



Original Research Article

Using natural marks in a spatially explicit capture-recapture framework to estimate preliminary population density of cryptic endangered wild cattle in Borneo

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ABSTRACT

The behaviour of cryptic tropical forest ungulates that are not identifiable from unique coat colour and patterns often impedes detectability and investigations of population density, which underpin conservation plans. The shy and endangered Bornean banteng has a declining trend, but quantifying this requires sufficient detections to estimate robust population parameters, which are currently unavailable. Using intensive camera trapping and individual identification from natural marks by two observers, we estimated the baseline population density of Bornean bantengs in Malua and Tabin forests in Sabah (Malaysian Borneo) using a spatially explicit capture-recapture framework. We also investigated the efficacy of two commonly-used survey methods (camera trapping and signs) that have previously failed to detect the species, by contrasting capture frequencies to estimate the probability of odds of capture. Density estimates and simulated 95% confidence limits were exceptionally low in both forests and with negligible differences arising from small disparities in the interpretation of natural marks. Density in Malua ranged from 0.5 individuals per 100 km² (0.21–1.48) to 0.56 (0.15–2.09), and in Tabin between 0.61 (0.32–1.16) to 0.95 (0.54–1.66). The capture odds were significantly greater for camera traps ($X^2 = 20$, $p < 0.001$, and $OR = > 4$, $p < 0.001$); sign survey efficacy declined at higher elevations and under dense canopy. Using natural marks for individual identification was resource-demanding, but provided robust population density parameters for an otherwise challenging species to detect. Extremely low-density estimates of Bornean bantengs highlights the urgency for greater control of poaching, which is almost certainly decimating the population. Rapid implementation of actions to mitigate against further losses are essential for halting the declining trend. The estimation of density parameters in other forests in Sabah that contain bantengs would set the context for our density estimates. It would additionally provide a basis for long-term population monitoring, and facilitate investigations into the effectiveness of enforcement strategies.

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1. Introduction

The cryptic nature of many forest-dwelling mammalian species complicates their detection and the estimation of population parameters, and this makes it problematic to substantiate population declines and establish conservation priorities (Norris et al., 2011). In such circumstances, standardised field surveys of large mammals are notoriously difficult to carry out, and this is particularly so in moist tropical forests where most species are lower in abundance (Espartosa et al., 2011). The Bornean banteng (*Bos javanicus lowi* or *lowii*) is a large-bodied, elusive and endangered wild bovid that dwells in tropical forest in Borneo. They are the only type of wild cattle found in Borneo and are thought to have arrived on the island during the Last Glacial Maximum; a large cave painting of the banteng in Kalimantan (Indonesian Borneo) is thought to be the oldest Palaeolithic cave art in the world, dating back a minimum of 40 ka (Aubert et al., 2018). The species is widely considered to be in decline, with losses highlighted over three decades ago (Davies and Payne, 1982). Their decline is primarily attributed to widespread loss of habitat and conversion to agro-intensive tree plantations that cultivate oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*) and fast-growing timber species (*Acacia* spp.), and to poaching for bushmeat and trophies (Penny C Gardner et al., 2016). Quantifying losses to the population that were sustained by poaching is exceptionally difficult, owing to the secretive trade in wildlife products of highly prized endangered species. Evidence of banteng poaching is opportunistic and infrequently obtained through social media accounts and anonymous reports. Occasionally, evidence is located in the field in Borneo that indicates at the direct impacts of the spiralling poaching problem upon this species (Fig. 1).

