | Crude protein (% DM)        | Neutral detergent fibre 'NDF' (% DM) | Acid detergent fibre 'ADF' (% DM) | <i>In vitro</i> digestibility (% DM) | Condensed tannin (propn. max conc.) |
|--|-------------------|---------------------------|-----------------------------|--------------------------------------|-----------------------------------|--------------------------------------|-------------------------------------|
| <i>Acacia nigrescens</i> Oliver (leaves)   | 30.5%             | 40.3 $\pm$ 4.7            | 12.6 $\pm$ 1.3              | 39.6 $\pm$ 1.2                       | 28.9 $\pm$ 0.9                    | 50.7 $\pm$ 3.3                       | 0.10 $\pm$ 0.03                     |
| (flowers)  | 18.6%             | 64.3 $\pm$ 5.9            | 22.1 $\pm$ 1.8              | 37.2 $\pm$ 2.0                       | 18.3 $\pm$ 0.9                    | 50.6 $\pm$ 4.5                       | 0.27 $\pm$ 0.06                     |
| <i>Acacia gerrardii</i> Benth. (leaves)  | 9.0%              | 44.8 $\pm$ 2.3            | 13.7 $\pm$ 1.1              | 44.3 $\pm$ 6.5                       | 27.6 $\pm$ 1.8                    | 49.6 $\pm$ 7.7                       | 0.11 $\pm$ 0.12                     |
| <i>Acacia robusta</i> Burchell (leaves)  | 6.5%              | 58.9 $\pm$ 7.3            | 17.7 $\pm$ 3.1              | 42.4 $\pm$ 7.2                       | 22.9 $\pm$ 1.8                    | 49.7 $\pm$ 9.8                       | 0.24 $\pm$ 0.15                     |
| <i>Acacia tortilis</i> (Forsk.) Hayne (leaves)   | 6.4%              | 39.9 $\pm$ 10.6           | 17.2 $\pm$ 0.7              | 41.2 $\pm$ 2.4                       | 30.1 $\pm$ 2.3                    | 47.4 $\pm$ 3.5                       | 0.10 $\pm$ 0.04                     |
| <i>Mangium senegalensis</i> (Lam.) Exell (leaves)  | 5.9%              | 51.9 $\pm$ 6.3            | 7.1 $\pm$ 1.0               | 43.6 $\pm$ 5.6                       | 26.1 $\pm$ 3.9                    | 27.3 $\pm$ 20.2                      | 0.52 $\pm$ 0.15                     |
| <i>Combretum hereroense</i> Schinz (leaves)  | 2.0%              | 43.0 $\pm$ 3.3            | 9.8 $\pm$ 0.6               | 28.3 $\pm$ 1.4                       | 26.4 $\pm$ 0.9                    | 40.2 $\pm$ 11.4                      | 0.86 $\pm$ 0.08                     |
| Multiple regression analysis (determination of giraffe feeding time). Std. $\beta \pm$ SE ( $t_{35}$ ) |                   | 0.02 $\pm$ 0.22 (0.09 ns) | -0.31 $\pm$ 0.23 (-1.37 ns) | -0.44 $\pm$ 0.21 (-2.11*)            | -0.25 $\pm$ 0.22 (-1.11 ns)       | -0.03 $\pm$ 0.18 (-0.19 ns)          | -0.96 $\pm$ 0.26 (-3.67***)         |

leaves had been stripped from the twigs (in the case of compound-leaved species, whole leaves were used rather than leaflets, since giraffes strip whole leaves from twigs and branches when browsing). The samples were then air-dried in paper bags hung in the shade.

On return to Pretoria, dried samples of flowers and foliage were weighed and the percentage dry matter determined. Samples were then milled to a powder and analysed for crude/total protein (Macro-Kjeldahl method using the Leco combustion system), acid detergent fibre (ADF) (Goering & van Soest 1970), neutral detergent fibre (NDF), *in vitro* digestibility (using sheep rumen liquor), and condensed tannin (CT) (proanthocyanidin assay using the butanol-HCl method; Wisdom *et al.* 1987) (Table 1). CT values were expressed as a proportion of the maximum concentration, since the agronomy assay has been developed for *Sorghum bicolor* tannin as the standard (Hattas 2003), which may not reflect absolute concentration of *A. nigrescens* tannin. Results of nutrient analyses for the seven browse types (water content, total protein, ADF, NDF, *in vitro* digestibility, and CT content as independent variables) were compared with data on giraffe browsing time (behavioural observations; du Toit 1988) as the dependent factor by multiple regression analysis, to determine whether specific attributes of browse types were associated with feeding preferences (see Belovsky & Schmitz 1991).

