Acta Oecologica 75 (2016) 54–62

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Giraffe browsing in response to plant traits

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ARTICLE INFO

Article history:
Received 1 May 2016
Received in revised form
27 June 2016
Accepted 5 July 2016

Keywords:
Accumulated browsing
Arusha National Park
Bite rate
Bite mass
Giraffa camelopardalis tippelskirchi
Intake rate

ABSTRACT

Intake rates by large herbivores are governed by among other things plant traits. We used Masai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie) as study animals, testing whether they as very large browsers would follow the Jarman–Bell principle and maximize intake rate while tolerating low forage quality. We worked in Arusha National Park, Tanzania. We investigated how intake rate was determined by bite mass and bite rate, and show that bite mass and bite rate were determined by plant characteristics, governed by inherent plant traits, plant traits acquired from previous years' browsing, and season. We predicted that; (1) bite mass would be larger in trees without spines than with (2) bite mass would be larger in the wet season than in the dry, (3) bite rate would be higher in spinescent trees than in non-spinescent, (4) bite rate and/or bite mass would increase with previous years' browsing, (5) bite mass, bite rate or browsing time per tree would be highest for high trees with large, although still available canopies. Visual observations were used to collect data on tree attributes, number of bites taken and time of browsing. Sample size was 132 observed giraffe. We found that bite mass was larger in spineless than in spinescent trees and was larger in the wet season than in the dry. Bite rate, but not bite mass, increased with increasing browsing in previous years and was highest on two to three meter high trees and in spinescent trees. Intake rate followed bite mass more than bite rate and was higher in spineless than in spinescent trees, higher in the wet season than in the dry, and tended to increase with tree height. Giraffe did not prioritize the highest intake rate, but browsed much on Acacias giving a high quality diet but a low intake rate.

1. Introduction

Understanding what tree traits govern giraffe, *Giraffa camelopardalis tippelskirchi* Matschie, bite mass and bite rate and, thus, influence intake rate is a fundamental step towards understanding giraffe, foraging ecology. Browsers encounter a wide range of food plants that vary in terms of morphology and chemistry with seasonal differences in availability and chemistry (Bergström, 1992; Dagg, 2014; Pellew, 1984c; Rooke et al., 2004; Shipley, 1999). The Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974) explains that large animals can feed on relatively poor quality forage (high concentration of fiber, low digestibility), because they have low metabolic requirement/gut capacity ratio compared to smaller herbivores (Demment and Van Soest, 1985). The metabolic requirement scales to body mass raised to about ¾ (metabolic mass), while the gut capacity scales isometrically to body mass (Demment and Van Soest, 1985). Feeding ecology and energy requirements of giraffes are comparatively well known (Cameron and du Toit, 2007; Dagg, 2014; du Toit, 1990b; Pellew, 1983, 1984b; Young and Isbell, 1991). How free-ranging giraffe's bite mass and bite rate determine intake rate and how these are affected by plant characteristics remains, however, relatively unclear (Pellew, 1984c).

Diet selection in herbivores is influenced by, among other factors, intake rate (Committee, 2007; Pretorius et al., 2016; Shipley et al., 1999; Wilson and Kerley, 2003b). Large bite mass reduces bite rate because it increases handling time (Gordon and Prins, 2008; Wilson and Kerley, 2003b) while small bite mass reduces handling time and increases bite rate (Iason et al., 2012). Handling time includes chewing time and increases with fibrousness and spinescence of the bite. The absolute bite rate also depends on mouth size of the animal (Shipley et al., 1994), but predicting bite

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http://dx.doi.org/10.1016/j.actao.2016.07.001
1146-609X/

rate on mouth size ignores the chewing time (Shipley et al., 1994). Plant attributes such as tree height, morphology following previous years' browsing, seasonal phenology, concentration of nitrogen and digestibility-reducing compounds and spinescence have impact on the bite mass and bite rate of browsers (Cooper and Owen-Smith, 1986; Freeland and Janzen, 1974; Renaud et al., 2003; Rooke et al., 2004; Sebata, 2013; Skarpe et al., 2007; Wilson and Kerley, 2003b). Spalinger et al. (1986) concluded that herbivores when given opportunity to select from a range of plants of high nutritional quality are likely to select on structural characteristics that might minimize handling time. A browser may crop 10,000 or 40,000 thousands bites from individual plants during a day (Illius and Gordon, 1990; Shipley, 2007) and the selection of which bite to consume has important consequences for the nutritional intake and thus for fitness (Shipley et al., 1999). It is hypothesized that a browser would select plants or plant parts that offer the highest intake rates of the quality required to meet the nutritional and energy demands (Skarpe et al., 2007).

Although spines cannot stop browsers from feeding they reduce the bite mass and intake rates (Cooper and Owen-Smith, 1986; Dziba et al., 2003; Rooke et al., 2004). Spines act as deterrents to herbivory by limiting access to leaves or shoots directing browsing towards leaf picking (Bergström, 1992; Gowda, 1996; Skarpe et al., 2012; Wilson and Kerley, 2003a) and may restrict the time spent browsing on individual plants (Hartley et al., 1997; Milewski and Madden, 2006). Spineless woody plants often offer opportunities for browsers to strip many leaves in one bite or to take a large twig bite, as different to spiny plants (Searle and Shipley, 2008; Shipley, 2007).

