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1   **Giraffe browsing in response to plant traits**

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8

9   **Abstract**

10   Intake rates by large herbivores are governed by among other things plant traits. We used

11   Masai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie) as study animals, testing

12   whether they as very large browsers would follow the Jarman–Bell principle and maximize

13   intake rate while tolerating low forage quality. We worked in Arusha National Park,

14   Tanzania. We investigated how intake rate was determined by bite mass and bite rate, and

15   show that bite mass and bite rate were determined by plant characteristics, governed by

16   inherent plant traits, plant traits acquired from previous years' browsing, and season. We

17   predicted that; (1) bite mass would be larger in trees without spines than with (2) bite mass

18   would be larger in the wet season than in the dry, (3) bite rate would be higher in spinescent

19   trees than in non-spinescent, (4) bite rate and/or bite mass would increase with previous years'

20   browsing, (5) bite mass, bite rate or browsing time per tree would be highest for high trees

21   with large, although still available canopies. Visual observations were used to collect data on

22   tree attributes, number of bites taken and time of browsing. Sample size was 132 observed

23   giraffe. We found that bite mass was larger in spineless than in spinescent trees and was larger

24   in the wet season than in the dry. Bite rate, but not bite mass, increased with increasing

25   browsing in previous years and was highest on two to three meter high trees and in spinescent

26 trees. Intake rate followed bite mass more than bite rate and was higher in spineless than in

27 spinescent trees, higher in the wet season than in the dry, and tended to increase with tree

28 height. Giraffe did not prioritize the highest intake rate, but browsed much on Acacias giving

29 a high quality diet but a low intake rate.

30 **Key words:** accumulated browsing, Arusha National Park, bite rate, bite mass, *Giraffa*

31 *camelopardalis tippelskirchi,* intake rate

32

33   INTRODUCTION

34 Understanding what tree traits govern giraffe, *Giraffa camelopardalis tippelskirchi* Matschie,

35 bite mass and bite rate and, thus, influence intake rate is a fundamental step towards

36 understanding giraffe, foraging ecology. Browsers encounter a wide range of food plants that

37 vary in terms of morphology and chemistry with seasonal differences in availability and

38 chemistry (Bergström, 1992; Dagg, 2014; Pellew, 1984c; Rooke et al., 2004; Shipley, 1999).

39 The Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974) explains that large animals

40 can feed on relatively poor quality forage (high concentration of fiber, low digestibility),

41 because they have low metabolic requirement/gut capacity ratio compared to smaller

42 herbivores (Demment and Van Soest, 1985). The metabolic requirement scales to body mass

43 raised to about ¾ (metabolic mass), while the gut capacity scales isometrically to body mass

44 (Demment and Van Soest, 1985). Feeding ecology and energy requirements of giraffes are

45 comparatively well known (Cameron and du Toit, 2007; Dagg, 2014; du Toit, 1990b; Pellew,

46 1983, 1984b; Young and Isbell, 1991). How free-ranging giraffe's bite mass and bite rate

47 determine intake rate and how these are affected by plant characteristics remains, however,

48 relatively unclear (Pellew, 1984c).

49   Diet selection in herbivores is influenced by, among other factors, intake rate (Committee,

50   2007; Pretorius et al., 2015; Shipley et al., 1999; Wilson and Kerley, 2003b). Large bite mass

51   reduces bite rate because it increases handling time (Gordon and Prins, 2008; Wilson and

52   Kerley, 2003b) while small bite mass reduces handling time and increases bite rate (Iason et

53   al., 2012). Handling time includes chewing time and increases with fibrousness and

54   spinescence of the bite. The absolute bite rate also depends on mouth size of the animal

55   (Shipley et al., 1994), but predicting bite rate on mouth size ignores the chewing time

56   (Shipley et al., 1994). Plant attributes such as tree height, morphology following previous

57   years' browsing, seasonal phenology, concentration of nitrogen and digestibility-reducing

58   compounds and spinescence have impact on the bite mass and bite rate of browsers (Cooper

59   and Owen-Smith, 1986; Freeland and Janzen, 1974; Renaud et al., 2003; Rooke et al., 2004;

60   Sebata, 2013; Skarpe et al., 2007; Wilson and Kerley, 2003b). Spalinger et al. (1986)

61   concluded that herbivores when given opportunity to select from a range of plants of high

62   nutritional quality are likely to select on structural characteristics that might minimize

63   handling time. A browser may crop 10 000 or 40 000 thousands bites from individual plants

64   during a day (Illius and Gordon, 1990; Shipley, 2007) and the selection of which bite to

65   consume has important consequences for the nutritional intake and thus for fitness (Shipley et

66   al., 1999). It is hypothesized that a browser would select plants or plant parts that offer the

67   highest intake rates of the quality required to meet the nutritional and energy demands

68   (Skarpe et al., 2007).

69   Although spines cannot stop browsers from feeding they reduce the bite mass and intake rates

70   (Cooper and Owen-Smith, 1986; Dziba et al., 2003; Rooke et al., 2004). Spines act as

71   deterrents to herbivory by limiting access to leaves or shoots directing browsing towards leaf

72   picking (Bergström, 1992; Gowda, 1996; Skarpe et al., 2012; Wilson and Kerley, 2003a) and

73   may restrict the time spent browsing on individual plants (Hartley et al., 1997; Milewski and

74 Madden, 2006). Spineless woody plants often offer opportunities for browsers to strip many

75 leaves in one bite or to take a large twig bite, as different to spiny plants (Searle and Shipley,

76 2008; Shipley, 2007).