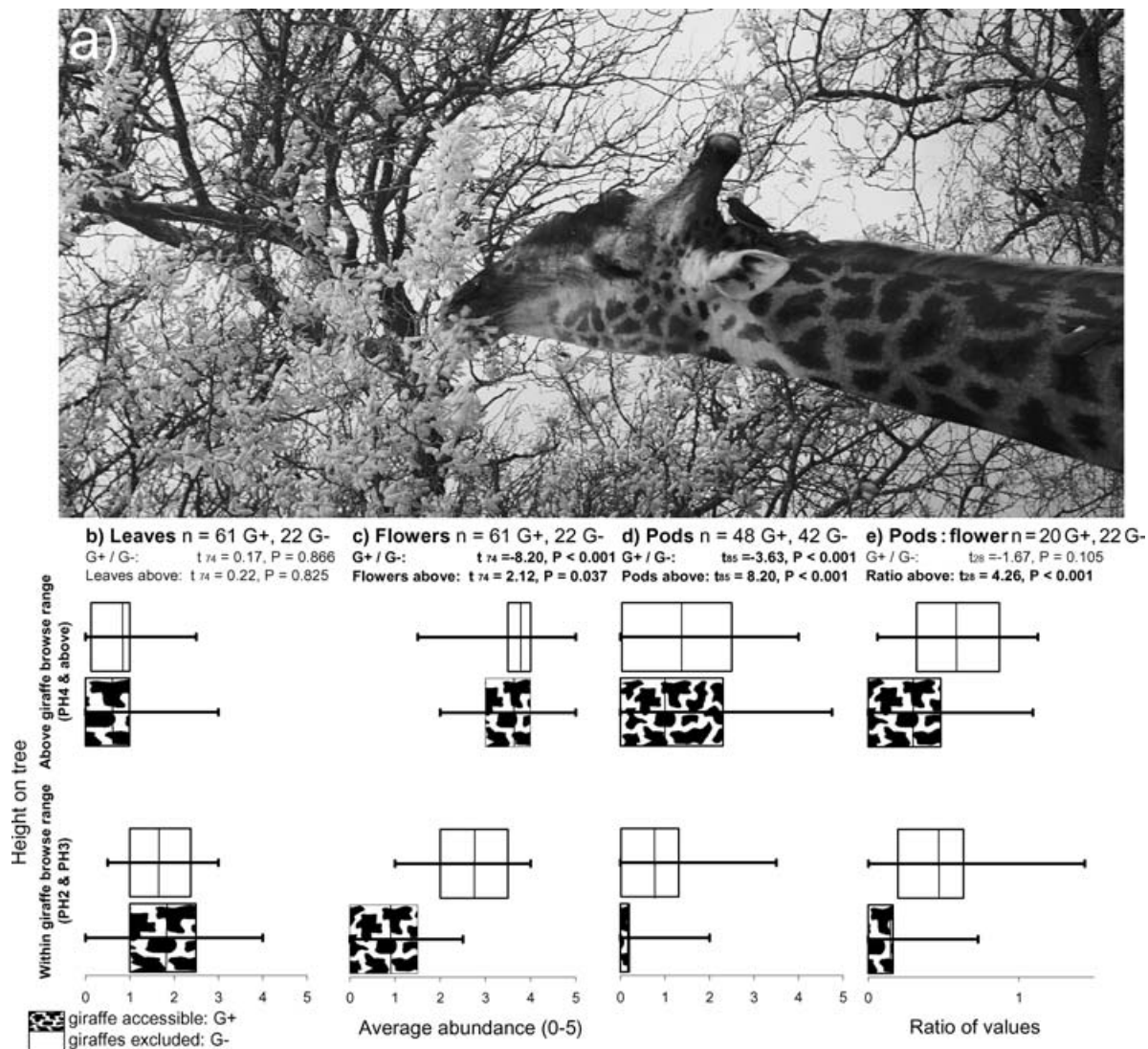
For all tests, the level of significance was  $P \leq 0.05$ . Data are reported throughout as mean  $\pm$  1 SD.