Sightings of the Bornean banteng are extremely rare, and establishing reliable estimates of their abundance are challenging due to their preference for secluded forest and wariness of humans. The most commonly used monitoring method for ungulate species like the banteng is counting dung pellets but encounter rates, dung morphology and incorrect species assignment can be problematic (Pfeffer et al., 2018). Dung defecation rate and the rate of decay have also been found to influence the estimation of population density but in elephants (Hedges et al., 2013). Visual surveys of ungulates are sometimes rendered impractical by low densities, extreme wariness, dense vegetation and difficult terrain (Gopalswamy et al., 2012). Camera traps used in conjunction with capture-recapture techniques or random encounter models can provide reliable population estimates where individuals may or may not be identifiable by pelage, tags or natural marks (Rowcliffe et al., 2008; Oyster et al., 2018; Pfeffer et al., 2018). Past surveys of Bornean bantengs noted infrequent encounters of dung pellets (Olsen, 2003), and the same issue prevented density estimations by Boonratana (1997) and Hedges and Meijaard (1999). Recent camera trap surveys have enabled investigations of the effect of forest edges on their use of the habitat (Brodie et al., 2014) and their occurrence using community occupancy models (Cheyne et al., 2016; Sollmann et al., 2017). More intensive camera trapping efforts specifically focused on the banteng have enabled investigations into their foraging behaviours and diet (Gardner et al., 2019) and their distribution across the landscape of Sabah, Malaysian Borneo (Lim et al., 2019). Identification of individual bantengs using natural marks visible in camera trap images has been used to investigate their body condition (Prosser et al., 2016), herd demography and sexual segregation (Journeaux et al., 2018), and behaviours in response to forest degradation (Gardner et al., 2018). No density estimates for the Bornean banteng are available, however, the ability to elucidate individuals from their natural marks may fortify population estimates when modelled in a spatially explicit capture-recapture framework. Furthermore, as bantengs have the ability to range large distances where forest extent is continuous (Gardner et al., 2014), the optimum spacing of camera trap units for modelling population parameters is difficult to gauge. Currently, their home-range size is not known, and studies that are conducted over small spatial scales may be influenced by repeated sampling of the same individuals. Individual identification of bantengs may serve to increase the robustness of population parameters and inform the sampling design of future field surveys.

A lack of data on banteng density impede long-term monitoring and management (Boonratana, 1997). Accurate estimations of their abundance are essential for substantiating their declining trend, identifying areas across their range in need of effective management and measuring the success of conservation actions. In light of the difficulties associated with surveying Bornean bantengs and the requirement for robust population parameters for monitoring and management, we conducted an intensive non-invasive camera trap survey and identified individuals using natural marks. We applied a sightings-only model using a spatially explicit capture-recapture framework to estimate density parameters in two tropical forests in Sabah (Malaysian Borneo). We then compared camera trap surveys with dung pellet and track surveys using

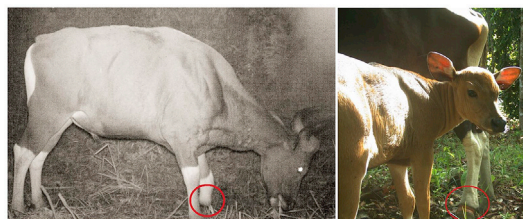


Fig. 1. The wild cattle of Borneo are targeted for bushmeat consumption and are often bycatch in snares, which result in potentially catastrophic injuries such as the loss of a limb. These images were documented using camera traps and are of two separate incidences of injuries sustained by Bornean bantengs in Sabah resulting from snares.

generalised estimating equations to fit a binomial generalised linear model to determine if the odds of capturing the species using these two methods differentiated substantially.

2. Materials and methods

2.1. Study areas

Camera trap and sign surveys for dung pellets and tracks were conducted in Tabin Wildlife Reserve and Malua Forest Reserve in Sabah (Fig. 2). Secondary lowland dipterocarp forest with areas of seasonal swamp and mangrove forest that are intersected by a vast network of abandoned logging roads were the prevailing conditions in both locations. Tabin (5° N, 118° E) is a large fragment of forest ($1,124$ km²) bounded by oil palm plantations with the exception of the north where nipah palm (*Nypa fruticans*) dominates in the riparian areas and is unsuitable habitat for bantengs. Tabin is connected to Sungai Kapur and Dagat Forest Reserves, and to Kulamba Forest Reserve along a narrow riparian corridor unsuitable for banteng dispersal. Until 1989, Tabin was extensively logged using conventional methods (Sabah Forestry Department, 2005); structural damage is still apparent in large expanses of scrubland across the reserve. The extraction of timber in Malua Forest Reserve (5° N, 117° E) ceased in 2007, but employed a combination of conventional, traditional (crawler tractor), and reduced impact logging (RIL) techniques including heli-logging in higher elevations and log-fisher logging (removal of logs via high cables). In 2013, an area of 339.96 km² was reclassified as a Class I Protection Forest and later certified with Forest Stewardship Council (FSC) certification. Consequently, it now comprises a mosaic of highly degraded and mature stands. Past forest fires have reduced biodiversity and inhibited natural regeneration (New Forests Ltd, 2008). Malua shares boundaries with other natural forest reserves: Kuamut, Ulu-Segama and Danum Valley forests, forming a large contiguous forest patch in central Sabah ($9,685$ km²).

