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African Journal of Ecology

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Title: Hierarchical foraging by giraffe in a heterogeneous savanna, Tanzania

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Key words: *Acacia xanthophloea, Arusha National Park, Browsing, Giraffa camelopardalis tippelskirchi Patch, Scale*

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Running title: Hierarchical foraging by giraffe

Words: 3481

Tables: 2

Figures: 4

Abstract

26

27 Understanding foraging decisions made by wildlife at different spatio-temporal scales is

28 important for wildlife management and conservation. We tested whether foraging decisions by

29 Masai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie*)* differed with scales; habitat, patch

30 and tree in a heterogeneous savanna. We collected data from Arusha National Park, Tanzania in

31 March-May and August-October 2013. Visual observations were used to collect data on foraging.

32 Measurements of tree height and stem height and scoring of accumulated browsing were made in

33 133 patches around trees where the giraffes had been seen browsing, and in a corresponding

34 number of available patches. A logistic regression with mixed effects model (GLMM),

35 descriptive statistics and preference indices data were analyzed by using R program. Giraffes

36 preferred *Acacia* shrub (PI = 2.8) and *Dodonea* shrub habitats (PI = 2.2), and for patch use

37 *Acacia xanthophloea* and *Dodonea viscosa*. Odds ratios correlated with FSAV (p = 0.001).

38 Between plant species, *A. xanthophloea* was the most preferred (p $<$ 0.001) and within plant

39 species, tree height (p $<$ 0.001) and score of accumulated browsing related positively to

40 foraging (p $<$ 0.001). Generally, giraffes selected for *A. xanthophloea* at all scales.

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Introduction

The probability to survive and reproduce among free-living animals depends on the foraging decisions they make at different temporal and spatial scales (Pyke, 1984; Senft *et al.*, 1987; Owen-Smith, Fryxell & Merrill, 2010). According to theory, foraging decisions determine; i) where to search for food; ii) which kind of food to select; iii) when to feed; and iv) when to stop feeding at a particular tree or patch (Pyke, 1984; Stokke, 1999; Owen-Smith *et al.*, 2010). Decisions are nested in a hierarchy of scales (Senft *et al.*, 1987; Skarpe *et al.*, 2000). Senft *et al.* (1987) noted four scales which herbivores are confronted with while foraging: the regional, landscape, patch and plant scale. We used habitat (Krausman, 1999) as our largest scale, and further used patch and plant scales. Habitats are resources and conditions in an area that meet the animal's requirements for survival and reproduction (Hall, Krausman & Morrison, 1997). Habitat selection may be influenced by resource availability, season, time of day, presence of predators and anthropogenic activities (Danell, Edenius & Lundberg, 1991). A patch refers to an array of plants available to an animal without moving (Ginnett & Demment, 1997). At the patch scale, the animal's foraging decisions may depend on food concentration, spatial arrangement, palatability and forage depletion (WallisDeVries, Laca & Demment, 1999; Searle, Hobbs & Shipley, 2005). At the plant scale, animals decide on which plant or plant part to forage. Accumulated browsing may influence animal's foraging decisions at the plant scale (Machida, 1979; Skarpe *et al.*, 2000; Bergqvist, Bergström & Edenius, 2003; Skarpe *et al.*, 2007). Accumulated browsing might increase, decrease or have no impact on forage value. Dry season or winter foraging often leaves the plant with fewer meristems, leading to few but large and sometimes more nutrient rich shoots, thus attracting more browsing (du Toit, Bryant & Frisby, 1990; Bergqvist *et al.*, 2003). Such browsing might develop into a 'feeding loop', where a plant is repeatedly browsed.

72   Here we investigated factors influencing foraging decisions of giraffe at three scales in a savanna

73   ecosystem in Tanzania. We asked whether criteria for foraging decisions differed between scales

74   and seasons. We predicted that at the habitat scale, selection will be influenced by physical

75   factors such as distance from water or predator avoidance; at a patch scale, by forage quantity;

76   and at a plant level by forage quality.