## RESULTS

### Browse patterns and giraffe foraging behaviour

Behavioural observations and data on distribution of flowers and pods suggest that giraffes eat substantial volumes of *A. nigrescens* flowers and significantly reduce seed set. A distinct browse line was observed for flowering trees in areas where giraffes occur (see also Hall-Martin 1974). Of the 63 giraffes observed feeding, 15 (seven adult males, five adult females and three sub-adults or juveniles) were feeding on *A. nigrescens* flowers, and individuals were observed with whole florets on their faces and necks. On 22 of 27 occasions when individuals moved between trees to feed, they remained browsing on the same plant species; on eight of these occasions giraffes moved between *A. nigrescens* trees to feed on flowers. Giraffe browsing range was observed to be PH2 and PH3 (*c.* 1.7–5.1 m) which corresponds to published values for average feeding height for adult females of 2.6 m, and 3.7 m for adult males (Birkett 2002, du Toit 1990b, Ginnett & Demment 1999).

Exposure to giraffes (Figure 1a) was associated with a significant reduction in abundance of *A. nigrescens* flowers



**Figure 1.** (a) Giraffe browsing on *Acacia nigrescens* flowers. Photo: Sally Hofmeyr. Comparison of the abundance of *Acacia nigrescens* (b) leaves, (c) flowers (d) fruit (pods), and (e) the fruit to flower ratio, within giraffe browsing range (PH2 and PH3), and above the reach of giraffes (PH4 and above), inside and outside areas accessible to giraffes. G+ = trees exposed to giraffes (inside the KNP but outside tourist camps); G- = trees not accessible to giraffes (inside tourist camps or outside the KNP). Statistics cited above each graph are a summary of multiple regression analyses carried out to determine whether the presence of giraffes (G+/G-) significantly affects leaves, flowers or fruiting indices, once the values for the same indices at the tops of the trees (above the reach of giraffes) have been taken into account. Values are the mean, quartile and range.

and pods, but not leaves (Figure 1b). Trees exposed to giraffes had significantly fewer flowers (Figure 1c) and fruit (Figure 1d) for heights within giraffe browse range (PH2 and PH3), than those from areas where giraffes were excluded (indicated as a significant G+/G- effect, once the numbers of flowers above and pods above the reach of giraffes had been taken into account). For the 42 trees that were re-visited to follow up fruit set, the fruit to flower ratio within giraffe browse range was not significantly reduced for trees exposed to giraffes, once the ratio on the tops of the trees had been taken into account (Figure 1e).

### Browse quality and defences

Given that giraffes consumed a significant number of *A. nigrescens* flowers, how do the flowers rate in terms of nutritional benefits and defences compared with other diet items? Condensed tannins (CT) were clearly the most significant factor that reflected giraffe feeding time (see results of multiple regression analysis; Table 1). Giraffe browse time was significantly correlated with condensed tannin ( $t_{35} = -3.67, P < 0.001$ ) and total fibre (NDF  $t_{35} = -2.11, P = 0.040$ ) content of different leaf and flower diets. Flowers contained close to three times as

much CT as *A. nigrescens* leaves, and had more CT than leaves of all the *Acacia* species examined; only the leaves of *Maytenus senegalensis* and *Combretum hereroense* contained higher CT levels. In terms of nutritional value, *A. nigrescens* flowers contained about 50% more water, almost twice as much protein and about 33% less lignin and cellulose (ADF) than *A. nigrescens* leaves (Table 1). Flowers had approximately the same amount of total fibre (NDF) and were about as digestible (*in vitro* assay) as *A. nigrescens* leaves.