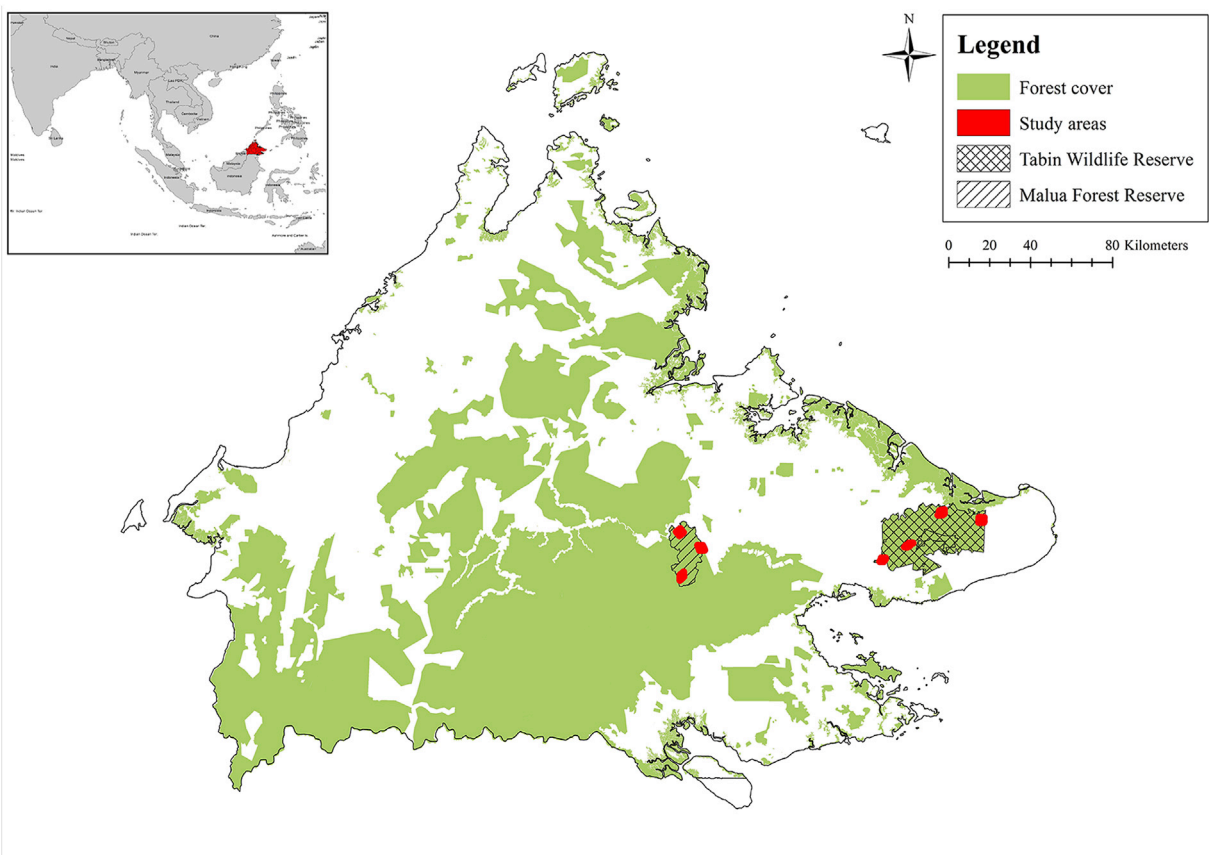


Fig. 2. The position of the Malaysian state of Sabah on the island of Borneo (inset) with the locations of the two study areas, the Protection Malua Forest Reserve and Tabin Wildlife Reserve, with the positions of the sampling stations within each grid where non-invasive sign surveys and camera trap surveys were conducted between the years 2011–2013. Maps were generated using ArcGIS® software version 10.1 by ESRI, with data from Natural Earth and the Sabah Forestry Department.

