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1   **The influence of logging upon the foraging behaviour and diet of the endangered**

2   **Borneo banteng**

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4   Penny C. Gardner[1,2β]*, Stephanie Ridge[1,2β], Jocelyn Goon Ee Wern[1] and Benoit

5   Goossens[1,2,3,4]*

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7   [1]Danau Girang Field Centre c/o Sabah Wildlife Department, Wisma Muis, 88100 Kota

8   Kinabalu, Sabah, Malaysia

9   [2]Organisms and Environment Division, School of Biosciences, Cardiff University, Sir

10   Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK

11   [3]Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia

12   [4]Sustainable Places Research Institute, Cardiff University, 33 Park Place, Cardiff CF10

13   3BA, UK

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15   [β] Penny C. Gardner and Stephanie Ridge contributed equally to this work.

16   [*] Corresponding authors

17   Email: Biodiversitymatters@protonmail.com (PCG), goossensbr@cardiff.ac.uk (BG)

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19   Running title: Logging influences bantengs' foraging ecology

20 **Abstract**

21 Logging causes soil compaction and alters the vegetation structure and plant diversity,

22 and ungulates must adapt to modified conditions if they are to survive. We investigated

23 the impact of logging upon the foraging ecology of the Borneo banteng using camera

24 traps and botanical surveys. General linear models were used to explore the effects of

25 site characteristics and plant diversity upon foraging duration, and plant specimens were

26 identified to confirm dietary preferences. Foraging events were recorded over 40,168

27 nights in five forests. Foraging duration significantly decreased in open areas

28 depauperate in species richness ($F=7.82$, $p= <0.01$), however it increased with elevation

29 ($F=3.46$, $p=0.05$). Their diet comprised of eight invasive species (*Mikania cordata* and

30 *Chromolaena odorata, Cyperus difformis, Fimbristylis littoralis* and *Scleria* sp.,

31 *Desmodium triflorium*, *Eleusine indica*, and *Selaginel* sp.), which are characteristic of

32 disturbed forest and fast to establish. Logging creates ideal conditions for these plants,

33 which are preferentially selected by bantengs. Whilst logging may increase forage, the

34 disturbances logging causes to the bantengs and the ensuing poaching may counteract

35 any positive benefits. Developing forest management strategies that incorporate

36 conservation of the bantengs may in-turn encourage more favourable conditions for

37 emergent timber species and also conserve this endangered wild cattle species.

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39 Keywords: Mammal community, Borneo, foraging behaviour, forest management,

40 logging impacts, forest degradation.

41 Declarations of interest: None.

42

Introduction

Since the 1970's, the timber and oil palm industries have increased in prevalence in

Sabah (Reynolds et al. 2011), with forests being logged to generate sites for agricultural

development, and fences erected to mark boundaries and electric wires to prevent crop

damage by elephants moving across their territory (Estes et al. 2012). Since 2010, the

forested area of Sabah was estimated to have been reduced by 168,493 km^2 or 30.2%

(Gaveau et al. 2014) and, as of 2011, only a meagre ~1.4 % (1,030 km^2) was covered by

Virgin Jungle Reserve (Reynolds et al. 2011). The remainder of natural forests are

predominantly secondary and highly degraded by repetitive interval logging (Gaveau et

al. 2014), which has resulted in alterations to the canopy and understory structure, and

changes in the abundance of different plant species (Costa and Magnusson 2003).

Timber harvesting also changes the way forest-dwelling mammals such as the Borneo

banteng (*Bos javanicus lowi*) behave and use the forest (Gardner et al. 2018), as it

creates gaps that facilitate species access to foraging sites and can alter the quantity and

quality of resources (Costa and Magnusson 2003). The extensive loss of forest habitat

across Sabah has now largely confined the Borneo banteng to secondary seasonal

swamp, lowland and upland mixed dipterocarp, and lower montane forests (Gardner and

Goossens, unpublished). Occupation of secondary forests may imply that the bantengs

show versatility and some resilience to habitat modification. They have been found to

congregate in larger herds along abandoned logging roads (Journeaux et al. 2018) and

forage for long durations in open canopy areas of recently-logged forests (Gardner et al.

