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

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Running title: Logging influences bantengs' foraging ecology
Abstract

Logging causes soil compaction and alters the vegetation structure and plant diversity, and ungulates must adapt to modified conditions if they are to survive. We investigated the impact of logging upon the foraging ecology of the Borneo banteng using camera traps and botanical surveys. General linear models were used to explore the effects of site characteristics and plant diversity upon foraging duration, and plant specimens were identified to confirm dietary preferences. Foraging events were recorded over 40,168 nights in five forests. Foraging duration significantly decreased in open areas depauperate in species richness (F=7.82, p= <0.01), however it increased with elevation (F=3.46, p=0.05). Their diet comprised of eight invasive species (*Mikania cordata* and *Chromolaena odorata, Cyperus difformis, Fimbristyliis littoralis* and *Scleria* sp., *Desmodium triflorium, Eleusine indica*, and *Selaginel* sp.), which are characteristic of disturbed forest and fast to establish. Logging creates ideal conditions for these plants, which are preferentially selected by bantengs. Whilst logging may increase forage, the disturbances logging causes to the bantengs and the ensuing poaching may counteract any positive benefits. Developing forest management strategies that incorporate conservation of the bantengs may in-turn encourage more favourable conditions for emergent timber species and also conserve this endangered wild cattle species.

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

Declarations of interest: None.
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
twining vines, grasses and sedges that may influence the growth of pioneer trees with
specific recruitment and establishment conditions (Pinard et al. 1996). These plant
infestations however, may also impact upon the diversity and abundance of the plants
available for banteng consumption, and influence how and when they forage within
secondary forests. Although probably a grazer by preference, bantengs should perhaps
be considered an intermediate feeder, like the close-relative gaur (*Bos gaurus*), since it
can and does consume a lot of browse and fruits depending on season and local food
availability (Timmins et al. 2008). Forage obtained by these two species is thought to be
similar and consist of grasses, sedges, herbs, soft vines, shrubs, and wild fruits such as
guava (*Myrataceae*) (Gad and Shyama 2009; Gardner et al. 2014), as well as bamboo,
flowers, and tree bark (Timmins et al. 2008), showing a wide and varied diet. As
bantengs are a ruminant they generate a large quantity of metabolic heat as forage is
broken down by fermentation in the rumen (Puniya et al. 2015); for this reason they
may be influenced by the degree of canopy cover available within their habitat, which
were found to influence a range of ungulates in Poland (Kuijper et al. 2009). Gad and
Shyama’s (2009) study on gaur revealed that the middle part of the day was spent
resting, ruminating and keeping cool in the shade, whilst domestic cattle species use
respiration and low night-time temperatures to cool their bodies (Dewell 2010). In
addition to shade, plant biomass may also be a factor that influences the bantengs’
selection of foraging sites, as ungulates base their foraging decisions on the selection of
patches that result in high protein and energy intake (Kuijper et al. 2009).
Ensuring an adequate food supply and suitable secure areas for foraging is problematic
when there is limited information on preferences. To better our understanding of
banteng feeding ecology, we investigated their foraging behaviour and the physical
characteristics of feeding sites across the landscape in Sabah by testing the hypotheses
that bantengs forage for longer in open degraded areas that have lower plant species richness, and that cooler ambient temperatures at higher elevations enable them to forage for longer. We also investigated their diet using a combination of botanical surveys and camera traps.