77 Effect of browsing in previous years on tree architecture (Mathisen et al., 2014; Skarpe et al.,

78 2007) might have an effect on the bite mass and/or on bite rate. Repeatedly browsed plants

79 might induce defenses in the form of chemicals and/or increased spinescence (Gowda, 1996;

80 Milewski et al., 1991; Rohner and Ward, 1997; Young, 1987). More often trees are reported

81 to respond by increased nitrogen concentration and/or decreased tannin concentration, thus

82 attracting more browsing (du Toit et al., 1990; Hartley et al., 1997; Scogings et al., 2011;

83 Searle and Shipley, 2008). Trees browsed in the dry season or winter have been found to

84 increase shoot size but reduce number of shoots in the following growing season, the potential

85 large bite size attracting more browsing (de Jager et al., 2009; Rooke et al., 2004).

86 Forage availability changes with seasons as trees change their phenology (Dziba et al., 2003;

87 Renecker and Hudson, 1986; White, 2012). During the dry season or winter, food availability

88 is low, as most of the leaves are fallen, shoots are lignified and the production of new shoots

89 or leaves is low, thus, it is expected that herbivore's bite mass will be small (Bergström, 1992;

90 Pellew, 1984c). In the wet season, however, trees grew new soft nutrient-rich shoots. Even the

91 thorns are first soft (Pellew, 1984d), and browsers might increase bite mass and/or bite rate.

92 Giraffes select which heights of trees to browse from. Small trees offer little canopy to

93 browse, while too large trees might have grown out of reach even for giraffe, offering little or

94 no browsing. Tree canopies have been modelled as spherical, hemi-spherical, conical

95 etc.(Fiala et al., 2006), and their upper surface area has been measured as a proxy for browse

96 availability. Many savanna trees have a proxy-hemi-spherical shape, and much browse is

97 available when the tree height approaches the maximum browsing height, 4.5 – 5.0 m. A tall

98   tree has also been suggested to have large shoots with much leaves on them (Cameron and du

99   Toit, 2007). If defences (tannins, phenolics, fiber) are produced to deter terrestrial herbivores

100   (Woodward and Coppock, 1995) and are costly for the plant, they would be expected to be

101   differentially distributed and having lower concentrations high up in the canopies (Feeny,

102   1976; Rhoades and Cates, 1976; Rooke et al., 2004).

103

104   Many previous giraffe studies have looked into browsing height in relation to plant physical

105   or chemical traits (Ciofolo and Le Pendu, 2002; du Toit, 1990a; Sauer, 1983; Woolnough and

106   du Toit, 2001; Young and Isbell, 1991) or competing browser species (Cameron and du Toit,

107   2007; du Toit, 1990a; Makhabu, 2005; O'Connor et al., 2015; Simmons and Altwegg, 2010).

108   Plant species eaten by giraffe has been recorded at least since the 1950's (Innis, 1958;

109   Verschuren, 1958) and continued with later studies such as Pratt and Anderson(1982) from

110   Arusha National Park, Pellew (1984a), Young and Isbell (1991) , Caister et al. (2003), Marais

111   et al. (2011) and Cornelius et al. (2012) to mention a few. Grazing is rarely reported (Seeber

112   et al., 2012) . Chewing or eating of bones and soil is common in some areas (Langman, 1978;

113   Western, 1971; Wyatt, 1971). Some have looked on browsing behavior of females contra

114   males (sexual segregation) (Caister et al., 2003; Ginnett and Demment, 1997, 1999; Leuthold

115   and Leuthold, 1978; Young and Isbell, 1991). Relatively few have looked on tree height

116   (instead of or in addition to browsing height)(Young and Isbell, 1991), and few have taken the

117   effort to record bite mass and bite rate to calculate intake rate (Pellew, 1984c). Still, intake

118   rate is critical for giraffe as a large browser, specializing on Acacias which generally seem to

119   give relatively low instantaneous intake rate compared to spine-less trees (Pellew, 1984c). In

120   this study we examined if plant characteristics, tree height, spinescense, seasonal phenology

121   and effect of previous years' browsing, had effect on the bite mass and bite rate and, hence,

122   on intake rate. These factors interact with each other and we hypothesized that bite mass and

123 bite rate largely depended on tree traits. We were interested in seeing how the different tree

124 traits affected bite mass and bite rate and how they determined intake rate. These factors are

125 not statistically independent, but in order to find how each depended on tree traits, we

126 analyzed all three independent of each other.

127 We predicted that; (1) bite mass would be larger in trees without spines than with (2) bite

128 mass would be larger in the wet season than in the dry, (3) bite rate would be higher in

129 spinescent trees than non-spinescent, (4) bite rate and/or bite mass would increase with

130 accumulated browsing, (5) bite mass, bite rate and browsing time per tree would be highest

131 for high trees with large, although still available canopies.

