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

3

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18

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 triflorum*, *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.

38

39 **Keywords:** Mammal community, Borneo, foraging behaviour, forest management,
40 logging impacts, forest degradation.

41 **Declarations of interest:** None.

42

43 **Introduction**

44 Since the 1970's, the timber and oil palm industries have increased in prevalence in
45 Sabah (Reynolds et al. 2011), with forests being logged to generate sites for agricultural
46 development, and fences erected to mark boundaries and electric wires to prevent crop
47 damage by elephants moving across their territory (Estes et al. 2012). Since 2010, the
48 forested area of Sabah was estimated to have been reduced by 168,493 km² or 30.2%
49 (Gaveau et al. 2014) and, as of 2011, only a meagre ~1.4 % (1,030 km²) was covered by
50 Virgin Jungle Reserve (Reynolds et al. 2011). The remainder of natural forests are
51 predominantly secondary and highly degraded by repetitive interval logging (Gaveau et
52 al. 2014), which has resulted in alterations to the canopy and understory structure, and
53 changes in the abundance of different plant species (Costa and Magnusson 2003).
54 Timber harvesting also changes the way forest-dwelling mammals such as the Borneo
55 banteng (*Bos javanicus lowi*) behave and use the forest (Gardner et al. 2018), as it
56 creates gaps that facilitate species access to foraging sites and can alter the quantity and
57 quality of resources (Costa and Magnusson 2003). The extensive loss of forest habitat
58 across Sabah has now largely confined the Borneo banteng to secondary seasonal
59 swamp, lowland and upland mixed dipterocarp, and lower montane forests (Gardner and
60 Goossens, unpublished). Occupation of secondary forests may imply that the bantengs
61 show versatility and some resilience to habitat modification. They have been found to
62 congregate in larger herds along abandoned logging roads (Journeaux et al. 2018) and
63 forage for long durations in open canopy areas of recently-logged forests (Gardner et al.
64 2018), and that logging influences their body condition (Prosser et al. 2016). Given that
65 little primary forest remains in Sabah, the environmental conditions and plant
66 availability in secondary forests is of utmost importance for the survival of large
67 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

168 ***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 odorata* 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

319 **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 suppress
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

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344

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445 **Figure and Table legends**

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

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

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

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

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

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

463 Table 3: Plant species consumed by Borneo bantengs in Sabah