2.2. Field surveys

Camera traps utilised in this study were Reconyx HyperFire™ HC500 or PC800, housed in locked heavy-duty security cases and positioned at a banteng-specific height of 100–150 cm. Each station comprised a pair of cameras that flanked a banteng trail or a general wildlife trail, which occasionally coincided with an abandoned logging road. Camera traps were deployed in large grids to cover a wide variety of habitat niches and to increase the probability of capture of the target species (Trolle et al., 2008). Grid spacing was smaller than previous banteng studies utilising grids (e.g. Gray, 2018) as banteng density was suspected to be much lower. Grids differed in geographical representation and in size; Four grids were deployed in Tabin; two grids comprised 25 stations and two further grids comprised 36 stations owing to an increase in resources. Three grids were deployed in Malua and each comprised 36 stations. Cameras for each grid were deployment over a relatively short duration (1–4 weeks) and after this set-up period all cameras ran continuously (with no time-delay) for a 90-day period, with 30-day checks. Cameras were then removed and deployed in a different grid located more than 10 km away to reduce resampling of herds. Each station represented a symmetrical grid cell size of 0.25 km², and was located at least 500m away from the reserve boundary. We utilised a higher density of cameras within each grid compared to other studies (Tobler et al., 2009; Thomas N. E. Gray et al., 2012; Sollmann et al., 2017) in order to increase detection of this cryptic bovid that was previously an issue for past studies (Boonratana, 1997; S. Hedges and Meijaard, 1999; Olsen, 2003). At each station we examined an area of 5m radius for dung pellets and tracks. This was conducted every 30-days to coincide with camera checks and to avoid undue disturbance to the species. The vegetation type at each station was categorised broadly as one of two prevailing forest types, namely 'seasonal freshwater swamp forest' or 'lowland dipterocarp forest'. The percentage leaf cover above each station was estimated from photos (Samsung WP10 all-weather 12.2 MP x5.0 camera on minimum optical zoom) converted to monochrome images using the software HabitApp, version 1.1 (MacDonald, 2014).

2.3. Spatially explicit capture-recapture modelling

Camera trap photographs of bantengs were manually examined for visible natural marks such as scars and disparities in horn morphology and pelage (Fig. 3) by two independent observers. Recapture histories of identified bantengs were created by each observer for each of the two forests, and then standardised to a survey period of 84 nights due to camera malfunction. The survey duration was arbitrarily split into three 28-camera trap night sighting occasions. Individuals of uncertain identity were treated as unidentified and incorporated in a sighting attribute (T_m), which detailed the number of unidentified individuals captured at each trap for each 28-day sighting occasion. A conservative approach would have been to discard this information, however that would have resulted in a substantial loss of data that took considerable effort and resources to acquire and would prevent the estimation of detection parameters. Spatially Explicit Capture-Recapture models in the package secr 3.2.0 (Efford, 2019) of R version 3.2.3 (R Core Development Team, 2015) were used to estimate three population parameters of D (density), g_0 and σ (σ); the latter two real parameters jointly define detection probability as a function of location (Efford, 2019). As identification of individuals was based on natural marks and without a prior identification period or 'marking session', a sighting-only model with an unknown fraction of individuals marked was adopted (Efford, 2019). Rather than reaching a consensus on banteng identifications, the recapture histories created by each observer were analysed separately to gauge the magnitude of difference in parameter estimates resulting from identification heterogeneity. A single-session capthist object was created for each of the four forest/observer combinations (e.g. Malua/observer 1, Malua/observer 2, Tabin/observer 1, Tabin/observer 2) using a count detector type, and included the T_m attribute of unidentified individuals. In preparation for modelling, four clipped masks were created for each forest/observer combination that buffered around each camera trap station and clipped to the spatial coordinates of the nearest forest boundary; neighbouring forest reserves



Fig. 3. A mature Bornean banteng bull in Sabah with natural marks (circled) used for identification purposes and to create a recapture history for estimating population parameters.