77   **Materials and methods**

78   *Study system*

79   We worked in Arusha National Park, Tanzania. It is situated on the eastern slopes of Mount Meru

80   (36^0 45′ E-3^0 15′ S), and has a total area of 137 km^2 (Martinoli *et al.*, 2006). Climate varies with

81   altitude and has two rainy seasons, the short rains of November and December and the long rains

82   of March to May, with rainfall around the lakes approximately 1100 mm per annum (Amubode

83   & Boshe, 1990; Martinoli *et al.*, 2006). The hottest season is January - February with mean

84   maximum temperature 25.4 degree centigrade while the cold season is June- August with mean

85   minimum temperature of 12.8 degree centigrade (Kahana, Malan & Sylvina, 2014). The soils

86   are mainly originated from the volcanic activities of Mount Meru (Tanapa, 2003). The vegetation

87   is savanna type with grasses, trees and shrubs. Our study species was Masai giraffe (*Giraffa*

88   *camelopardalis tippelskirchi Matschie).* Giraffes live in sub-humid to semi-arid savannas (Dagg,

89   1971; Dagg, 2014). The average height is about 5 m and a mass about one ton (Estes, 1991;

90   Ginnett *et al.*, 1997). They are ruminants and browsers feeding on a variety of plant species and

91   parts with *Acacia* spp being their principal food (Pellew, 1984; Milewski, Young & Madden,

92   1991).

93

94 *Used patches*

95   Visual observations of foraging giraffe were conducted, during   March-May (wet season) and

96 August-October (dry season) between 06h00 and 18h00. We travelled all the roads in our study

97 area (total odometer recorded 17 km) in a way that gave equal coverage. The roads were narrow

98 and less used, and we presume that the bias of sampling from them was small (Stokke, 1999;

99 Wallgren *et al.*, 2009). We drove at a speed of 20 - 30 km an hour. As soon as a browsing adult

100 giraffe was observed within ~50 m from the road, the car was stopped and observations started.

101 Tree species browsed and habitat type were recorded. After the observation was terminated, two

102 sampling plots were laid out; a used plot and an available plot. These plots represent the patches

103 in the foraging decision scale. Hence, the used plot represented the used patch   containing the

104 newly browsed plant or plants in the centre. It had a radius of 4 m (area 50 m^2) meaning that a

105 giraffe standing in its center should reach or be directly aware of all trees within the patch. The

106 available patches of the same size were constructed 100 m from the used patches by walking to

107 the right perpendicular to the direction in which the giraffe moved off.   Hence, the available

108 patch was a randomly selected area available for giraffe to feed in. The design in principle

109 followed Stokke (1999). A total of 266 patches (n=133 used, n=133 available) were sampled and

110 a total of 29 available tree species were recorded. In the patches all trees (including all woody

111 plants > 0.5 m high) were registered by species, tree height, stem height and accumulated

112 browsing. Tree height referred to the height from the ground to the tip of the highest living shoot

113 (Næsset & Økland, 2002) and stem height referred to the height from the ground to the lowest

114 living branch (Deblonde & Ledent, 2001). Tree height and stem height were measured up to 5 m

115 using a graded wooden measuring rod and heights greater than 5 m were estimated in relation to

116 the rod. The accumulated effect on growth form of previous browsing was estimated for each tree

117   on a 4-degree scale. The 4 levels were: 0 = no sign of previous browsing, 1 = old browsing

118   visible but tree growth form had not changed, 2 = old browsing visible and growth form had

119   changed and 3 = old browsing visible and growth form had strongly changed (Skarpe *et al.*, 2007;

120   Mathisen *et al.*, 2014). Giraffes were not individually recognized, and the same animal was likely

121   recorded more than once.

122   *Data analysis*

123   *Habitat use*

124   Our largest spatial scale was the habitat, defined according to Hall and Krausman (1997). We

125   identified four habitats from field observations: (1) *Acacia* shrub (AS) dominated by *Acacia*

126   *xanthophloea*, (2) *Dodonea* shrub (DS), dominated by *Dodonea viscosa,* (3) Grass forb shrub

127   (GFS) dominated by grasses and forbs, and (4) Tall shrub or forest (TS) dominated by tall trees

128   mainly *Euclea divinorum.* We determined distance covered by the different habitats along the

129   roads and calculated percentage available of each habitat in the area (Table 1). A habitat