Materials and methods

Study Sites

Field surveys were conducted in five reserves across Sabah that represented different classes of protection (refer to Sabah Forestry Department., (2006) for a description of forest classes) and management (Fig. 1), namely Tabin Wildlife Reserve (TWR), Malua Forest Reserve (MFR), Maliau Basin Conservation Area (MBCA), Sipitang Forest Reserve (SPT) and Sapulut Forest Reserve (SPL). MBCA is a Class 1 protected primary and secondary forest reserve and part of the Yayasan Sabah Forest Management Area (Reynolds et al. 2011). Due to the inaccessibility of the basin, this study focused on the southern edge buffer zone, which is characterised by riparian, lowland (below 300m) and hill (300-750m) mixed dipterocarp forest (Wong Kochummen et al. 1985). TWR is situated on Sabah’s east coast, and this Class 7 Wildlife Reserve contains small sections of virgin jungle reserve with the surrounding area made up of secondary seasonal freshwater swamp, lowland and hill mixed dipterocarp forest. MFR is a secondary Class 1 forest that consists of lowland, hill and seasonal swamp dipterocarp forest. In 2011 it achieved forest stewardship council (FSC) certification and is now fully protected from future logging (Reynolds et al. 2011). SPT and SPL are both commercial forest reserves (Class 2) and, at the time of this study, active logging was taking place. SPT is managed by Sabah Forest Industries (SFI) and consists of primary and secondary lowland hill forest, riparian and upper hill forest (750-1200m) (Wong Kochummen et al. 1985), and
Industrial Tree Plantation (ITP) planted with fast-growing *Acacia/Eucalyptus* species.

SPL is located on the central southern edge of Sabah, to the south west of MBCA and is made up of lowland and hill dipterocarp and montane forest. The study covered areas of natural forest management (NFM) and ITP managed by Sapulut Forest Development Sdn. Bhd. since 2003. All study sites in SPL were located in NFM areas.

**Data collection**

A total of 368 Reconyx Hyperfire HC500 and PC800 camera trap stations were deployed across the five forests for at least 90 days. This duration was previously found to be sufficient for obtaining robust estimated of population size of bantengs in Sabah (Gardner 2015). Two different categories of canopy extent which broadly represented leaf cover of the camera viewpoint (‘open’ when canopy leaf cover was less than 50% and ‘closed’ when canopy leaf cover exceeded 50%). Surveys were conducted at different times and cameras were distributed in a grid format and/or on an ad-hoc basis, with the disparity arising from two different studies of bantengs by Gardner (2015) and Gardner and Goossens (unpublished). Cameras operated for 24/7, with three consecutive photos taken at one-second intervals, with no time lapse. Grids of cameras were defined by access (on-foot, by boat or vehicle), with a minimum of 500m between stations and from unsealed roads to reduce disturbance. This distance was previously found to incur only low correlation, as bantengs were found to be low density and were not frequently captured at neighbouring cameras (Gardner 2015). Ad-hoc cameras were positioned in locations where banteng signs were encountered or, in their absence, alongside a wildlife trail, and set at a height between 1-1.5m high to coincide with the widest part of the body. Photographic capture events of bantengs confirmed their presence, and the performance and the time spent foraging was calculated from the time
of the first photograph when feeding began, until the time of the last photograph when
the feeding ceased or when the individual(s) moved out of the station viewpoint. Events
were classed as independent when 30 minutes or more had elapsed between the prior
and subsequent captures, and these events were stratified according to forest name,
canopy extent, elevation, ambient temperature and plant species richness.

The diet of bantengs was investigated in the first instance by inspecting all camera trap
photographs for the presence of bantengs that were foraging. The corresponding event
data from these images was extracted and used for modelling foraging behaviours (as
detailed below). The taxonomic identification of the plant forage was investigated to
species level by using botanical surveys which were conducted at camera trap stations
where bantengs were photographed foraging. Confirmation of plant forage from feeding
signs and/or bite marks was not factored into the vegetation surveys as they were
nonconcurrent to the camera trapping surveys. Surveys were conducted post-hoc using a
5 m line transect perpendicular to the station. Every visually-distinct plant, including all
obtainable parts (i.e. flower, stem etc) was photographed, labelled, sampled and stored
following the protocols in the literature (Mealor and Mealor 2010; Queensland
Herbarium 2010). Species that occurred at multiple stations were not collected; this
reduced unnecessary removal from forests that were regenerating. Specimens were
formally identified by a botanist at the Sepilok Forest Research Centre managed by the
Sabah Forestry Department. Distinction of plant species consumed by bantengs in front
of cameras from those plants that were arbitrarily collected at each site was conducted
by cross-comparison of specimens with camera trap photographs of foraging bantengs.
Plant species richness was calculated for every station where the botanical surveys were
conducted by using the Shannon-Wiener diversity index.
Statistical modelling