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133   MATERIALS AND METHODS

134 **Study system**

135 The present study was carried out in Tanzania in Arusha National Park (36^0 45´ E-3^0 15´ S),

136 during March-May, wet season, and August-October, dry season, 2013. The whole park is

137 552 km^2 in size (Tanapa, 2016). Arusha National Park is in the low land characterized by

138 savanna vegetation with grasses and trees (Razzetti and Msuya, 2002). Most of the soils

139 originate from volcanic activities of Mount Meru (Beesley, 1972; Razzetti and Msuya, 2002;

140 Tanapa, 2003). The area is within the regime of two rainy seasons, the short rains of

141 November and December and the long rains of March to May with annual precipitation

142 ranging geographically between 1300 mm and 2400 mm (Beesley, 1972; Kahana et al., 2014;

143 Martinoli et al., 2006; Vesey-FitzGerald, 1974). The hottest season is in January and February

144 with an mean monthly maximum temperature of 27^0C while the coldest season is from June

145 to August with an mean monthly minimum temperature of 11^0C (Meteoblue, 2016). The area

146 is rich in water including permanent rivers and lakes; and temporal water courses which all

147 are used by giraffes and other animals. Common tree species include *Juniperus procera,*

148 *Croton macrostachyus, Euclea divinorum, Dodonea viscosa* and *Acacia xanthophloea*

149 (Beesley, 1972; Pratt and Anderson, 1982; Tanapa, 2003). Mammals in the area include

150 african buffalo, *Syncerus caffer*, bushbuck, *Tragelaphus scriptus*, red duiker, *Cephalophus*

151 *harveyi* , giraffe, *Giraffa camelopardalis* and plains zebra, *Equus quagga*, (Pratt and

152 Anderson, 1982; Tanapa, 2003), and, uncommon, but potentially with great impact, elephant,

153 *Loxodonta africana.*

154 The study animal was Masai giraffe that was the dominant subspecies in the park. Giraffes

155 live in sub-humid to semi-arid savannas (Dagg, 1971, 2014). They are ruminants and *Acacia*

156 specialist browsers, browsing on leaves, shoots, thorns, flowers, seed pods and fruits

157 (Bergström, 1992; Dagg, 2014; du Toit, 2003; Pellew, 1984b). They live in mixed loose

158 groups of two to about 35 animals, males may be solitary (Dagg, 2014; Leuthold, 1979).

159 **Data collection**

160 *Browsing observations and measured variables:* Giraffe browsing was observed visually from

161 a four-wheel-drive car driven about 20 km h^{-1} along the park roads in the north eastern part of

162 Arusha National Park. The length of the road transect driven each day, was about 25 km.

163 When a giraffe was observed browsing within about 50 m from the road the car was stopped

164 and observation started. The most visible or nearby mature giraffe was chosen in a group. We

165 chose only mature giraffe for observation in order to reduce variation in the feeding data.

166 During the observation we recorded tree species browsed, and spinescence as "Yes" or "No"

167 (Table 1). A spinescent tree here refers to a tree with long straight (up to about 7 cm) and/or

168 short hooked, (usually < 1 cm) usually paired, spines (Cooper et al., 2003; Cooper and Owen-

169 Smith, 1986). We also recorded number of bites taken and time a giraffe fed on a certain tree.

170 An accumulated browsing score was given to each browsed tree. Accumulating browsing

171   score was defined as the cumulative effect of browsing in previous years on tree architecture

172   (Mathisen et al., 2014; Skarpe et al., 2007). The effect of accumulated browsing was

173   estimated for each tree on a four degree scale classified as; 0 = no sign of previous browsing,

174   1 = old browsing visible but tree growth form not changed, 2 = old browsing visible and

175   growth form changed and 3 = old browsing visible and growth form strongly changed

176   (Mathisen et al., 2014; Skarpe et al., 2007). We used a stop watch to record time of browsing

177   on each tree. We started the watch when the giraffe noose was about 5 cm from plant material

178   and stopped it when the giraffe stopped browsing or chewing. If the giraffe reassumed

179   browsing on the same tree the clock was started again and time-taking was continued. If it

180   selected another tree the watch was started anew from 0. Each giraffe was observed for

181   maximum 15 min. Mean recording time was 2.2 ± 0.13 SE min. A GPS position for the

182   observation was recorded. We measured tree height of all browsed trees up to 5 m. using a

183   marked wooden rod and taller trees had height estimated as, for example, 1.4 times the rod

184   height equals 7 m, double the rod height is 10 m. We recorded bite diameter (mm with one

185   decimal) using a caliper, measuring the shoot diameter just below where the shoot was bitten

186   off by giraffe, on five shoots per browsed tree. We calculated the bite mass of the five most

187   browsed plant species representing 61% of the total number of bites (Table 1). To estimate

188   biomass per bite we sampled shoots with leaves. We collected shoots from each species with

189   diameters of 1.0 mm, 2.0 mm, 3.0 mm, 4.0 mm and 5.0 mm, including the diameters bitten by

190   the giraffe. For each diameter, we collected 10 shoots per species. Collected shoots were

191   oven dried for 24 h at 65^{0}C (Cleve et al., 1990) and then weighted to obtain dry mass for each

192   bite diameter.