130   preference index (PI) was determined by dividing the proportion of browsed patches in a habitat

131   with the proportion of the habitat available (Krueger, 1972; Uresk, 1984; Kauhala & Auttila,

132   2009) (Table 1). PI < 1 was regarded as habitat avoidance and PI > 1 as habitat preference

133   (Hammerschlag, Heithaus & Serafy, 2010). We investigated if tree density, tree species diversity

134   and tree height per patch for all patches (used and available) differed among habitat types. A

135   Shannon-Wiener species diversity index within each habitat was determined using the following

136   formula;

$$\text{Diversity} H' = -\sum_{i=1}^{S} p_i \ln p_i$$

137

138   Where *S* is the number of tree species in a patch, *pi* is the proportion of individuals of species *i*

139   and *ln* is the natural logarithm (Spellerberg & Fedor, 2003; Magurran, 2004; Kent, 2011). We

140   calculated tree density (number of trees over area) and averages of tree height and stem height

141   per patch. Because we had more than one dependent variable and several measures of dependent

142   variables on the same patches, a multivariate analysis of variance (MANOVA) was performed in

143   the R program (Crawley, 2007). Benjamini-Yekutieli adjusted p-values test for multiple

144   comparisons was applied to control the false discovery rate in order to avoid inflating the

145   probability of getting an effect (i.e. committing a type I error) while there was none (Benjamini &

146   Yekutieli, 2001; Crawley, 2007). The false discovery rate was chosen as it is a more robust and

147   less stringent test than family-wise error rate tests which are considered to be conservative

148   methods (Benjamini & Hochberg, 1995; Crawley, 2007).

149   *Patch use*

150   Within habitats, we calculated species preference indices for all browsed species (Table 2) using

151   the following formula:

152   PI = *Number of species A in the diet / Number of all species in the diet*

153   *Number of species A in the environment / Number of all species in the environment*

154   A preference index > 1 was regarded as preferred and < 1 was regarded as avoidance (Table 2).

155   Feeding site attractiveness values (FSAV) were calculated to determine differences in vegetation

156   palatability between used and available patches for all patches in each habitat. Patch use was

157   investigated separately for *Acacia* and *Dodonea* habitats for which enough data were available.

158   We used a formula of FSAV adopted from Manly *et al*. (1992) and Stokke (1999) which states;

$$\text{FSAV} = \sum_{i=1}^{n} P_i \cdot B_i$$

159

160   Where P_i is the proportion of species i in the patch, B_i is the preference index for species i, and n

161   is the number of species in the patch. A generalized mixed effects model (GLMM) in R 2.8.0

162   (http://cran.r-project.org/) program with lme4 package using glmer command was used to

163   determine the probability of a patch being browsed. GLMM was chosen for its robustness in

164   handling data that are non-independent. It allows interactions for both continuous and discrete

165   variables as well as continuous independent and dependent variables (Zuur *et al.*, 2009). We used

166   a logistic model, where the response variable was the probability of a patch to be browsed (0/1,

167   family=binomial). Predictor variables included were: FSAVs, tree density, tree height, stem

168   height, season (wet and dry) and Shannon-Wiener diversity index. Statistical assumptions

169   including collinearity and homogeneity of variances were investigated for the full model using

170   variance inflation factors and pair functions detection tools in R (Zuur, Ieno & Elphick, 2010).

171   Backward stepwise selection was performed to find the most parsimonious model that explained

172   the probability of a patch being browsed. Both in *Acacia* and *Dodonea* patch analysis, tree

173   density and stem height were dropped from the models because they were confounded. Since

174   available patches were not necessarily unbrowsed, we presented the results as odds ratios which

175   show relative patch use instead of probabilities of patch selection.

176   *Browsing selection between and within species in the used patches*

177   Our smallest scale was to work within browsed patches to find differences in browsing selectivity

178   between and within tree species. To determine differences in browsing selectivity between

179   species, we picked the three most common and most browsed species having $\geq$ 10 browsed trees

180   each (Table 2) and fitted with our model. A logistic model with mixed effects was used. Whether

181   a tree was browsed or not was the response variable and tree species was the predictor variable.