The species richness of each camera trap station was calculated using the Vegan package (Oksanen et al. 2012) in RGui version 3.2.3. Using the continuous data of plant species richness, elevation and ambient temperature, and the categorical data of site type (old logging road, open scrub and road verge), canopy extend (closed, open), and forest name (MFR, TWR, MBCA, SPL, SPT), we modelled the effects upon the foraging duration (minutes) of bantengs using a general linear model (GLM) with a Gamma error family and an identity link function in the lme4 package (Douglas et al. 2017). Model selection was conducted by dropping non-significant terms using the drop1 function, and model validation was conducted using graphical plots of the standardised residuals, Shapiro-Wilk test for normality, Fligner-Killeen test of homogeneity of variances and comparison of AIC weighting. Graphs were created using the ggplot2 library (Wickham and Chang 2016).

Results

Our stations were deployed in natural forest, ITP and scrub that ranged in elevation, from 0 to 1,379m above sea level with an average of ~250m. The numbers of camera trap stations established in each forest were as follows: TWR = 130, MFR = 148, MBCA = 27, SPT = 33, SPL = 30. During the surveys some camera traps suffered from electronic failure or theft which resulted in shorter operating periods, with a minimum of 10 days and a maximum of 373 days. Grids of cameras in TWR and MFR resulted in a higher survey effort, with the most camera trap nights obtained from MFR (14,760) and the least in SPL (2,578). A total of 40,168 camera trap nights were documented between April 2011 to May 2014 and during this time a total of 345 incidences of foraging were recorded at 37 out of 368 stations. Observations indicated that bantengs
foraged for periods lasting between 1-197 minutes, with an average duration of 17 minutes. With respect to botanical surveys, they were conducted at a later time to camera trap surveys and it was not possible to sample species richness at all sites where foraging occurred, owing to a number of factors resulting in inaccessibility but also regrowth of highly invasive plants. Investigations of the foraging duration data indicated a zero-bounded asymmetrical shape that benefited from a power transformation prior to modelling. Five models were fitted to the data to explain foraging duration; systematic removal of non-significant interactions and terms led to the exclusion of an interaction between elevation and temperature, and the exclusion of terms temperature and forest name. An initial null model was fit and subsequent models specified different combinations of terms and interactions. A GLM that specified the foraging duration explained by an interaction between plant diversity and canopy extent plus a main effect of elevation was the best fitting model (Table 1, model 4), with normally-distributed standardised residuals and explained the highest proportion of the variation (R²=22%) but had the fourth smallest AIC (Table 2, model 4). In general, foraging duration significantly declined as plant species richness increased (Z=0.07 ± 0.03, p= < 0.05, Table 1, model 4). More specifically, foraging duration significantly declined as plant species richness increased in open canopy areas (F=7.82, p= < 0.01, Table 2, model 4, Fig. 2). Foraging duration also increased as elevation increased (F=3.46, p=0.05, Table 2, model 4, Fig. 3), however no temperature effect was observed. A total of 48 plant specimens from 22 plant families were collected from 25 sites where bantengs were observed foraging. Plant species richness of the 25 sites can be found in Appendix 1. Eight species from 5 plant families were foraged by bantengs evident in camera trap photographs (Table 3 and Fig. 4). At the family level,
Cyperaceae and Asteraceae were the most prevalent, whilst at the species-level *Mikania cordata* was the most prevalent and was found in all five forests.