Effect of browsing in previous years on tree architecture (Mathisen et al., 2014; Skarpe et al., 2007) might have an effect on the bite mass and/or on bite rate. Repeatedly browsed plants might induce defenses in the form of chemicals and/or increased spinescence (Gowda, 1996; Milewski et al., 1991; Rohner and Ward, 1997; Young, 1987). More often trees are reported to respond by increased nitrogen concentration and/or decreased tannin concentration, thus attracting more browsing (du Toit et al., 1990; Hartley et al., 1997; Scogings et al., 2011; Searle and Shipley, 2008). Trees browsed in the dry season or winter have been found to increase shoot size but reduce number of shoots in the following growing season, the potential large bite size attracting more browsing (de Jager et al., 2009; Rooke et al., 2004).

Forage availability changes with seasons as trees change their phenology (Dziba et al., 2003; Renecker and Hudson, 1986; White, 2012). During the dry season or winter, food availability is low, as most of the leaves are fallen, shoots are lignified and the production of new shoots or leaves is low, thus, it is expected that herbivore's bite mass will be small (Bergström, 1992; Pellew, 1984c). In the wet season, however, trees grew new soft nutrient-rich shoots. Even the thorns are first soft (Pellew, 1984d), and browsers might increase bite mass and/or bite rate.

Giraffes select which heights of trees to browse from. Small trees offer little canopy to browse, while too large trees might have grown out of reach even for giraffe, offering little or no browsing. Tree canopies have been modelled as spherical, hemi-spherical, conical etc.(Fiala et al., 2006), and their upper surface area has been measured as a proxy for browse availability. Many savanna trees have a proxy-hemi-spherical shape, and much browse is available when the tree height approaches the maximum browsing height, 4.5–5.0 m. A tall tree has also been suggested to have large shoots with much leaves on them (Cameron and du Toit, 2007). If defences (tannins, phenolics, fiber) are produced to deter terrestrial herbivores (Woodward and Coppock, 1995) and are costly for the plant, they would be expected to be differentially distributed and having lower concentrations high up in the canopies (Feeny, 1976; Rhoades and Cates, 1976; Rooke et al., 2004).

Many previous giraffe studies have looked into browsing height in relation to plant physical or chemical traits (Ciofolo and Le Pendu, 2002; du Toit, 1990a; Sauer, 1983; Woolnough and du Toit, 2001; Young and Isbell, 1991) or competing browser species (Cameron and du Toit, 2007; du Toit, 1990a; Makhabu, 2005; O'Connor et al., 2015; Simmons and Altwegg, 2010). Plant species eaten by giraffe has been recorded at least since the 1950's (Innis and Christine, 1958; Verschuren, 1958) and continued with later studies such as Pratt and Anderson (1982) from Arusha National Park, Pellew (1984a), Young and Isbell (1991), Caister et al. (2003), Marais et al. (2011) and Cornelius et al. (2012) to mention a few. Grazing is rarely reported (Seeber et al., 2012). Chewing or eating of bones and soil is common in some areas (Langman, 1978; Western, 1971; Wyatt, 1971). Some have looked on browsing behavior of females contra males (sexual segregation) (Caister et al., 2003; Ginnett and Demment, 1997, 1999; Leuthold and Leuthold, 1978; Young and Isbell, 1991). Relatively few have looked on tree height (instead of or in addition to browsing height) (Young and Isbell, 1991), and few have taken the effort to record bite mass and bite rate to calculate intake rate (Pellew, 1984c). Still, intake rate is critical for giraffe as a large browser, specializing on Acacias which generally seem to give relatively low instantaneous intake rate compared to spine-less trees (Pellew, 1984c). In this study we examined if plant characteristics, tree height, spinescense, seasonal phenology and effect of previous years' browsing, had effect on the bite mass and bite rate and, hence, on intake rate. These factors interact with each other and we hypothesized that bite mass and bite rate largely depended on tree traits. We were interested in seeing how the different tree traits affected bite mass and bite rate and how they determined intake rate. These factors are not statistically independent, but in order to find how each depended on tree traits, we analyzed all three independent of each other.

We predicted that; (1) bite mass would be larger in trees without spines than with (2) bite mass would be larger in the wet season than in the dry, (3) bite rate would be higher in spinescent trees than non-spinescent, (4) bite rate and/or bite mass would increase with accumulated browsing, (5) bite mass, bite rate and browsing time per tree would be highest for high trees with large, although still available canopies.

2. Materials and methods

2.1. Study system

The present study was carried out in Tanzania in Arusha National Park (36° 45′ E-3° 15′ S), during March–May, wet season, and August–October, dry season, 2013. The whole park is 552 km^2 in size (Tanapa, 2016). Arusha National Park is in the low land characterized by savanna vegetation with grasses and trees (Razzetti and Msuya, 2002). Most of the soils originate from volcanic activities of Mount Meru (Beesley, 1972; Razzetti and Msuya, 2002; Tanapa, 2003). The area is within the regime of two rainy seasons, the short rains of November and December and the long rains of March to May with annual precipitation ranging geographically between 1300 mm and 2400 mm (Beesley, 1972; Kahana et al., 2014; Martinoli et al., 2006; Vesey-FitzGerald, 1974). The hottest season is in January and February with a mean monthly maximum temperature of 27 °C while the coldest season is from June to August with a mean monthly minimum temperature of 11 °C (Meteoblue, 2016). The area is rich in water including permanent rivers and lakes; and temporal water courses which all are used by giraffes and other animals. Common tree species include *Juniperus procera, Croton macrostachyus, Euclea divinorum, Dodonea viscosa* and *Acacia xanthophloea* (Beesley, 1972; Pratt and Anderson, 1982;