182   We used a logistic model with mixed effects (GLMM) for *A. xanthophloea* and *D. viscosa* to

183   analyse browsing preferences within species. We used a simple logistic model without mixed

184   effect (GLM) for *E. divinorum* because of small sample size that could not warrant incorporating

185   the random effects in the model. For each model, we checked for statistical assumptions as

186   explained above (Zuur *et al.*, 2010).

187   Within the *A. xanthophloea* model, the probability of a tree to be browsed was the response

188   variable, while tree height, stem height and accumulated browsing were fixed effects, and plot

189   identification was the random intercept (Bennington & Thayne, 1994). Stem height was dropped

190   from the model as it was confounded with tree height. Backward stepwise selections were

191   performed to find the most parsimonious model that explained selectivity. A p-value ≤ 0.05 was

192   used as determining criteria for inclusion or exclusion of variables in the model. A similar model

193   was used to analyse tree selection within *D. viscosa.* However, accumulated browsing level 0 was

194   excluded as there were no previously non-browsed trees. For *E. divinorum,* predictor variables

195   included were similar to the other species. Accumulated browsing level 3 and 0 were excluded as

196   there were no data on these levels.

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201 **Results**

202 *Habitat use*

203 We identified four habitat types and compared the proportion of patches browsed in a habitat to

204 the proportion of the habitat available (PI). *Acacia* shrub (PI = 2.8) and *Dodonea* shrub (PI = 2.2)

205 habitats were preferred (PI>1), whereas, Grass forbs shrub habitat (PI = 0.2) and Tall shrub

206 habitat (PI = 0.5) were avoided (PI<1) (Table 1). MANOVA results revealed that there was a

207 mean difference in tree species diversity ($F_{3,\ 129} = 7.32$, p = 0.001), tree density ($F_{3,\ 129} = 7.61$, p =

208 0.001) and tree height ($F_{3,\ 129} = 7.96.7$, p = 0.001) among habitats, Pillai = 0.42 ($F_{3,\ 129} = 7.07$, p =

209 0.001, Table 1).

210 *Patch use*

211 *Acacia and Dodonea habitats*

212 There was a strong correlation between the use of a patch within *Acacia* shrub habitat and the

213 FSAV. Odds ratios of patch use increased with increasing FSAV ($\chi^2_{1,\ 56} = 13.55$, p = 0.001, Figure

214 1a). Within *Dodonea* shrub habitat, odds ratios of patches being used also correlated with FSAV

215 ($\chi^2_{1,\ 32} = 2.49$, p = 0.013; Figure1b). In both models, species diversity ($\chi^2_{1,\ 56} = 0.11$, p = 0.73),

216 tree height ($\chi^2_{1,\ 56} = 0.86$, p = 0.35) and season ($\chi^2_{1,\ 55} = 0.31$, p = 0.57) for *Acacia* patches and

217 species diversity ($\chi^2_{1,\ 32} = 1.11$, p = 0.29) , tree height ($\chi^2_{1,\ 32} = 1.96$, p = 0.16) and season ($\chi^2_{1,\ 31} =$

218 0.19, p = 0.65) for *Dodonea* shrub variables, were dropped from the models because they were

219 not significant. The significant predictor variable was FSAV for both *Acacia* and *Dodonea*

220 patches.

221

222   *Plant use between and within species*

223   We compared differences in use between *A. xanthophloea, D. viscosa* and *E. divinorum* (Table

224   2). The odds ratios for *A. xanthophloea* to be browsed was 9.9 (95% Cl: 4.2, 23.2) times higher

225   than for *D. viscosa* and 12.3 (95% Cl: 5.7, 26.8) times higher than for *E. divinorum* (F_2,

226    $_{142}$=35.46, P < 0.001). Only *A. xanthophloea* (PI = 1.8), *Croton macrostachyus* (PI = 1.4) and

227   possibly *Warburgia ugandensis* (PI = 1.1) had preference indices >1, other species had PI < 0.5

228   (Table 2).

229   Within *A. xanthophloea* the parsimonious model for browsing probability had two predictor

230   variables: tree height and accumulated browsing. The probability of an *A. xanthophloea* to be

231   browsed increased with height ($\chi^2_{1, 118}$ = 1.68; p < 0.001) and with increasing accumulated

232   browsing level ($\chi^2_{3, 115}$ = 18.99; p < 0.001; Figure 2).