that adjoined the study sites were included due to the contiguous forest coverage and the bantengs' ability to range across boundaries. The clipped mask for Tabin included Sungai Kapur and Dagat forest reserves, and for Malua it included Danum Valley Conservation Area, Kuamut and Ulu Segama forest reserves. The buffer distances for the clipped masks were estimated using the average spatial scale parameter σ calculated from three functions: 1) RPVS, 2) suggest buffer and 3) esa plot. The optimum mask grid cell spacing was identified by trialling a range of sizes from $0.05\text{--}2\sigma$ upon density using a parsimonious null model. Due to the relatively small dataset, we constructed three parsimonious likelihood-based sighting-only unknown-marks Poisson distribution models with a half normal detection function that were fitted once, and then refitted by maximising a pseudolikelihood and setting 1,000 simulations to adjust for overdispersion arising from the unidentified bantengs. The most parsimonious model specified the clipped mask and fixed the detection parameters g_0 and σ as constant. The parameter pID (proportion of individuals identified) was also fixed to be constant because our dataset did not contain a marking session prior to sightings. The second model retained the same structure but with the addition of a density surface covariate for the distance to the nearest forest boundary, which was created within `seccr`. The least parsimonious model was a hybrid mixture model that retained the clipped mask and constant detection parameters g_0 , σ and also pID , but included a class covariate with two factors (male and female) to estimate density for each gender class and to estimate the sex ratio parameter ($pmix$). Density estimates were converted to the number of individuals per 100 km^2 . Adjustment of overdispersion was estimated from the original and refitted models, and model fit was evaluated from the AICc weighting of refitted models.

2.4. Comparison of survey methods

We investigated the differences in the two survey methods, including the survey duration and environmental conditions, by using generalised estimating equations to fit a binomial generalised linear model (GEEGLM) in the package `geepack` (Højsgaard et al., 2006) using software R. This approach is appropriate for binomial datasets that are characterised by within-cluster correlation or longitudinal correlation (Vaughan et al., 2007). We constructed a binary dataset by specifying presence/absence of bantengs according to the camera trap station, the grid number and the forest of origin, and included leaf canopy cover, elevation, survey duration and habitat type as covariates. Potential autocorrelation arising from neighbouring stations was modelled using an exchangeable correlation structure, which assumed equal correlation among all sampling locations within each cluster (i.e. each grid) (Fieberg et al., 2010). Interaction terms were included between the survey method, survey duration and elevation. The final model was selected based on backwards deletion of non-significant terms and interactions, and an ANOVA of the Wald statistic was used to compute significance values of terms and interactions. GEEGLM estimates and standard errors for the explanatory variables were expressed as the ratio of the odds of capturing bantengs (OR) for ease of interpretation (Lipsitz et al., 1991; Vaughan et al., 2007).

3. Results

3.1. Population density

Camera traps functioned between 29 and 175 days depending on the location and ability to perform checks in secluded and sometimes flooded locations. A total of 23,424 trap nights were obtained. A convex polygon around camera locations estimated our study areas as 18.75 km^2 in Malua and 20.5 km^2 in Tabin. Twenty-nine photographic captures of bantengs were obtained from 230 camera trap locations during the standardised survey period, with a higher proportion originating from Tabin. In total, observer 1 identified 32 unique individuals; 16 males, 16 females, and observer 2 identified 29; 14 males, 15 females. None of the identified bantengs were recaptured in more than one grid indicating that our survey grid areas were geographically closed during the relatively short survey period of 84 days.

The trialling of σ values for clipped masks resulted in different optimum grid cell spacing that ranged between $0.1\text{--}0.3\sigma$ and buffer distances between 1427 and 2415m for each of the four datasets (Table 1). Models that specified a density surface covariate for the distance to the forest boundary and a gender detection covariate were too complex for the limited number of identified individuals that were recaptured. The most parsimonious model with no surface or detection covariates computed density parameters for all datasets. For the Malua datasets, refitting of the model with simulations resulted in 68% and 75% reductions in the overdispersion parameter (overdispersion = 1.0) for observer 1 and 2, respectively. The mean density for bantengs identified by observer 1 was $D = 0.55$ individuals per 100 km^2 (95% confidence limits: 0.21–1.48), with detection probability estimated at $g_0 = 0.08$ (0.04–0.16) and a spatial scale movement parameter of $\sigma = 758\text{ m}$ (565–1016 m).

Table 1

The clipped mask specifications developed for each forest and observer combination, which were used to compute density parameters in Spatially explicit Capture-Recapture models.