## DISCUSSION

Giraffes do not appear to be the 'ideal' non-flying mammal pollinator according to the criteria set out by Carthew & Goldingay (1997). Firstly, the animal should be a regular and predominantly non-destructive flower visitor. Giraffes certainly do visit flowering *Acacia nigrescens* regularly, but appear to be highly destructive. Secondly, when visiting the flowers the animal should pick up pollen and transport it between flowering plants. Giraffes were observed with whole *A. nigrescens* florets on their faces and moved directly between trees when browsing, so they have the potential to carry large amounts of pollen between individual trees. The distances that giraffes can travel (up to 20 km in a day; du Toit 1990a) would improve the value of their service as pollen vectors. Thirdly, proof is needed that successful pollination does occur as a result of visitation, and that this pollination leads to the production of seed. In this respect, giraffes appear to do *A. nigrescens* a disservice, since their destructive browsing on flowers (see also Hall-Martin 1974) was associated with significantly reduced *A. nigrescens* fruit set in the present study.

Predator satiation is one of the theories for the ultimate advantage of mast seeding (Kelly 1994). Similarly, highly synchronized and abundant flowering might reduce the detrimental effect of giraffe browsing, since copious flowers may mean that a certain level of florivory can be tolerated. Mass flowering strategies, displayed by many *Acacia* species, mean that they produce potentially viable flowers hugely in excess of the resources they have to invest in seed production, leading to resource matching by selective abortion (and abscission) of fertilised ovules and small seed pods (Bawa & Webb 1984). Consequently, *Acacia* species almost invariably exhibit a very low pod to flower ratio (Gassama-Dia *et al.* 2003, Raju & Rao 2002, Tandon *et al.* 2001, see also review by Kenrick 2003). Low fruit set may be due to inadequate pollination (Moncur *et al.* 1991, Tandon *et al.* 2001), or alternatively only a small proportion of the florets may be fertile: the remainder are the equivalent of petals, simply to attract pollinators (Ross 1979) or disseminate pollen (Kearns & Inouye 1993), and therefore largely expendable. Large

numbers of staminate flowers represent a powerful visual and olfactory advertisement, as well as abundant reward for a limited pool of pollinators (Stone *et al.* 2003). Abundant, synchronous flowering, beyond the resources available for fruit set, may therefore ensure that the giraffe population is unable to consume sufficient flowers to significantly decrease overall *A. nigrescens* reproductive output (du Toit 1992). We noted that trees exposed to giraffes (and other browsers also) had lower overall fruit set, possibly reflecting the fact that these trees have fewer resources to allocate to seed: they were exposed to intense browsing and possibly also limited water availability (by contrast, giraffe-excluded trees were protected from browsing whilst those within tourist camps might also have more water available). This difference might suggest that fruit set in *A. nigrescens* is restricted by resource limitation, rather than insufficient pollination.

An increase in condensed tannin (CT) content was significantly correlated with a reduction in giraffe feeding time on different plant species, which presumably reflects forage quality for these animals. Condensed tannins (CT) were measured given their role as a deterrent for mammalian herbivores, especially ruminants (Cooper & Owen-Smith 1985, Owen-Smith *et al.* 1993, Robbins *et al.* 1987) and tannin concentration has previously been associated with avoidance of certain plant foods by giraffes (Caister *et al.* 2003, Furstenburg & van Hoven 1994). *Acacia nigrescens* flowers contain  $\sim 3 \times$  more CT than *A. nigrescens* leaves and more CT than three of the five species of alternative browse. Condensed tannins are complex secondary metabolites that are therefore expensive to produce (Harborne 1991); their primary function may be to defend plant tissues against microbial or fungal attack (Cooper & Owen-Smith 1985, Kantar *et al.* 1996) and advantageous herbivore-deterrent properties may be secondary or incidental (Cooper & Owen-Smith 1985). Several studies, however, have found high CT levels in the flowers of various trees, shrubs and forbs, which may be associated with protecting the valuable flowers against herbivory (Frutos *et al.* 2002, Hyder *et al.* 2002, Robbins *et al.* 1987). For example, vervet monkeys in Kenya consume large quantities of flowers of two *Acacia* species: when both are available, monkeys prefer *A. tortilis* flowers, which have CT concentrations only 25–33% of those in *A. xanthophloea* flowers (Wrangham & Waterman 1981).