193   **Statistical analysis**

194   *Bite mass, biting rate browsing time and intake rate*. Biting rate (bites.min^{-1}) was calculated

195   by dividing number of bites taken with browsing time (minutes). To estimate bite mass (g dry

196   weight) we constructed regression curves of the relationship between bite diameter and

197   biomass per shoot diameter, and evaluated the shape of the regression curve based on the best

198   fit to residuals. This was carried out for the five most common species where we had enough

199   data. The model that best described the relationship between bite dimeter and bite mass was a

200   quadratic regression curve (second order polynomial, Table 3). The general formula was $y =$

201    $\beta x^2 - \beta x + e$ (Table 3), where; y represented the biomass (g), β represented slope and x^2

202   represented the quadratic effect on bite diameter (mm), x represented bite diameter (mm) and

203   e represented the error term. Intake rate (g min^{-1}) was calculated from the combination of bite

204   rate and bite mass (i.e. bite rate $\times$ bite mass = intake rate) (Haschick and Kerley, 1997; Sebata

205   and Ndlovu, 2010). Browsing time here refers to the time a giraffe spent feeding on one plant.

206   Moreover, for each plant species shown in Table 3, we calculated average bite mass, average

207   bite rate and average intake rate.

208   *Modelling and data exploration.* We used a linear regression model with mixed effects using

209   the lm4 package in the R program (2.8.0)(RCoreTeam, 2014) to analyze factors influencing

210   bite mass, bite rate, browsing time per tree and intake rate. Linear mixed effects models were

211   applied because they are efficient in handling continuous, categorical variables and non-

212   independence (Zuur et al., 2009). We used observation number (giraffe) as a random

213   intercept, as each observation included several trees. Our predictor variables were

214   spinescence, tree height, accumulated browsing and season (dry and wet). Accumulated

215   browsing level zero was removed from analysis because there was only one previously

216   unbrowsed tree. A full model was made and statistical assumptions including homogeneity of

217   variances, normality and outliers were checked by using detection tools; histogram and Q-Q

218   plot for normality, residuals versus fitted values for homogeneity and influence plot for

219   outliers (Zuur et al., 2010). Response variables were transformed using the function natural

220   logarithm to fulfill assumptions of normality and homoscedasticity of bite rate, bite mass,

221   browsing time and intake rate as well as explanatory variable tree height for outliers. Stepwise

222   backward selection procedures were carried out to select a model with only significant

223   predictors (Crawley, 2007). We used the function lme and maximum likelihood estimation

224   "ML" to compare models with different variables (Zuur et al., 2009). A p-value 0.05 criterion

225   was used to exclude non-significant variables in the model, but tree height and intake rate (P

226   = 0.06) (Table 2) was included as a tendency. Moreover, we used a polynomial term

227   command in R to fit our response i.e. bite rate , intake rate and time spent browsing per tree to

228   tree height as they showed a quadratic relationship (lmer (y ~ I(*height* ^ 2)) (Biggs and Smith,

229   2002; Fox, 2003). It should be noted that Acacia *xanthophloea* was the only common

230   spinescent species eaten by giraffe, so results allocated to a spinescent tree might as well

231   refer to this particular species.

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242   Table 1: Sample size, number of bites, tree height, spinescence and accumulating browsing

243   levels for giraffe feeding in trees in Arusha National Park.

Tree species	Sample size (n) by season.		Number of bites	Tree height (m) ± SE	Spinescence	Accumulated browsing levels.		
	Wet	Dry				1	2	3
Acacia xanthophloea	98	83	7580	1.8 ± 0.05	Yes	4	3	173
Dodonea viscosa	6	1	140	1.7 ± 0.26	No	0	2	5
Euclea divinorum	4	10	478	4.5 ± 0.26	No	8	5	1
Olea africana	0	2	117	1.4 ± 0.33	No	0	0	2
Warburgia ugandensis	0	3	50	4.1 ± 1.24	No	1	1	1

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251 Table 2: Backward model selection for linear mixed effects models analyzing factors

252 influencing, respectively, bite mass, biting rate, browsing time per tree and intake rate.

253 Likelihood ratio (L. ratio) was used to compare if models with and without the variable under

254 consideration best fitted with the data.

Response	Explanatory variables	Df	L. ratio	P-value
Bite mass	Accumulated browsing	2	0.36	0.84
	Season	1	22.92	<.0001***
	Tree height	1	1.39	0.24
	Spinescence	1	43.40	<.0001***
Bite rate	Accumulated browsing	2	10.62	0.005**
	Season	1	0.82	0.36
	Tree height	1	3.84	0.05*
	Spinescence	1	13.25	<.0001***
Browsing time	Accumulated browsing	2	0.36	0.50
	Season	1	22.92	0.14
	Tree height	1	1.39	0.02**
	Spinescence	1	43.40	0.56
Intake rate	Accumulated browsing	2	3.69	0.24
	Season	1	10.39	0.0001***
	Tree height	1	5.63	0.06
	Spinescence	1	16.86	<.0001***
	Accumulated browsing	2	3.69	0.24

255 * $P \leq 0.05$; ** $P < 0.01$; ***$P < 0.0001$

256

RESULTS

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258   We determined giraffe intake rate using the tree species shown in Table 1 and 3. It should be

259   noted that giraffes had many bites from *Acacia xanthophloea* (7580) compared to other tree

260   species (885), which may, thus, be less robust for regression equations.