Forest	Identifier	No. of mask cells	Cell spacing	Cell spacing (m)	Buffer
Malua Forest Reserve	Observer 1	3150	0.3σ	201.35	2414.54
	Observer 2	2008	0.1σ	270.30	2702.95
Tabin Wildlife Reserve	Observer 1	3161	0.1σ	191.80	1918.03
	Observer 2	1427	0.1σ	142.68	1426.78

For observer 2, estimates were almost comparable but confidence limits were marginally wider owing to more unidentified individuals: Mean density was $D = 0.56$ individuals per 100 km^2 (95% confidence limits: 0.15–2.09), detection probability was $g_0 = 0.05$ (0.01–0.15), and the spatial scale movement parameter was $\sigma = 671 \text{ m}$ (454–992 m). For Tabin, simulations reduced overdispersion by 78% for both observers (overdispersion = 1.0), and mean density was estimated at $D = 0.95$ individuals per 100 km^2 (95% confidence limits: 0.54–1.66), detection probability at $g_0 = 0.20$ (0.12–0.32) and spatial scale movement at $\sigma = 562 \text{ m}$ (422–749 m) for observer 1. The density parameters of Tabin bantengs that were identified by observer 2 were $D = 0.61$ (95% confidence limits: 0.32–1.16), detection probability $g_0 = 0.18$ (0.10–0.31) and movement $\sigma = 542 \text{ m}$ (366–864 m).

3.2. Probability odds of capturing bantengs using two common survey methods

Out of the total 230 survey locations, 39 were located in seasonal freshwater swamp and 192 in lowland dipterocarp forest. The elevation of the stations ranged between 0 and 405m above sea level, and the leaf canopy cover above the stations varied between 25 and 99%. Two grids failed to capture bantengs on camera trap and no fresh signs in these locations were observed during our surveys. Conversely, only six observations of banteng signs were recorded across the 230 stations; no fresh dung pellets were encountered. Significantly more presence records were obtained using camera traps than using sign surveys ($\chi^2 = 20$, $p < 0.001$, Table 2 and $OR = > 4$, $p < 0.001$, Table 3). Survey duration and habitat type did not significantly influence the two sampling methods, however elevation did ($\chi^2 = 5$, $p < 0.05$); tracks were recorded less frequently as elevation increased ($OR = 0.98$, $p < 0.05$). There was also a marginal effect of leaf canopy cover upon the survey method, with fewer tracks detected when leaf cover was denser ($OR = 0.96$, $p = 0.07$). Within-cluster correlation between the stations was low ($r^2 = 32\%$), indicating that bantengs were not recorded consecutively at neighbouring points in the grid, and the close proximity (500m) between the stations did not cause undue bias.

Whilst not a focus of this study, we obtained substantial evidence of armed and unarmed poachers, snares and castoff shotgun shells within the two reserves, although no direct observations of carcasses were ever made and no prosecutions were brought about during the time of this study.

During our surveys we did not observe any signs of banteng remains stemming from poaching activity, however, it is worth noting that we did observe signs of encroachment and illegal resource use within and around the study areas. These included harvesting of gaharu/sandalwood and timber, snaring using ropes and string, fishing, a discarded homemade crossbow, shotgun cartridge shells and direct and indirect encounters of armed hunters. It remains unknown if any banteng deaths resulted from these activities. Reports of banteng deaths in other forest reserves, that stemmed from hunting using firearms, were received during the timing of this survey; the carcasses of two mature bulls were extracted from the central forest in Sabah using motorboat during the hours of darkness, and then transported to a village by using an off-road vehicle.

4. Discussion

Our intensive camera trapping effort provided sufficient photographic captures of multiple individuals with natural marks that were suitable for identification, and facilitated the first modelling of density parameters for this subspecies. These natural marks induced a small amount of variability by the two observers, but translated to negligible differences in estimates, equating to 0.01 and 0.34 individuals per 100 km^2 in Malua and Tabin, respectively. The exceptionally low-density estimates in both locations is of grave concern. Tabin supports a marginally higher density of bantengs; it has been in a recovering state

Table 2

Analysis of variance (ANOVA) of the means for the final GEEGLM model terms and interactions (), with the chi-squared test statistic (χ^2), degrees of freedom (d.f.), significance value (ANOVA P value) and significance of the relationship ranging from marginal to highly significant: .-0.05, * < 0.05 = lower threshold, ** < 0.01, *** < 0.001 = highly significant, N/A = no significance.