2018), and that logging influences their body condition (Prosser et al. 2016). Given that

little primary forest remains in Sabah, the environmental conditions and plant

availability in secondary forests is of upmost importance for the survival of large

mammals like the banteng. Sites heavily disturbed by logging can be infested by

68   twining vines, grasses and sedges that may influence the growth of pioneer trees with

69   specific recruitment and establishment conditions (Pinard et al. 1996). These plant

70   infestations however, may also impact upon the diversity and abundance of the plants

71   available for banteng consumption, and influence how and when they forage within

72   secondary forests. Although probably a grazer by preference, bantengs should perhaps

73   be considered an intermediate feeder, like the close-relative gaur (*Bos gaurus*), since it

74   can and does consume a lot of browse and fruits depending on season and local food

75   availability (Timmins et al. 2008). Forage obtained by these two species is thought to be

76   similar and consist of grasses, sedges, herbs, soft vines, shrubs, and wild fruits such as

77   guava (Myrataceae) (Gad and Shyama 2009; Gardner et al. 2014), as well as bamboo,

78   flowers, and tree bark (Timmins et al. 2008), showing a wide and varied diet. As

79   bantengs are a ruminant they generate a large quantity of metabolic heat as forage is

80   broken down by fermentation in the rumen (Puniya et al. 2015); for this reason they

81   may be influenced by the degree of canopy cover available within their habitat, which

82   were found to influence a range of ungulates in Poland (Kuijper et al. 2009). Gad and

83   Shyama's (2009) study on gaur revealed that the middle part of the day was spent

84   resting, ruminating and keeping cool in the shade, whilst domestic cattle species use

85   respiration and low night-time temperatures to cool their bodies (Dewell 2010). In

86   addition to shade, plant biomass may also be a factor that influences the bantengs'

87   selection of foraging sites, as ungulates base their foraging decisions on the selection of

88   patches that result in high protein and energy intake (Kuijper et al. 2009).

89   Ensuring an adequate food supply and suitable secure areas for foraging is problematic

90   when there is limited information on preferences. To better our understanding of

91   banteng feeding ecology, we investigated their foraging behaviour and the physical

92   characteristics of feeding sites across the landscape in Sabah by testing the hypotheses

93   that bantengs forage for longer in open degraded areas that have lower plant species

94   richness, and that cooler ambient temperatures at higher elevations enable them to

95   forage for longer. We also investigated their diet using a combination of botanical

96   surveys and camera traps.

97

98   **Materials and methods**

99   *Study Sites*

100   Field surveys were conducted in five reserves across Sabah that represented different

101   classes of protection (refer to Sabah Forestry Department., (2006) for a description of

102   forest classes) and management (Fig. 1), namely Tabin Wildlife Reserve (TWR), Malua

103   Forest Reserve (MFR), Maliau Basin Conservation Area (MBCA), Sipitang Forest

104   Reserve (SPT) and Sapulut Forest Reserve (SPL). MBCA is a Class 1 protected primary

105   and secondary forest reserve and part of the Yayasan Sabah Forest Management Area

106   (Reynolds et al. 2011). Due to the inaccessibility of the basin, this study focused on the

107   southern edge buffer zone, which is characterised by riparian, lowland (below 300m)

108   and hill (300-750m) mixed dipterocarp forest (Wong Kochummen et al. 1985). TWR is

109   situated on Sabah's east coast, and this Class 7 Wildlife Reserve contains small sections

110   of virgin jungle reserve with the surrounding area made up of secondary seasonal

111   freshwater swamp, lowland and hill mixed dipterocarp forest. MFR is a secondary Class

112   1 forest that consists of lowland, hill and seasonal swamp dipterocarp forest. In 2011 it

113   achieved forest stewardship council (FSC) certification and is now fully protected from

114   future logging (Reynolds et al. 2011). SPT and SPL are both commercial forest reserves

115   (Class 2) and, at the time of this study, active logging was taking place. SPT is managed

116   by Sabah Forest Industries (SFI) and consists of primary and secondary lowland hill

117   forest, riparian and upper hill forest (750-1200m) (Wong Kochummen et al. 1985), and

118   Industrial Tree Plantation (ITP) planted with fast-growing *Acacia/Eucalyptus* species.

119   SPL is located on the central southern edge of Sabah, to the south west of MBCA and is

120   made up of lowland and hill dipterocarp and montane forest. The study covered areas of