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268   Table 3: Average , bite diameter, bite mass, bite rate, intake rate and regression equations for each tree species for giraffe feeding in Arusha

269   National Park during wet and dry season.

Tree species	Bite diameter (mm) ± SE	Bite mass (g) ± SE		Bite rate (bites min^{-1}) ± SE		Intake rate (g min^{-1}) ± SE		Regression equation (y= bite mass, x= bite diameter)
		Wet	Dry	Wet	Dry	Wet	Dry	
Acacia xanthophloea	1.6 ± 0.02	0.21 ± 0.02	0.12 ± 0.01	21 ± 0.66	19 ± 0.56	4.48 ± 0.41	2.37 ± 0.24	$y = 0.53x^2 - 1.28x + 0.81$
Dodonea viscosa	1.8 ± 0.11	0.87 ± 0.21	0.05 ± -	13 ± 1.85	21±-	10.71 ± 2.73	8.01 ± 5.66	$y = 0.48x^2 + 0.07x - 0.84$
Euclea divinorum	1.6 ± 0.11	0.55 ± 0.1	0.54 ± 0.11	12 ± 1.99	12 ± 1.43	6.75 ± 1.78	5.79 ± 0.77	$y = 0.76x^2 - 1.85x + 1.29$
Olea africana	1.4 ± 0.08	0	0.19 ± 0.02	-	18 ± 1.05	-	3.33 ± 0.15	$y = 0.76x^2 - 1.85x + 1.29$
Warburgia ugandensis	2.6 ± 0.14	0	1.53 ± 0.19	-	10 ± 1.33	-	16 ± 3.49	$y = 0.69x^2 - 2.22x + 2.62$

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Bite mass

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272   Spinescence and season were found to be determinant factors affecting bite mass. The bite

273   mass (g) of giraffe was larger in trees with no spines than in spiny trees (Figure 1a).

274   Moreover, bite mass was larger in the wet season than in the dry (Figure1b).
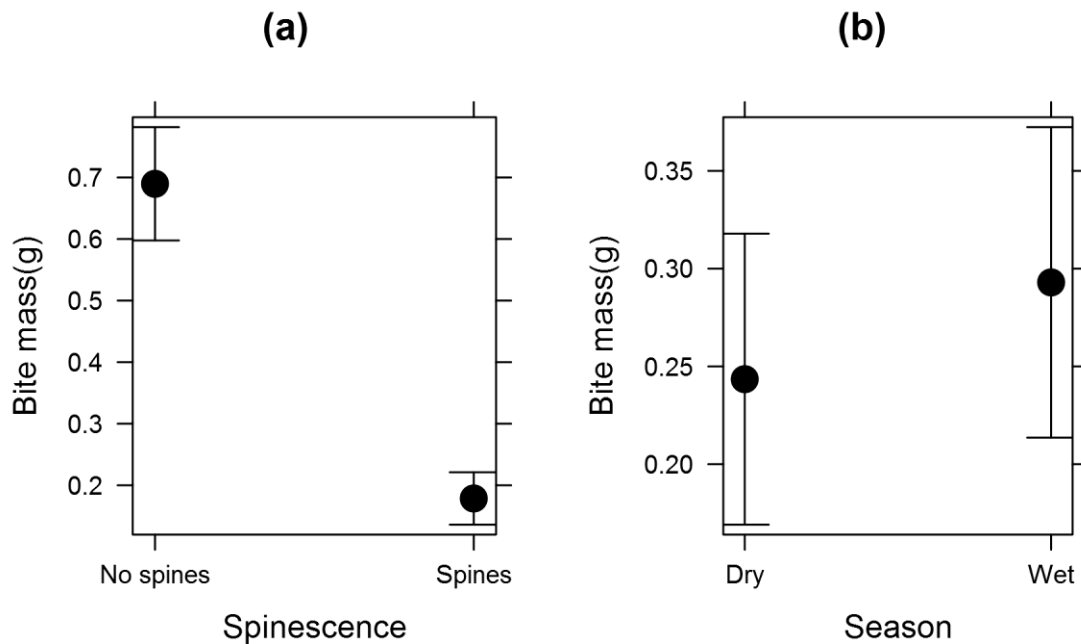
Figure 1: Effect of spinescence and season on the bite mass of giraffe. Mean values are shown at the middle (point) while error bars above and below the mean show confidence intervals 95% upper and lower. (a) effect of spinescence on the bite mass of giraffe, (b) effect of season on the bite mass of giraffe.

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Bite rate

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283   Three variables, spinescence, accumulated browsing and tree height (Table 2) were found to

284   be factors influencing bite rate of giraffe. Giraffe had higher bite rates (bites min^{-1}) from

285   plants with spines than those without (Figure 2a). Bite rate increased with accumulated

286   browsing (Figure 2b). Bite rate peaked at trees of about 2.2 m and decreased with increasing