233   Within *D. viscosa,* the odds ratio for accumulated browsing 3 was 1.1 (95% CI: 0.55, 2.2) times

234   higher than for level 1 and 1.7 (95% CI: 1.03, 2.8) times higher than for level 2   ($F_{2, 12}$ = 0.18, P

235   < 0.001).

236   Within *E. divinorum,* there was a positive correlation between tree height and the probability of

237   being browsed ($\chi^2_{1, 44}$ = 30.5; p <0.001; Figure 3).There were non-significant correlation between

238   accumulated browsing and the probability of *E. divinorum* being browsed ($\chi^2_{1, 43}$ = 0.005; p =

239   0.94).

240

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Discussion

Habitat use

The results supported our hypotheses for patch and tree selection, but not for selection of habitats. Habitat selection by large herbivores is often associated with forage availability, water or predator avoidance (Mysterud *et al.*, 1999; Van Beest *et al.*, 2010). Giraffe generally drink regularly, although in areas without water they have adapted to survive without drinking for long periods (Skinner & Chimimba, 2005; Smit, Grant & Devereux, 2007; Valeix *et al.*, 2008; Dagg, 2014; Okello *et al.*, 2015). Giraffe move several kilometers per day (Berry, 1978; du Toit, 2001; Fennessy, 2009) and the mean distance to water was less than 3 km for all sampling patches. Thus, water was not an important criterion for habitat selection. Further, large predators were virtually absent from the study area (Tanapa, 2003). *Acacia* shrub habitat had lowest tree density, but the other preferred habitat *Dodonea* shrub had the highest (Table1), suggesting tree density was not important for selection. Both preferred habitats had low tree height possibly related to predator avoidance, but could also be a result of the search for *A. xanthophloea,* that generally was low (Table 1). Giraffes selected for high forage availability. Similar consistency of selection criteria across scales was recorded by Schaefer and Messier (1995) and by Skarpe *et al*. (2007). Other studies found selection criteria to change with spatial scale (Wilmshurst *et al.*, 1999; Boyce *et al.*, 2003; Fortin *et al.*, 2003). Pratt and Anderson (1982) reported that *C. macrostachyus* was selected by giraffe in Arusha National Park. It has the second highest preference index (1.4) after the *A. xanthophloea* (1.8) Table (2). Today it is uncommon for unknown reason. A population estimate of giraffes in Arusha National Park in 1980s was 462 individuals, in 2000-2003 360 individuals (Pratt & Anderson, 1985; Tanapa, 2003) and now it is estimated to be less than 100

264   (*Pers.comm. park staff*). Generally, giraffe prefers *Acacia* species (Pellew, 1983; Pellew, 1984;

265   du Toit *et al.*, 1990; Parker, Bernard & Colvin, 2003; Waweru, 2007).We thus found giraffe to

266   select habitats according to forage availability, *A. xanthophloea* shrub and, *D. viscosa* shrub,

267   whereas habitats with little of *A. xanthophloea*, Grass forbs shrubs and Tall shrubs were avoided.

268   *Patch use*

269   Giraffe are highly selective browsers, and were found to select patches with high density of the

270   most palatable tree species rather than selecting, for example, sparse trees for predator avoidance.

271   We tested possible contributing variables but found them not significant. The probability of use

272   of a patch correlated only with the FSAV depending on preference indices of the species in the

273   patch. *A. xanthophloea* was the only common species with a positive preference index (1.8) other

274   less common species being *C. macrostachyus* (1.4) and *W. ugandensis* (1.1). Odds ratios of patch

275   selection within *Acacia* shrub and *Dodonea* shrub increased with increasing FSAVs, suggesting

276   that giraffe selected used patches depending on quantity of preferred species (Table 2), almost

277   entirely *A. xanthophloea*.