121   natural forest management (NFM) and ITP managed by Sapulut Forest Development

122   Sdn. Bhd. since 2003. All study sites in SPL were located in NFM areas.

123

124   *Data collection*

125   A total of 368 Reconyx Hyperfire HC500 and PC800 camera trap stations were

126   deployed across the five forests for at least 90 days. This duration was previously found

127   to be sufficient for obtaining robust estimated of population size of bantengs in Sabah

128   (Gardner 2015). Two different categories of canopy extent which broadly represented

129   leaf cover of the camera viewpoint ('open' when canopy leaf cover was less than 50%

130   and 'closed' when canopy leaf cover exceeded 50%). Surveys were conducted at

131   different times and cameras were distributed in a grid format and/or on an ad-hoc basis,

132   with the disparity arising from two different studies of bantengs by Gardner (2015) and

133   Gardner and Goossens (unpublished). Cameras operated for 24/7, with three

134   consecutive photos taken at one-second intervals, with no time lapse. Grids of cameras

135   were defined by access (on-foot, by boat or vehicle), with a minimum of 500m between

136   stations and from unsealed roads to reduce disturbance. This distance was previously

137   found to incur only low correlation, as bantengs were found to be low density and were

138   not frequently captured at neighbouring cameras (Gardner 2015). Ad-hoc cameras were

139   positioned in locations where banteng signs were encountered or, in their absence,

140   alongside a wildlife trail, and set at a height between 1-1.5m high to coincide with the

141   widest part of the body. Photographic capture events of bantengs confirmed their

142   presence, and the performance and the time spent foraging was calculated from the time

143   of the first photograph when feeding began, until the time of the last photograph when

144   the feeding ceased or when the individual(s) moved out of the station viewpoint. Events

145   were classed as independent when 30 minutes or more had elapsed between the prior

146   and subsequent captures, and these events were stratified according to forest name,

147   canopy extent, elevation, ambient temperature and plant species richness.

148   The diet of bantengs was investigated in the first instance by inspecting all camera trap

149   photographs for the presence of bantengs that were foraging. The corresponding event

150   data from these images was extracted and used for modelling foraging behaviours (as

151   detailed below). The taxonomic identification of the plant forage was investigated to

152   species level by using botanical surveys which were conducted at camera trap stations

153   where bantengs were photographed foraging. Confirmation of plant forage from feeding

154   signs and/or bite marks was not factored into the vegetation surveys as they were

155   nonconcurrent to the camera trapping surveys. Surveys were conducted post-hoc using a

156   5 m line transect perpendicular to the station. Every visually-distinct plant, including all

157   obtainable parts (i.e. flower, stem etc) was photographed, labelled, sampled and stored

158   following the protocols in the literature (Mealor and Mealor 2010; Queensland

159   Herbarium 2010). Species that occurred at multiple stations were not collected; this

160   reduced unnecessary removal from forests that were regenerating. Specimens were

161   formally identified by a botanist at the Sepilok Forest Research Centre managed by the

162   Sabah Forestry Department. Distinction of plant species consumed by bantengs in front

163   of cameras from those plants that were arbitrarily collected at each site was conducted

164   by cross-comparison of specimens with camera trap photographs of foraging bantengs.

165   Plant species richness was calculated for every station where the botanical surveys were

166   conducted by using the Shannon-Wiener diversity index.

167

Statistical modelling

169 The species richness of each camera trap station was calculated using the Vegan

170 package (Oksanen et al. 2012) in RGui version 3.2.3. Using the continuous data of plant

171 species richness, elevation and ambient temperature, and the categorical data of site type

172 (old logging road, open scrub and road verge), canopy extend (closed, open), and forest

173 name (MFR, TWR, MBCA, SPL, SPT), we modelled the effects upon the foraging

174 duration (minutes) of bantengs using a general linear model (GLM) with a Gamma error

175 family and an identity link function in the lme4 package (Douglas et al. 2017). Model

176 selection was conducted by dropping non-significant terms using the drop1 function,

177 and model validation was conducted using graphical plots of the standardised residuals,

178 Shapiro-Wilk test for normality, Fligner-Killeen test of homogeneity of variances and

179 comparison of AIC weighting. Graphs were created using the ggplot2 library (Wickham

180 and Chang 2016).