Condensed tannins are thought to deter ruminant browsing by binding to proteins in the plant cell walls and rendering them inaccessible to the animals' gut microflora (Cooper & Owen-Smith 1985, Hattas 2003). Cooper *et al.* (1988), however, suggested that a trade-off between tannin and protein content may make protein-rich browse a favoured choice despite high CT content. This may explain why *A. nigrescens* flowers, with almost

three times as much CT as leaves, but also with twice the protein content, are nevertheless heavily utilized by giraffes as browse during September. In fact, during the period of this study, giraffes consumed almost every inflorescence within reach.

In conclusion, high condensed tannin concentrations clearly do not deter giraffe browsing and *A. nigrescens* flowers are afforded little other protection, being exposed both physically and temporally to intense predation by giraffes. Additionally, flowers are comparable nutritionally to other browse, which is itself also limited in availability. For the plants, the costs of exposure experienced by flowering in September may be outweighed by the benefits of avoiding competition with sympatric *Acacia* species. We recorded a variety of insect visitors to *A. nigrescens* inflorescences during our field study, presumably attracted by the nectar and pollen resources available (Fleming, Hofmeyr & Nicolson, unpubl. data). Coupled with the successful fruitset on the tops of these trees, it seems likely that *A. nigrescens* may rely on insect or bird visitors, but not giraffes, in order to effect pollination. Finally, giraffes were plainly highly destructive and detrimental to the trees' overall fecundity during the season we examined. If they have a role as pollinators of *A. nigrescens*, then it would appear to be confined to years of superabundant, highly synchronized flowering, or could be in terms of greater quality of pollination service, which may be revealed by genetic analysis of seed.

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## LITERATURE CITED

- BAWA, K. S. & WEBB, C. J. 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *American Journal of Botany* 71:736–751.
- BELOVSKY, G. E. & SCHMITZ, O. J. 1991. Mammalian herbivore optimal foraging and the role of plant defenses. Pp. 1–28 in Palo, R. T. & Robbins, C. T. (eds.), *Plant defences against mammalian herbivory*. CRC Publishing, Boca Raton, FL.
- BIRKETT, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology* 40:276–282.
- CAISTER, L. E., SHIELDS, W. M. & GOSSER, A. 2003. Female tannin avoidance: a possible explanation for habitat and dietary segregation of giraffes (*Giraffa camelopardalis peralta*) in Niger. *African Journal of Ecology* 41:201–210.
- CARTHEW, S. M. & GOLDINGAY, R. L. 1997. Non-flying mammals as pollinators. *Trends in Ecology and Evolution* 12:104–108.
- CODD, L. E. W. 1951. *Trees and shrubs of the Kruger National Park*. Government Printer, Pretoria, South Africa. 192 pp.
- COOPER, S. M. & OWEN-SMITH, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142–146.
- COOPER, S. M., OWEN-SMITH, N. & BRYANT, J. P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75:336–342.
- DU TOIT, J. T. 1988. *Patterns of resource use within the browsing ruminant guild in the central Kruger National Park*. Ph.D., University of the Witwatersrand, Johannesburg.
- DU TOIT, J. T. 1990a. Giraffe feeding on *Acacia* flowers: predation or pollination? *African Journal of Ecology* 28:63–68.
- DU TOIT, J. T. 1990b. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28:55–61.
- DU TOIT, J. T. 1992. Winning by a neck. *Natural History* 8:29–32.
- FRUTOS, P., HERVAS, G., RAMOS, F., GIRALDEZ, F. J. & MANTECON, A. R. 2002. Condensed tannin content of several shrub species from a mountain area in northern Spain, and its relationship to various indicators of nutritive value. *Animal Food Science and Technology* 95:215–226.
- FURSTENBURG, D. & VAN HOVEN, W. 1994. Condensed tannin as anti-defoliate agent against browsing by giraffe (*Giraffa camelopardalis*) in the Kruger National Park. *Comparative Biochemistry and Physiology A* 107:425–431.
- GASSAMA-DIA, Y. K., SANÉ, D. & N'DOYE, M. 2003. Reproductive biology of *Faidherbia albida* (Del.) A. Chev. *Silva Fennica* 37:429–436.
- GERTENBACH, W. P. D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26:9–121.
- GINNETT, T. F. & DEMMENT, M. W. 1999. Sexual segregation by Masai giraffes at two spatial scales. *African Journal of Ecology* 37:93–106.
- GOERING, H. K. & VANSOEST, P. J. 1970. *Forage fibre analysis (apparatus, regions, procedures and some applications)*. USDA ARS: Agricultural Handbook 379. US Government Printing Office, Washington, D.C.
- HALL-MARTIN, A. J. 1974. Food selection by Transvaal lowveld giraffe as determined by analysis of stomach contents. *Journal of the South African Wildlife Management Association* 4:191–202.
- HARBORNE, J. B. 1991. The chemical basis of plant defence. Pp. 45–59 in Palo, R. T. & Robbins, C. T. (eds.), *Plant defences against mammalian herbivory*. CRC Press, Boca Raton, FL.
- HATTAS, D. 2003. In search of a universal condensed tannin standard. *African Journal of Range and Forage Science* 20:136.
- HYDER, P. W., FREDRICKSON, E. L., ESTELL, R. E., TELLEZ, M. & GIBBENS, R. P. 2002. Distribution and concentration of total phenolics, condensed tannins, and nordihydroguaiaretic acid