278   *Plant use*

279   Within used patches in *Acacia* shrub and *Dodonea* shrub habitats giraffe selected primarily *A.*

280   *xanthophloea. A. xanthophloea* has long straight spines (Table 2), probably reducing bite size of

281   the giraffe (Gowda, 1996; Skarpe *et al.*, 2012). The probability of *A. xanthophloea* to be browsed

282   increased with its height and degree of accumulated browsing. The selection of large trees has

283   been explained by higher allocation of defense compounds in younger than in mature trees

284   (Danell, Bergström & Dirke, 1990; du Toit *et al.*, 1990; Nordengren, Hofgaard & Ball, 2003).

285   However, a screening of small and large trees in Botswana failed to find any consistent

286 differences (Rooke *et al.*, 2004). The preference for previously browsed trees (du Toit *et al.*,

287 1990; Makhabu & Skarpe, 2006) could be caused by persistent differences between trees.

288 However, changes in "browsed" trees affecting future herbivory have been found following

289 random allocation of trees to simulated or natural browsing (Bergström, Skarpe & Danell, 2000;

290 Makhabu *et al.*, 2006). This has been explained by fewer buds on browsed trees, hence, fewer

291 shoots are growing larger. Sometimes they are also more nutrient rich and poorer in defence

292 compounds, offering a large bite of good quality forage (Danell *et al.*, 2003; Rooke & Bergström,

293 2007).

294 This study showed that giraffe in Arusha National Park selected primarily for *A. xanthophloea*.

295 At habitat scale, giraffe selected for *Acacia* shrub and *Dodonea* shrub habitats. At patch scale

296 giraffe selected quantity of preferred species according to FSAV, and at tree scale within and

297 between species giraffe selected for quality as expressed by tree height and accumulated

298 browsing.

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454   Table 1: Preference indices, MANOVA results with means and standard errors among habitat types for species

455   diversity, tree density and tree height in Arusha National Park

Habitat type	Distance along roads of habitat (km)	Proportion (%) of habitat available	Number of browsed patches per habitat	Proportion of patches browsed (%) per habitat	Proportion of patches browsed over proportion of habitat available (preference index)	Species diversity (H´)	Tree density (per m^2)	Tree height (m)
Acacia Shrub	3.3	19.5	73	54.9	2.8	0.22 ± 0.05	0.05 ± 0.01	1.53 ± 0.16
Dodonea Shrub	1.9	11.2	33	24.8	2.2	0.48 ± 0.09	0.11 ± 0.01	1.56 ± 0.29
Grass forb shrub	7.5	44.3	12	9.0	0.2	0.66 ± 0.14	0.06 ± 0.02	2.98 ± 0.42
Tall shrub	4.2	24.8	15	11.3	0.5	0.70 ± 0.13	0.07 ± 0.02	3.01 ± 0.39
Total distance	**16.9**	**100**	**133**	**100**				

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466 Table 2: List of important tree species representing preference indices, mean tree height, spinescence and percentage accumulated browsing recorded in the
467 patches

Tree species	Spinescence	Number of browsed trees in the used patches	Number of not browsed trees in the used patches	Preference index	Mean tree height (m) in browsed patches	Mean tree height (m) in unbrowsed patches	% accumulated browsing in the browsed patches (by levels)				% accumulated browsing in the unbrowsed patches (by levels)				Total number of trees in the browsed patches	Total number of trees in the unbrowsed patches
							0	1	2	3	0	1	2	3		
Acacia xanthophloea	Yes	191	111	1.8	1.7	1.6	2.0	4.3	4.3	89.4	1.3	2.7	8.7	87.3	302	150
Croton macrostachyus	No	2	2	1.4	3.5	0	0	25	75	0	0	66.7	33.3	0	4	3
Warburgia ugandensis	No	2	3	1.1	1.1	0	0	20	20	60	50	0	25	25	5	4
Maytenus senegalensis	Yes	2	9	0.5	1.6	0	9.1	0	63.6	27.3	0	0	0	100	11	1
Euclea divinorum	No	16	76	0.5	2.6	0	41.3	37	14.1	7.6	58.5	21.5	9.2	10.8	92	65
Dodonea viscosa	No	11	63	0.4	1.9	1.7	35.1	5.4	12.2	47.3	14.3	18.1	38.1	29.5	74	105
Carissa edulis	Yes	2	14	0.4	1.1	1.1	0	6.3	43.7	50	28.6	7.1	14.3	50	16	14
Olea africana	No	4	32	0.3	1.4	1.2	8.3	5.6	11.1	75	0	18.5	22.2	59.3	36	27
Rhus natalensis	No	2	17	0.3	1.6	1.2	5.3	15.8	26.3	52.6	21.4	14.3	21.4	42.9	19	14