181

182 **Results**

183 Our stations were deployed in natural forest, ITP and scrub that ranged in elevation,

184 from 0 to 1,379m above sea level with an average of ~250m. The numbers of camera

185 trap stations established in each forest were as follows: TWR = 130, MFR = 148,

186 MBCA = 27, SPT = 33, SPL = 30. During the surveys some camera traps suffered from

187 electronic failure or theft which resulted in shorter operating periods, with a minimum

188 of 10 days and a maximum of 373 days. Grids of cameras in TWR and MFR resulted in

189 a higher survey effort, with the most camera trap nights obtained from MFR (14,760)

190 and the least in SPL (2,578). A total of 40,168 camera trap nights were documented

191 between April 2011 to May 2014 and during this time a total of 345 incidences of

192 foraging were recorded at 37 out of 368 stations. Observations indicated that bantengs

193 foraged for periods lasting between 1-197 minutes, with an average duration of 17

194 minutes. With respect to botanical surveys, they were conducted at a later time to

195 camera trap surveys and it was not possible to sample species richness at all sites where

196 foraging occurred, owing to a number of factors resulting in inaccessibility but also

197 regrowth of highly invasive plants.

198   Investigations of the foraging duration data indicated a zero-bounded asymmetrical

199 shape that benefited from a power transformation prior to modelling. Five models were

200 fitted to the data to explain foraging duration; systematic removal of non-significant

201 interactions and terms led to the exclusion of an interaction between elevation and

202 temperature, and the exclusion of terms temperature and forest name. An initial null

203 model was fit and subsequent models specified different combinations of terms and

204 interactions. A GLM that specified the foraging duration explained by an interaction

205 between plant diversity and canopy extent plus a main effect of elevation was the best

206 fitting model (Table 1, model 4), with normally-distributed standardised residuals and

207 explained the highest proportion of the variation ($R^2=22\%$) but had the fourth smallest

208 AIC (Table 2, model 4). In general, foraging duration significantly declined as plant

209 species richness increased ($Z=0.07 \pm 0.03$, $p=<0.05$, Table 1, model 4). More

210 specifically, foraging duration significantly declined as plant species richness increased

211 in open canopy areas ($F=7.82$, $p= <0.01$, Table 2, model 4, Fig. 2). Foraging duration

212 also increased as elevation increased ($F=3.46$, $p=0.05$, Table 2, model 4, Fig. 3),

213 however no temperature effect was observed.

214   A total of 48 plant specimens from 22 plant families were collected from 25 sites

215 where bantengs were observed foraging. Plant species richness of the 25 sites can be

216 found in Appendix 1. Eight species from 5 plant families were foraged by bantengs

217 evident in camera trap photographs (Table 3 and Fig. 4). At the family level,

218   Cyperaceae and Asteraceae were the most prevalent, whilst at the species-level *Mikania*

219   *cordata* was the most prevalent and was found in all five forests.

220

221   **Discussion**

222   We found evidence to support our hypothesis that bantengs spent a greater duration of

223   time foraging in open degraded areas that have lower plant species richness; an overall

224   negative trend was observed, whereby bantengs foraged for shorter periods as the plant

225   species richness index increased in degraded open canopy areas. The foraging durations

226   recorded within three logged forests in Sabah by Gardner et al. (Gardner et al. 2018)

227   ranged between 2-174 minutes (95% CI = 0-217) and were not dissimilar to the

228   durations observed by this study (1-197 minutes with an average of 17). Furthermore, as

229   the present study investigated a larger number of forest reserves across a wider region

230   and utilised a larger number of survey nights, our foraging durations are believed to

231   accurately reflect their diet and foraging behaviours. Whilst not statistically significant,

232   the opposite trend in foraging behaviour was observed for closed canopy areas, whereby

233   bantengs showed a tendency to forage for longer when species richness was greater.