287   and decreasing tree height (Figure 3c).
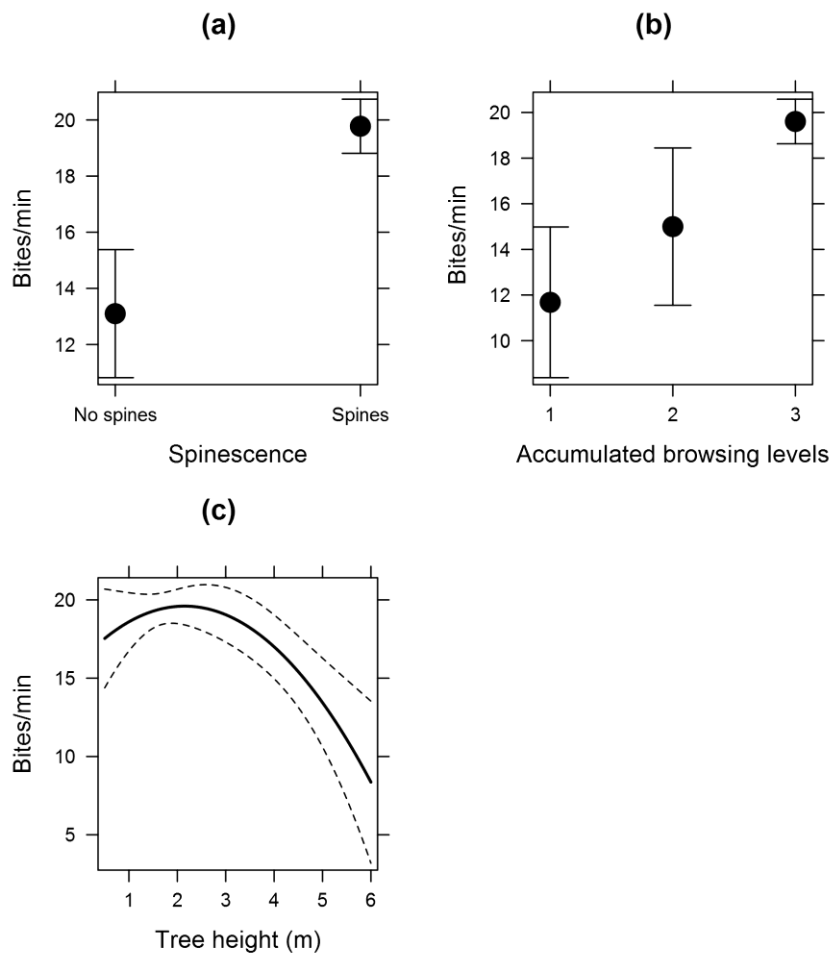
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289   Figure 2: Effects of spinescence accumulated browsing and tree height in relation to bite rate

290   of giraffe. Middle points show mean number of bites taken per minute, and the error bars with

291   95% confidence intervals. (a) effect of spinescence on bite rate (b) effect of accumulated

292   browsing levels on bite rate. (c) relationship between bite rate and tree height. The dashed

293   lines represent 95% confidence interval, upper and lower.

294   **Browsing time per plant**

295   We found that only tree height (Table 2) was affecting the time a giraffe spent browsing on a

296   particular tree (Figure 3). The browsing time was longest at a tree height of 3–4 m and was

297   reduced both in higher and lower trees (Figure 3).
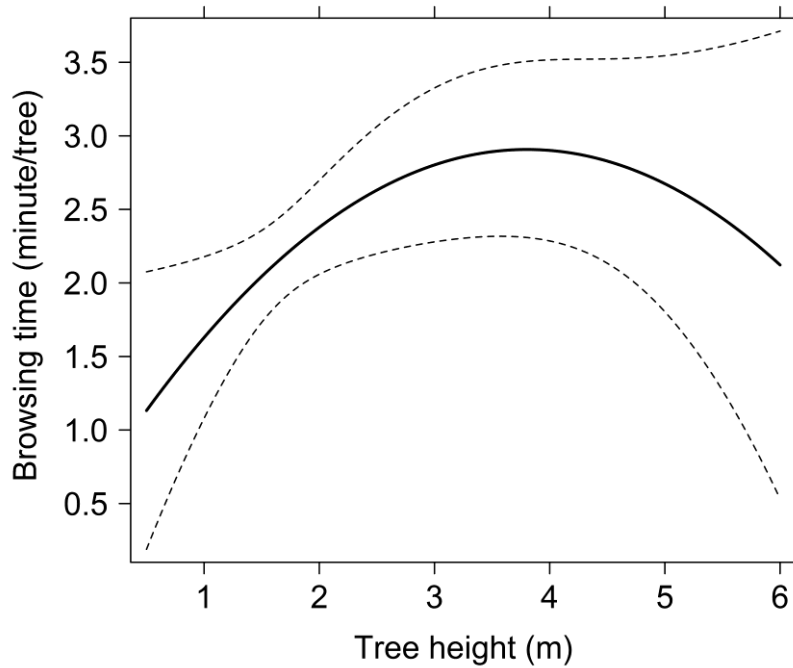
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299   Figure 3: The relationship between time spent browsing per tree and tree height. The dashed

300   lines represent upper and lower 95% confidence interval.

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303   **Intake rate**

304   Giraffe intake rate was higher from trees without spines than from spinescent trees (Figure

305   4a). Intake rate (g min^{-1}) was significantly lower in the dry season compared to the wet

306   (Figure 4b). Intake rate increased with increasing tree height (Figure 4c). Intake rate was low

307   up to 3 m. then started to increase with increasing tree height (Figure 4c).