Model No.	Model description	Terms	χ^2	d.f.	ANOVA P value	Significance
1	Banteng ~ Method + GridR	Method	20	1	<0.001	***
2	Banteng ~ Method * Survey duration + GridR	Method	20	1	<0.001	***
		Survey duration	1	1	N/A	N/A
		Method:Survey	0	1	N/A	N/A
3	Banteng ~ Method * Canopy + Method * Elevation + Method * Habitat + GridR	Method	20	1	<0.001	***
		Canopy	12	1	<0.001	***
		Elevation	5	1	0.05	*
		Habitat	1	1	N/A	N/A
		Method:Canopy	1	1	N/A	N/A
		Method:Elevation	5	1	0.05	*
		Method:Habitat	0	1	N/A	N/A
4	Banteng ~ Method * Canopy + Method * Elevation + GridR	Method	20	1	<0.001	***
		Canopy	12	1	<0.001	***
		Elevation	5	1	<0.05	*
		Method:Canopy	2	1	N/A	N/A
		Method:Elevation	5	1	<0.05	*

Table 3

Description of GEEGLM model estimates transformed to the probability of Odds of Ratios to determine the differences in survey methods and the effect of environmental factors. An interaction () between covariates, with lower and upper standard and the significance of the relationship (p value) denoted by: N/A = no significance, . = 0.05 (marginal), * = <0.05, ** = <0.01, *** = <0.001 highly significant.

Model No.	Model description	Term	OR Estimate	OR lower std err	OR upper std err	P value	Correlation ± SE (%)
1	Banteng ~ Method + GridR	MethodSign	0.16	0.11	0.24	***	35 ± 0.39
2	Banteng ~ Method * Survey + GridR	MethodSign	0.02	0.00	0.33	N/A	36 ± 12
		Survey	1.08	1.05	1.11	**	
		MethodSign:Survey	1.02	0.99	1.04	N/A	
3	Banteng ~ Method * Canopy + Method * Elevation + Method * Habitat + GridR	MethodSign	16.83	5.12	55.28	N/A	31 ± 0.85
		Canopy	0.95	0.93	0.97	*	
		Elevation	0.99	0.98	1.00	N/A	
		HabitatSeasonal	0.49	0.25	0.97	N/A	
		Swamp					
		MethodSign:Canopy	0.96	0.94	0.98	.	
		MethodSign:elevation	0.98	0.98	0.99	*	
		MethodSign:Habitat	0.58	0.19	1.74	N/A	
		Swamp					
4	Banteng ~ Method * Canopy + Method * Elevation + GridR	MethodSign	9.96	1.65	60.12	N/A	32 ± 0.60
		Canopy	0.95	0.94	0.97	*	
		Elevation	0.99	0.99	1.00	N/A	
		MethodSign:Canopy	0.96	0.94	0.98	.	
		MethodSign:Elevation	0.99	0.98	0.99	*	

for three decades, and therefore probably offers greater refuge from human-driven disturbances occurring along the forest-plantation boundary and a large expanse of natural forest to evade poachers. Due to this relatively lengthy regeneration period and the abandonment of logging roads following the cessation of harvesting activity, vegetation closure has occurred over the majority of vehicular access points into the forest, and this offers indirect protection to large mammals targeted for consumption or resource use. Density estimates and the probability of detecting individuals in Malua was lower. This may be due, in part, to recent habitat disturbance from timber harvesting and frequent vehicle activity along the access roads that traverse the forest, which may cause displacement into adjacent forest. The distances moved by bantengs in Malua were marginally greater and, whilst these bantengs have the ability to roam across a larger contiguous patch of forest, our trapping area was small relative to the potential distances bantengs are able to traverse over longer periods of time (10–23 km in Gardner et al., 2014). Qualifying home ranging sizes by enlarging the trap spacings would be a valuable addition to our understanding of their ecology, providing a sufficient number of identifiable bantengs are recaptured to facilitate modelling using the spatially explicit capture-recapture framework.