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Figure legends

Figure 1a and b**:** The relationship between FSAV and odds ratios of a patch being used; a) within *Acacia* shrub habitat and b) within *Dodonea* shrub habitat. Dotted lines are standard errors (SE). Data were collected from used patches and available patches within habitats.

Figure 2: Probability of *Acacia xanthophloea* being browsed as influenced by tree height and accumulated browsing. Levels were defined as: 0 = no sign of previous browsing, 1 = old browsing visible but tree growth form had not changed, 2 = old browsing visible and growth form had changed and 3= old browsing visible and growth form had strongly changed.

Figure 3: Probability of *Euclea divinorum* being browsed as influenced by tree height. Dotted lines are standard errors (2*SE).
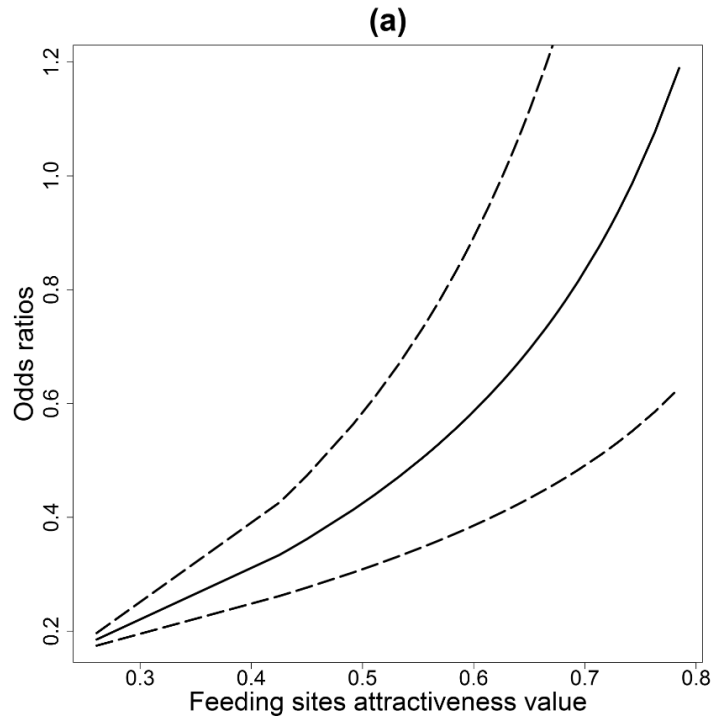
490 Figure 1a and b

(a)

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(b)