(a)

(b)

(c)

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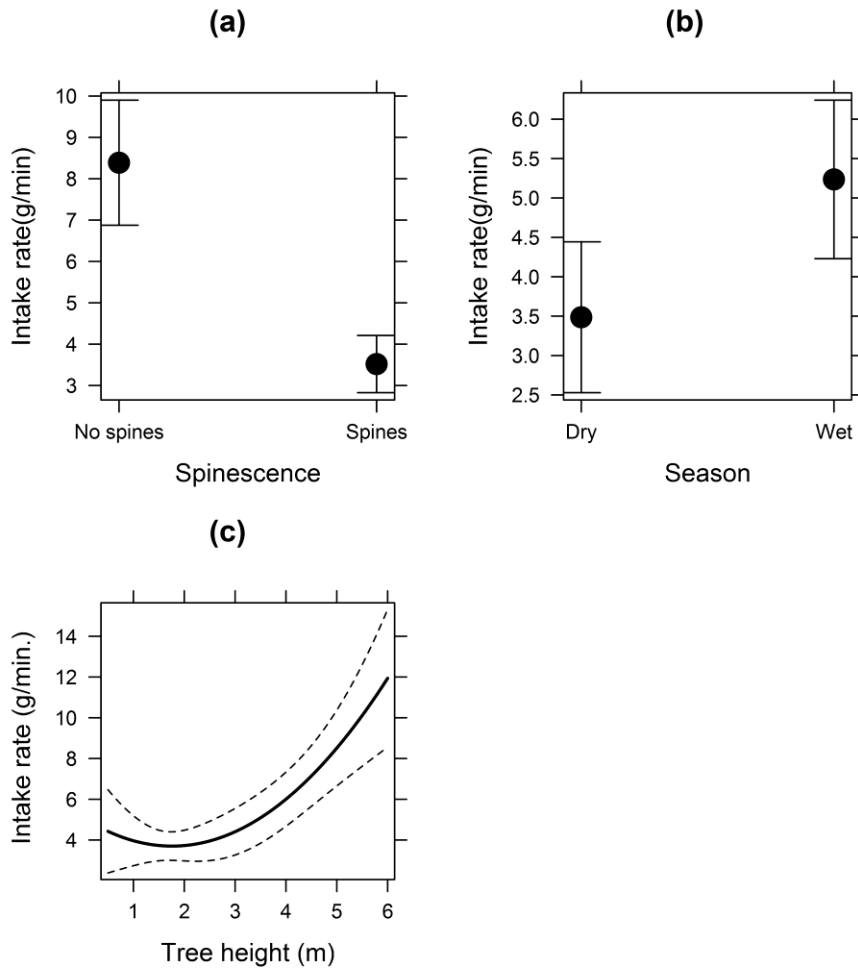
Figure 4: Intake rate of giraffe in relation to spinescence, season and tree height. Mean values are shown as the middle point while error bars above and below the mean show confidence intervals 95% upper and lower, (a) effect of spinescence on the intake rate , (b) effect of season on intake rate, (c) effect of tree height on intake rate. The dashed lines represent upper and lower 95% confidence interval.

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318 DISCUSSION

319 The data support some of our predictions; (1) bite mass was larger in trees without spines than

320 with, (2) bite mass was larger in the wet season than in the dry (3) bite rate was higher in

321 spinescent trees than in non-spinescent. Some predictions were partly supported; (5) browsing

322 time spent per tree and bite rate were unimodally distributed with a maximum browsing time

323 in 3 to 4 m high trees, and maximum bite rate in about 2.2 m high trees, (4) bite rate, but not

324 bite mass, increased with accumulated browsing.

325 **Bite mass**

326 Bite mass decreased with spinescence and was larger in the wet season than in the dry. Our

327 results concur with those presented by Pellew (1984c). Spines deter herbivory by preventing

328 access to shoot biting and to leaf stripping thus forcing animals to pick small bites of leaves

329 between the spines (Bergström, 1992; Gowda, 1996; Skarpe et al., 2012; Wilson and Kerley,

330 2003a). That bite mass is limited by spines and increases if they are removed is known from

331 studies on different browsing animal species (Cooper and Owen-Smith, 1986; Skarpe et al.,

332 2012). It seems shoots are the most valuable resource for the tree, and the long straight spines

333 mainly deter shoot biting (Gowda, 1996; Rosenthal and Kotanen, 1994). Leaf picking

334 between the spines gives small bite mass, particularly when leaves are small as in *Acacia*

335 *xanthophloea* (Cooper and Owen-Smith, 1986; Pellew, 1984b; Sebata and Ndlovu, 2010).

336 The spineless tree species that were most browsed by giraffe offered in most cases larger bite

337 mass, but did not seem as palatable. In Pellew's (1984c) study the non-spinescent trees gave

338 about double the bite mass compared to the Acacias. In the wet season most woody plants

339 have new leafy soft and nutritious shoots growing and even the thorns are first soft. Such

340 shoots are selected by giraffes, taking large bites (Cooper and Owen-Smith, 1986; Ginnett and

341 Demment, 1997; Parker and Bernard, 2006; Pretorius et al., 2016). In the late dry season food

342   availability is usually lower as shoots are lignified with hard and sharp spines, most leaves

343   are fallen and the production of new shoots is negligible, while browsers have been tapping

344   the resource since last growing season, all factors leading to a reduction in bite mass

345   (Bergström, 1992; Pellew, 1984c).