234   Depauperate plant species richness in open degraded banteng foraging sites contrasts

235   the results from other studies that compared biodiversity in logged and unlogged forests

236   in Borneo (Berry et al. 2010). This disparity may be due to seedling and sapling

237   recruitment failure and differences in the length of the regeneration period between the

238   forests studied (Sodhi et al. 2010), the bantengs' preferential selection of sites naturally

239   low in species richness, or even the locations where cameras were established (i.e. areas

240   unobstructed by trees rich in diversity). Given the similar low diversity of forage

241   detected in banteng faeces by Matsubayashi et al. (2007), the selection of camera sites

242   may not be responsible for the differences in diversity between logged sites. Our results

243   also indicated that bantengs increased the time they spent foraging at higher elevations,

244   which contrasts with findings by Chaiyarat et al. (2018), which identified 78% of

245   presence records of Burmese bantengs in Thailand were found in habitat ranging

246   between 101-200m, with no sites occurring above 401m high. Longer foraging at higher

247   elevations in Sabah may be due to the widescale loss of forest habitat at lower

248   elevations (for agriculture), to anthropogenic disturbances in lower elevations causing

249   the species to take refuges in more secluded habitat at higher elevations, or to wider

250   variation in the elevation of study sites. Food density is likely to be one of the other

251   main driving forces for these behavioural tendencies; when large canopy openings are

252   generated by logging there is a sudden increase in light at the forest floor, which

253   facilitates an invasion of exotic plants (Duclos et al. 2013). The vast network of logging

254   roads serve as pathways for the spread of these species (Döbert et al. 2017) but also as

255   paths for bantengs because they are less inhibited by trees (Kuijper et al. 2009). Over

256   time, forage almost certainly becomes scarcer because the regenerating canopy shades

257   out understorey invasive pioneers, therefore the time invested in feeding under a closed

258   canopy is probably reduced. Degraded open canopy areas supporter larger herds and the

259   greater plant biomass means the herd can spend a longer period of time feeding, without

260   having to move to search for new forage (Kuijper et al. 2009; Journeaux et al. 2018) but

261   this is conditional on the proximity to the forest border (Journeaux et al. 2018) and on

262   the provision of dense forest where they can seek shade, cool body temperatures, and

263   evade human disturbances (Gardner et al., 2018). The greater biomass has propagated

264   higher body condition scores (i.e. greater fat reserves) in bantengs inhabiting forest that

265   was in the early stages of regeneration (Prosser et al. 2016). As a large-bodied mammal,

266   Borneo bantengs require mature forest with a dense canopy where they are able to take

267   refuge from the sun and to cool core body temperature (Gardner et al., 2018), but we did

268   not find any evidence to suggest that cooler ambient temperatures at higher elevations

269   had an influence on foraging behaviours in this study.

270   In general, the foraging behaviours that we observed are not dissimilar to other

271   banteng subspecies and ungulates; Burmese bantengs in Lao People's Democratic

272   Republic concentrated within dry dipterocarp forest that had extensive and dense

273   ground of grassy forage (Steinmetz 2004), and Javan bantengs spent 50% of their

274   grazing time in meadows colonised by grasses and legumes (Sumardja and Kartawinata

275   1977), which included one species (*D. trifolium*) we found to be consumed by Borneo

276   banteng. Similarly, the forest buffalo (*Syncerus caffer nanus*) in west Africa was more

277   abundant in open grassy and sedge meadows which offered abundant quantities of

278   favoured food (Blake 2002), and the moose (*Alces alces*) in Canada significantly

279   increased usage of forest that was in the early stages of natural regeneration (10 years)

280   and the post-harvesting and management influenced their forage availability (Boan et al.

281   2011). Likewise, the sympatric sambar deer (*Cervus unicolor*) also forage within open

282   areas and along logging roads in Borneo (Meijaard and Sheil 2008).

283

284   The small number of plant species identified as banteng forage, relative to the large

285   number of specimens collected at foraging sites, are common in occurrence within

286   Sabah and highly adapted to exploit degraded soils. The two most prevalent species, *M.*

287   *cordata* and *Eleusine indica,* are fast to establish on disturbed land (CABI 2013b; CABI

288   2014b). *M. cordata* is a native fast-growing creeping vine that is easily spread by

289   humans and the wind and can regenerate from broken stems (CABI 2013b). *E. indica* is

290   a problematic weed in Malaysia and is an aggressive colonizer; it has the ability to grow

291   in direct sunlight enabling it to establish in post-logging bare soil (CABI 2014b).