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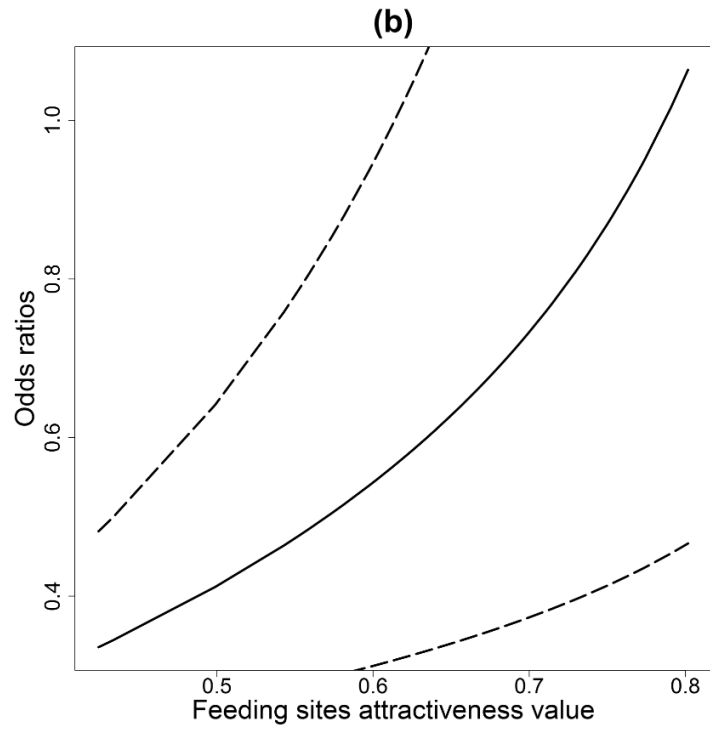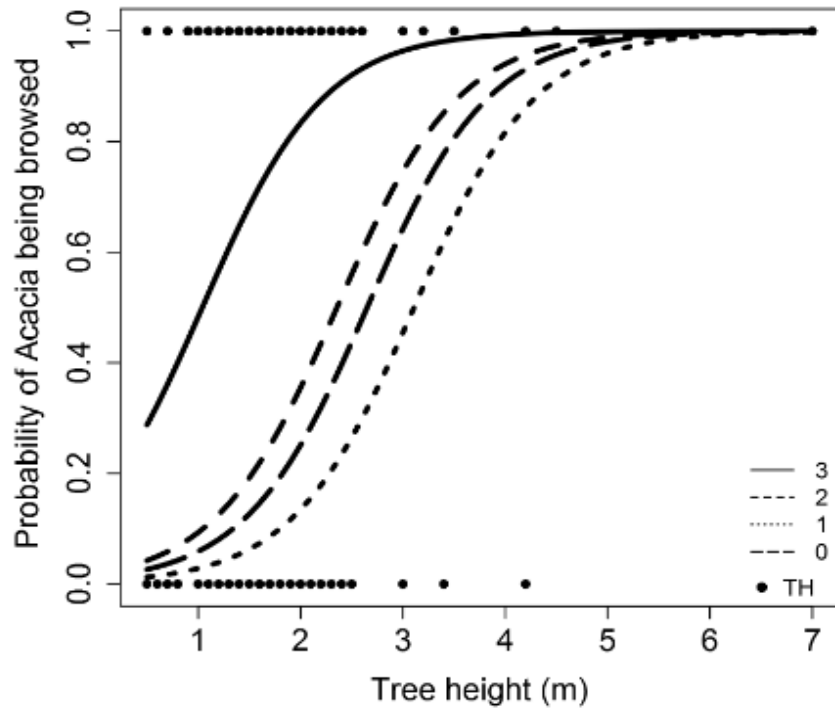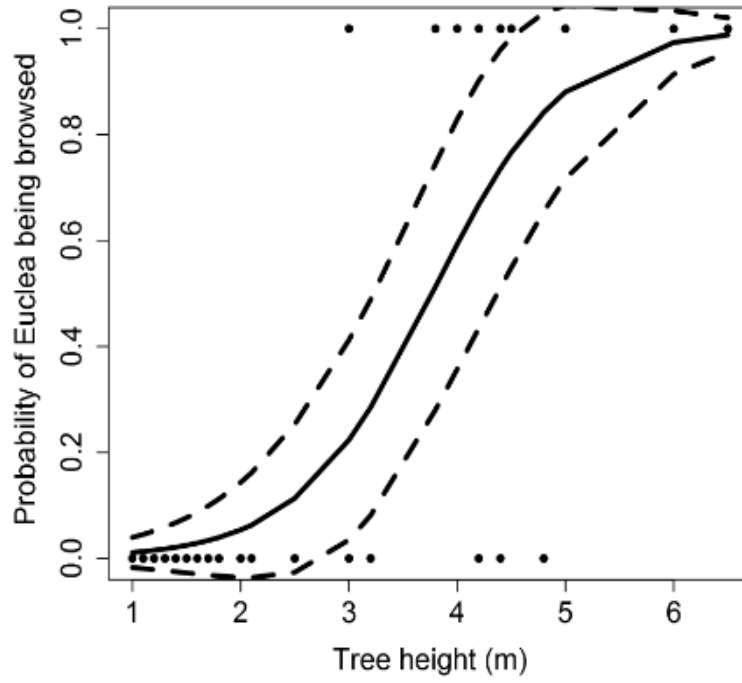494   Figure 2

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Figure 3

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