**Discussion**

We found evidence to support our hypothesis that bantengs spent a greater duration of time foraging in open degraded areas that have lower plant species richness; an overall negative trend was observed, whereby bantengs foraged for shorter periods as the plant species richness index increased in degraded open canopy areas. The foraging durations recorded within three logged forests in Sabah by Gardner et al. (Gardner et al. 2018) ranged between 2-174 minutes (95% CI = 0-217) and were not dissimilar to the durations observed by this study (1-197 minutes with an average of 17). Furthermore, as the present study investigated a larger number of forest reserves across a wider region and utilised a larger number of survey nights, our foraging durations are believed to accurately reflect their diet and foraging behaviours. Whilst not statistically significant, the opposite trend in foraging behaviour was observed for closed canopy areas, whereby bantengs showed a tendency to forage for longer when species richness was greater.

Depauperate plant species richness in open degraded banteng foraging sites contrasts the results from other studies that compared biodiversity in logged and unlogged forests in Borneo (Berry et al. 2010). This disparity may be due to seedling and sapling recruitment failure and differences in the length of the regeneration period between the forests studied (Sodhi et al. 2010), the bantengs’ preferential selection of sites naturally low in species richness, or even the locations where cameras were established (i.e. areas unobstructed by trees rich in diversity). Given the similar low diversity of forage detected in banteng faeces by Matsubayashi et al. (2007), the selection of camera sites may not be responsible for the differences in diversity between logged sites. Our results
also indicated that bantengs increased the time they spent foraging at higher elevations, which contrasts with findings by Chaiyarat et al. (2018), which identified 78% of presence records of Burmese bantengs in Thailand were found in habitat ranging between 101-200m, with no sites occurring above 401m high. Longer foraging at higher elevations in Sabah may be due to the widescale loss of forest habitat at lower elevations (for agriculture), to anthropogenic disturbances in lower elevations causing the species to take refuges in more secluded habitat at higher elevations, or to wider variation in the elevation of study sites. Food density is likely to be one of the other main driving forces for these behavioural tendencies; when large canopy openings are generated by logging there is a sudden increase in light at the forest floor, which facilitates an invasion of exotic plants (Duclos et al. 2013). The vast network of logging roads serve as pathways for the spread of these species (Döbert et al. 2017) but also as paths for bantengs because they are less inhibited by trees (Kuijper et al. 2009). Over time, forage almost certainly becomes scarcer because the regenerating canopy shades out understorey invasive pioneers, therefore the time invested in feeding under a closed canopy is probably reduced. Degraded open canopy areas supporter larger herds and the greater plant biomass means the herd can spend a longer period of time feeding, without having to move to search for new forage (Kuijper et al. 2009; Journeaux et al. 2018) but this is conditional on the proximity to the forest border (Journeaux et al. 2018) and on the provision of dense forest where they can seek shade, cool body temperatures, and evade human disturbances (Gardner et al., 2018). The greater biomass has propagated higher body condition scores (i.e. greater fat reserves) in bantengs inhabiting forest that was in the early stages of regeneration (Prosser et al. 2016). As a large-bodied mammal, Borneo bantengs require mature forest with a dense canopy where they are able to take refuge from the sun and to cool core body temperature (Gardner et al., 2018), but we did
not find any evidence to suggest that cooler ambient temperatures at higher elevations had an influence on foraging behaviours in this study.

In general, the foraging behaviours that we observed are not dissimilar to other banteng subspecies and ungulates; Burmese bantengs in Lao People’s Democratic Republic concentrated within dry dipterocarp forest that had extensive and dense ground of grassy forage (Steinmetz 2004), and Javan bantengs spent 50% of their grazing time in meadows colonised by grasses and legumes (Sumardja and Kartawinata 1977), which included one species \( D. \text{ trifolium } \) we found to be consumed by Borneo banteng. Similarly, the forest buffalo \( \text{Syncerus caffer nanus} \) in west Africa was more abundant in open grassy and sedge meadows which offered abundant quantities of favoured food (Blake 2002), and the moose \( \text{Alces alces} \) in Canada significantly increased usage of forest that was in the early stages of natural regeneration (10 years) and the post-harvesting and management influenced their forage availability (Boan et al. 2011). Likewise, the sympatric sambar deer \( \text{Cervus unicolor} \) also forage within open areas and along logging roads in Borneo (Meijaard and Sheil 2008).