- (NDGA) in creosotebush (*Larrea tridentata*). *Biochemical Systematics and Ecology* 30:905–912.
- KANTAR, F., HEBBLETHWAITE, P. D. & PILBEAM, C. J. 1996. Factors influencing disease resistance in high and low tannin *Vicia faba*. *Journal of Agricultural Science* 127:83–88.
- KEARNS, C. A. & INOUE, D. W. 1993. *Techniques for pollination biologists*. University Press of Colorado, Niwot, CO. 583 pp.
- KELLY, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9:465–470.
- KENRICK, J. 2003. Review of pollen-pistil interactions and their relevance to the reproductive biology of *Acacia*. *Australian Systematic Botany* 16:119–130.
- MONCUR, M. W., MORAN, G. F. & GRANT, J. E. 1991. Factors limiting seed production in *Acacia mearnsii*. Pp. 20–25 in Turnbull, J. W. (ed.), *Advances in tropical Acacia research*. Australian Centre for International Agricultural Research, Canberra.
- OWEN-SMITH, N., ROBBINS, C. T. & HAGERMAN, A. E. 1993. Browse and browsers: interactions between woody plants and mammalian herbivores. *Trends in Ecology and Evolution* 8:158–160.
- RAJU, A. J. S. & RAO, S. P. 2002. Pollination ecology and fruiting behaviour in *Acacia sinuata* (Lour.) Merr. (Mimosaceae), a valuable non-timber forest plant species. *Current Science* 82:1466–1471.
- ROBBINS, C. T., HANLEY, T. A., HAGERMAN, A. E., HJELJORD, O., BAKER, D. L., SCHWARTZ, C. C. & MAUTZ, W. W. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98–107.
- ROSS, J. H. 1979. A conspectus of the African *Acacia* species. *Memoirs of the Botanical Survey of South Africa* 44:1–155.
- STONE, G. N., RAINE, N. E., PRESCOTT, M. & WILLMER, P. G. 2003. Pollination ecology of acacias (Fabaceae, Mimosoideae). *Australian Systematic Botany* 16:103–118.
- TANDON, R., SHIVANNA, K. R. & MOHAN RAM, H. Y. 2001. Pollination biology and breeding system of *Acacia senegal*. *Botanical Journal of the Linnean Society* 135:251–262.
- VAN WYK, B. & VAN WYK, P. 1997. *Field guide to trees of southern Africa*. Struik, Cape Town.
- WISDOM, C. S., GOZALEZ-COLOMA, A. & RUNDEL, P. W. 1987. Ecological tannin assays. Evaluation of proanthocyanidins, protein binding assays and protein precipitating potential. *Oecologia* 72:395–401.
- WRANGHAM, R. W. & WATERMAN, P. G. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *Journal of Animal Ecology* 50:715–731.