As these are the first published density estimates for the Bornean banteng, it is not yet known if these are representative of the population across Sabah or the whole island of Borneo, but given that bantengs are more prevalent in Sabah, the density in Kalimantan (Indonesian Borneo) is unlikely to be greater. In contrast to other banteng subspecies, we found the density of Bornean bantengs to be exceptionally low (0.5–0.95 per 100 km²), particularly compared to estimates of Burmese banteng (*B. j. birmanicus*) in Cambodia (0.9 ± 0.1 km²) by Gray et al. (2012) and Thailand (1.8 ± 0.5 km²: combined with *B. gaurus*) by Srikosamataru (1993), which are considerably greater. The low density of Bornean bantengs may be a natural occurrence, governed by limited forage availability in dense forest. However, in light of their apparent declining population over the past three decades (Davies and Payne, 1982; Boonratana, 1997; Olsen, 2003) their low-density status in these two forests is almost certainly a consequence of widespread habitat loss and fragmentation, coupled with past off-take by hunters, which probably accelerated when forest was first opened up for timber extraction (Sodhi et al., 2004). Today, interval timber harvesting facilitates rapid access to locations containing rare biodiversity due to the well-managed road infrastructure; the success of poachers using vehicles to hunt and extract carcasses for bushmeat and trophies are often testified in local newspapers (Sario, 2015a, 2015b, 2016). The frequent losses of individuals in a low-density ungulate species that has slow recruitment and a long parental investment can comprise their ability to recover, even if the poaching is controlled (Steinmetz et al., 2010).

Exceptionally low encounter rates of Bornean banteng signs were noted by two previous studies (Boonratana, 1997; S. Hedges and Meijaard, 1999). Given the low-density of Bornean bantengs and the detection difficulties observed during this study, sign surveys offer little yield relative to the amount of resources required, and are not advocated for future surveys aiming to locate and quantify the population. This method almost certainly has less precision in Sabah owing to the topographical and wet climatic conditions that will erode signs, however it probably affords better precision in other countries, as they typical inhabit dry dipterocarp forest at low elevations in Cambodia (Phan and Gray, 2010) and open savannah in Java (Indonesia) (Pudiyatmoko, 2017).

5. Conservation and management

There is an urgent need to halt further losses of Bornean banteng individuals and control the poaching for bushmeat and opportunistic illegal resource use in Sabah, as it threatens to cause the extinction of this wild bovid. An intervention of this

nature needs to be collaborative with concession holders and state government, and conducted in such a way that it leads to conservation of the species, sustainable management of timber or tree products in forests that are managed on a commercial scale, and inclusion of the local community. Due consideration of the material needs of the local community is also fundamental; extreme poverty can drive the need to construct makeshift firearms and source bushmeat, whilst the more affluent source tactical equipment for a weekend of sport hunting. Further loss of banteng habitat, irrespective of granted concessions or planned revision of forest boundaries, should also be avoided; preserving large forested patches with connectivity is essential for sustaining large herds and maintaining their social behaviours (Journeaux et al., 2018), and for providing them with refuge from disturbances caused by timber harvesting and encroachment (Gardner et al., 2018).

Our study has provided key information on the banteng's population ecology that is long overdue, however, modelling baseline density estimates for other locations outlined by Lim et al. (2019) is vital future work, and would be complimentary to enforcement strategies. This information would provide a current quantitative description of the population that is currently lacking. With repetition, density estimates would facilitate a comprehensive investigation into the effectiveness of such enforcement strategies and provide insight into the changes that occur to the population following timber harvesting. They may also provide estimates of vital rates such as survival and recruitment, which are of fundamental importance to the understanding of population ecology. Camera trap data that has been collected by concession holders and other researchers may provide a foundation for modelling densities in some well-studied locations, but the bias in the sampling design and the methods used may give rise to inconsistency or imprecise estimates of abundance. Recently, a large-scale and long-term dataset on Bornean bantengs was used to investigate their habitat and potential connectivity across the Sabah landscape (Lim et al., 2019). This camera trap data encompassed 14 reserves of varying protection classes and management histories, and holds considerable potential for estimating population parameters at the landscape scale and investigating the effects of forest management upon survival. Commercially-managed natural forests that are in the early stages of recovery probably support higher densities of bantengs in the short term. Bantengs are adept at exploiting pioneer vegetation within degraded forests (Gardner et al., 2019), and have been found to have a higher body condition in forest that is harvested using reduced impact logging methods (Prosser et al., 2016). It is conceivable that the temporary abundance of pioneer forage across degraded areas in the forest actually aids banteng survival and recruitment. Using natural marks to estimate density parameters and locate the reserves where density is highest may provide clues as to the forest management techniques that most complement the conservation of wild cattle.

Declarations of interest

None.

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