292   *Chromolaena ordorata* was previously introduced to Sabah and is also a highly

293   competitive weed (CABI 2014a); a previous study found it to be highly abundant in

294   logged forest (Döbert et al. 2017). *Cyperus difformis* has a very short life cycle (~1

295   month) so is able to spread quickly once established and is able to exploit clay soils

296   (CABI 2013a) like those found in SPT. *Fimbristylis littoralis*, like *E. indica*, generates

297   large numbers of seeds, which can be transferred by humans, animals, water and wind,

298   allowing rapid colonisation of an area (CABI 2014b; CABI 2014c). Once established in

299   an area *F. littoralis* has the ability to change the dynamics of an ecosystem, benefitting

300   its own growth and disrupting other established species (CABI 2014c). This study

301   indicates the bantengs' diet consists mainly of invasive plants and that they may

302   actually benefit from greater quantities of biomass after logging, however, it is possible

303   that bantengs also forage upon other less common plants not observed during this study,

304   and that they may not expend much time in exploiting less prevalent plants as they may

305   provide high nutritional or mineral value. As such, bantengs perform an important

306   ecosystem service by grazing heavily on invasive pioneer plants (Dobson et al. 2006),

307   which are not necessarily transient in the regrowth process and can alter the trajectory of

308   forest succession (Brown and Gurevitch 2004). Commonalities in diet species richness

309   compared to other studies were approximately comparable, with 11 species (three more

310   than the present study) detected by Matsubayashi et al. (2007) from faecal screening of

311   bantengs in one forest in Sabah. In terms of plant species diversity however, there were

312   marked contrasts in the number of graminoids detected, with Matsubayashi et al. (2007)

313   noting the presence of nine graminoids whereas we only detected one. In comparison to

314   other banteng subspecies, marked differences were evident in both forage species

315   richness and diversity; 23 plant species were foraged by Burmese bantengs (*B. j.*

316   *birmanicus*) in Thailand (Chaiyarat et al. 2018) but only one plant species, the flowering

317   shrub *C. odorata,* was foraged by both Bornean bantengs and Burmese bantengs.

318

Conclusion

320 Logging and forest regeneration in Sabah create environmental conditions that are

321 favourable for exotic invasive plant species and influence the foraging behaviours and

322 diet of bantengs. Consequently, bantengs play an important role as an ecosystem

323 engineer in suppressing the growth of undesirable pioneers that are quick to colonize

324 open areas where the canopy is damaged and may suppress the growth of economically-

325 important emergent tree species. Bantengs may prosper from additional forage available

326 in high volumes, but only when seclusion and/or security measures safeguards them

327 against disturbance and poaching at a time when they are undertaking an essential

328 activity in a more exposed location. Conservation of bantengs within commercial

329 forests may be key to minimising the growth of invasive exotic plants that supress

330 growth of valuable timber species, but forest management needs to ensure their survival

331 by effecting anti-poaching strategies and ensure the availability of large and dense forest

332 refuges where they may evade harvesting activities and encroachment. Such a

333 harmonious approach to forest management may be more beneficial for the bantengs

334 and for timber productivity in the longer term.

335

344

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Figure and Table legends

Fig. 1: The locations of the study sites across the Malaysian state of Sabah on the island of Borneo. The map was generated using ArcGIS® software version 10.1 by ESRI, with data from Natural Earth and the Sabah Forestry Department.

Fig. 2: The significant linear relationships between plant species richness and canopy extent upon the foraging duration of Bornean bantengs.

Fig. 3: The significant positive relationship between elevation (metres) upon the foraging duration of Bornean bantengs (minutes).

Fig 4: Plant species that constitute the bantengs' diet (top left-right) *Mikania cordata*, *Chromolaena odorata*, *Cyperus difformis*, (middle left-right) *Fimbristlis littoralis*, *Scleria* sp., *Disodium triflorium*, (bottom left-right) *Eleusine indica*, *Selaginel* sp. and a juvenile male banteng foraging in Malua Forest Reserve.

Table 1: General linear model coefficients with stepwise model selection based on AIC values on the foraging duration of Borneo bantengs in Sabah (Malaysian Borneo) explained by plant species richness, canopy extent, elevation, ambient temperature and forest name.

Table 2: F statistics using single term deletions estimated from the general linear models on the foraging duration of Borneo bantengs.

Table 3: Plant species consumed by Borneo bantengs in Sabah