346   **Bite rate**

347   Giraffe's bite rates increased with spinescence and accumulated browsing, but decreased with

348   tree heights above and below about 2.2 m. The higher bite rate on spinescent trees seems to be

349   related to smaller bite mass and shorter handling time (Bergström, 1992; Cooper and Owen-

350   Smith, 1986; Pellew, 1984c; Skarpe et al., 2012). Giraffes here may not bite many spines, but

351   crop what is outside the outmost spine pair, and pick leaves between the spines, both giving

352   small bites. In our area the only common spinescent tree is *Acacia xanthophloea,* which has

353   small leaves, which in combination with spines, further contributes to a small bite mass and a

354   high bite rate (Cooper and Owen-Smith, 1986; Pellew, 1984c) . Where giraffe crop shoots

355   with spines the handling and chewing is slowed down and spinescent trees might hence have

356   a lower biting rate than non-spiny trees (Belovsky et al., 1991; Cooper and Owen-Smith,

357   1986; Gowda, 1996). In trees without spines, we found giraffes having access to large shoots

358   or to strip many leaves at a time thus needing more time to chew and handle the bite, reducing

359   the bite rate, as is frequently found (Bergström, 1992; Gowda, 1996; Pellew, 1984c; Searle

360   and Shipley, 2008).

361   Giraffe's bite rate was highest at a tree height of ca. 2.2 m, declining with increasing and

362   decreasing tree height. This is mainly below the tree height where giraffe stayed the longest

363   (3-4 m.). Possibly the low browsing height gave small bites, particularly as the canopy is

364   within reach for other browsers and, hence, a high bite rate (Young and Isbell, 1991).

365 Giraffe's bite rate increased with increasing accumulated browsing. Browsed trees undergo

366 both morphological and chemical changes often attracting further browsing (Bergström et al.,

367 2000; du Toit et al., 1990; Makhabu et al., 2006). Bite mass did not increase with

368 accumulated browsing, which could depend on giraffes biting outside the outmost thorns,

369 which might remain at about the same shoot diameter (Skarpe et al., 2012). Another reason

370 could be that these trees are browsed by obligate browsers, mainly giraffe, the whole year,

371 and could respond to wet season browsing with more small shoots, offering small bites and

372 high biting rate, while dry season browsing would lead to fewer bigger shoots, big bites and

373 lowered bite rate (Bergström and Danell, 1987, 1995; Bergström et al., 2000).

374 **Browsing time per tree**

375 We found a clear relationship between time spent foraging per tree by giraffes and tree height,

376 with longer time spent on rather tall trees, three to four meters high. The explanation may be

377 that more shoots and leaves are available above the browsing height of smaller competing

378 browsers (Cameron and du Toit, 2007; Stokke and du Toit, 2000) such as bushbucks, which

379 were the most common browser in Arusha National Park besides the giraffe (Haschick and

380 Kerley, 1997). To avoid competition with bushbuck a tree height of >1.2 m would be enough

381 (Haschick and Kerley, 1997). A tall tree is likely to have a large canopy and to offer more

382 shoots and leaves to browse than a shorter tree, until it grows too big and gets out of reach

383 also for giraffe. Thus, forage availability and hence browsing time, shows a unimodal

384 relationship with tree height, with little browse available and short browsing time on short

385 trees and on very tall trees and longer time spent on trees of about three to four meters height.

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389 **Intake rate**

390 Intake rate is the product of bite mass and bite rate, and is governed by a trade-off between

391 quantity and quality (Van Wieren, 1996). Generally, a larger bite gives lower quality, as a

392 larger proportion of lignified shoot is included, and a smaller proportion of bark and leaves

393 (Shipley et al., 1999). Low quality forage tends to be a common resource, whereas high

394 quality forage is scarce (Demment and Van Soest, 1985; McNaughton et al., 1988).

395 According to the Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974), large

396 herbivores need large quantities of food, but tolerate low quality whereas small herbivores

397 require small amounts of high quality food. Thus, large sized browsers, like giraffe, ought to

398 select plants that offer large bite mass and high intake rate in order to meet its energy

399 requirements, tolerating low nutrient concentration (Bell, 1971; Geist, 1974; Jarman, 1974;

400 Senft et al., 1987). Our results showed that giraffes instead browsed on Acacias offering small

401 bites, high bite rate and low intake rate. *Acacia xanthophloea* was selected by giraffe in

402 Arusha National Park (Mahenya et al., 2016) and has been shown to have high concentration

403 of nitrogen and relatively low concentration of defense compounds compared to other species

404 (Khanyile et al., 2014; Wrangham and Waterman, 1981). The giraffe preference for Acacia,

405 where it is available, is well known (Bergström, 1992; Dagg, 2014; Pellew, 1984c; Sauer,

406 1983; Sauer et al., 1982) but is rarely seen in relation to intake rate.

407 <div align="center">CONCLUSIONS</div>

408 We found the giraffe to select for Acacia, obviously not cropping the spines, but taking

409 comparatively small bites with a high bite rate. The variation in bite mass was larger than that

410 in bite rate, and intake rate followed bite mass, being positively related to non-spinescence, to

411 the wet season and to relatively tall plants.

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