The small number of plant species identified as banteng forage, relative to the large number of specimens collected at foraging sites, are common in occurrence within Sabah and highly adapted to exploit degraded soils. The two most prevalent species, \( M. \text{ cordata} \) and \( \text{Eleusine indica} \), are fast to establish on disturbed land (CABI 2013b; CABI 2014b). \( M. \text{ cordata} \) is a native fast-growing creeping vine that is easily spread by humans and the wind and can regenerate from broken stems (CABI 2013b). \( \text{E. indica} \) is a problematic weed in Malaysia and is an aggressive colonizer; it has the ability to grow in direct sunlight enabling it to establish in post-logging bare soil (CABI 2014b). \( \text{Chromolaena ordorata} \) was previously introduced to Sabah and is also a highly
competitive weed (CABI 2014a); a previous study found it to be highly abundant in
logged forest (Döbert et al. 2017). *Cyperus difformis* has a very short life cycle (~1
month) so is able to spread quickly once established and is able to exploit clay soils
(CABI 2013a) like those found in SPT. *Fimbristylis littoralis*, like *E. indica*, generates
large numbers of seeds, which can be transferred by humans, animals, water and wind,
allowing rapid colonisation of an area (CABI 2014b; CABI 2014c). Once established in
an area *F. littoralis* has the ability to change the dynamics of an ecosystem, benefitting
its own growth and disrupting other established species (CABI 2014c). This study
indicates the bantengs’ diet consists mainly of invasive plants and that they may
actually benefit from greater quantities of biomass after logging, however, it is possible
that bantengs also forage upon other less common plants not observed during this study,
and that they may not expend much time in exploiting less prevalent plants as they may
provide high nutritional or mineral value. As such, bantengs perform an important
ecosystem service by grazing heavily on invasive pioneer plants (Dobson et al. 2006),
which are not necessarily transient in the regrowth process and can alter the trajectory of
forest succession (Brown and Gurevitch 2004). Commonalities in diet species richness
compared to other studies were approximately comparable, with 11 species (three more
than the present study) detected by Matsubayashi et al. (2007) from faecal screening of
bantengs in one forest in Sabah. In terms of plant species diversity however, there were
marked contrasts in the number of graminoids detected, with Matsubayashi et al. (2007)
noting the presence of nine graminoids whereas we only detected one. In comparison to
other banteng subspecies, marked differences were evident in both forage species
richness and diversity; 23 plant species were foraged by Burmese bantengs (*B. j.
birmanicus*) in Thailand (Chaiyarat et al. 2018) but only one plant species, the flowering
shrub *C. odorata*, was foraged by both Bornean bantengs and Burmese bantengs.
Conclusion

Logging and forest regeneration in Sabah create environmental conditions that are favourable for exotic invasive plant species and influence the foraging behaviours and diet of bantengs. Consequently, bantengs play an important role as an ecosystem engineer in suppressing the growth of undesirable pioneers that are quick to colonize open areas where the canopy is damaged and may suppress the growth of economically-important emergent tree species. Bantengs may prosper from additional forage available in high volumes, but only when seclusion and/or security measures safeguards them against disturbance and poaching at a time when they are undertaking an essential activity in a more exposed location. Conservation of bantengs within commercial forests may be key to minimising the growth of invasive exotic plants that supress growth of valuable timber species, but forest management needs to ensure their survival by effecting anti-poaching strategies and ensure the availability of large and dense forest refuges where they may evade harvesting activities and encroachment. Such a harmonious approach to forest management may be more beneficial for the bantengs and for timber productivity in the longer term.

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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*, *Selaginell* 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