Herd demography, sexual segregation and the effects of forest management on Bornean banteng *Bos javanicus lowi* in Sabah, Malaysian Borneo

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ABSTRACT: Between 1973 and 2010, 39.5% of Sabah's (Malaysian Borneo) natural forest cover was lost to deforestation and conversion to agriculture, thus the remaining population of endangered Bornean banteng (*Bos javanicus lowi*) is being driven towards extinction. The Bornean banteng's herd demography, sexual segregation and the effects of forest management were investigated at 393 camera locations in six forest reserves using generalized estimating equations (GEEs) fitted via generalized linear models (GLMs). A total of 43,344 camera trap nights and 832 independent banteng events were captured at 93 locations. The identification of 183 bantengs included 22 herds (>1 individual) and 12 solitary bulls, with a herd size range of 2-21. Significantly larger herds were observed in forest with <8 years of post-logging regeneration (PLR), whereas herds were smaller in forest with <3, 4 and 16 years of PLR. Within these forests, herds were significantly larger along logging roads than in open sites and on forest trails. Herds were significantly larger in upland compared to lowland dipterocarp forest, however were significantly smaller when closer to the forest border. Bachelor herds being observed as frequently as mixed sex herds, and a significantly higher capture frequency of female herds in the dry season, supported the theory of sexual segregation. Frequency of calf births was highest in March and September, and significantly more calf captures occurred in June and July. This study contributes to a better understanding of banteng ecology and will assist in the effective management to provide suitable habitat for re-population and their longevity.

KEY WORDS: Endangered species, *Bos javanicus lowi,* Forest management, Demography, Sexual segregation, Camera trapping

INTRODUCTION

Tropical forests are the richest terrestrial ecosystem on Earth (Gentry 1992) and contain many of the world’s ‘biodiversity hotspots’ (Myers et al. 2000), yet are experiencing the greatest forest loss of all forest domains, with loss increasing by 210,100 ha/year (Hansen et al. 2013). Between 1990 and 2010, tropical forest cover was reduced from 1635 million ha to 1514 million ha, with 32.9 million ha lost in Southeast Asia (Achard et al. 2014). Overexploitation and agricultural activities are the primary threats to species worldwide (Maxwell et al. 2016). Crop, livestock and tree plantations are the major direct causes of tropical deforestation. Logging, mining and petroleum development also contribute directly to tropical deforestation, however, they additionally promote deforestation indirectly by increasing the accessibility to otherwise remote areas and facilitating poaching (Butler & Laurance 2008). Sparsely populated areas are being cleared rapidly, for example, the Amazon for large-scale cattle ranching and industrial soy farming, and Southeast Asia including Borneo, Sumatra, and New Guinea for oil palm and rubber plantations (Sodhi & Ehrlich 2010). Of the three major tropical regions, Southeast Asian forests are experiencing the highest rates of forest loss (Sodhi et al. 2004), therefore requires urgent conservation attention.

Forest cover in Borneo is being lost at approximately twice the rate of other tropical forests in the world (Gaveau et al. 2014). Between 1973 and 2010, 39.5% of forest in Sabah, Malaysian Borneo, was lost to selective logging, fire and conversion to oil palm and timber plantations (Gaveau et al. 2014). Of this forest loss, 97% occurred in habitat suitable for the Bornean banteng (*Bos javanicus lowi*) (Gaveau et al. 2014; Gardner et al. 2016), likely to be the rarest mammal in Sabah now that the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) has been declared extinct in the wild in Malaysia (Havmøller et al. 2015).

Banteng (*Bos javanicus*) is a sexually dimorphic wild cattle species and is categorised as ‘Endangered’ by the IUCN Red List of Threatened Species (Gardner et al. 2016). The most recent global population estimate of banteng is 8,000 (Gardner et al. 2016). Three subspecies of banteng are recognised: Java banteng (*B. j. javanicus*) found in Java and Bali, Burma banteng (*B. j. birmanicus*) existing on the Asian mainland, and finally the Bornean banteng (*B. j. lowi*) present in Borneo (Hassanin & Ropiquet 2007), in Sabah, Kalimantan and possibly Sarawak (Gardner et al. 2014). The first survey of the Bornean banteng carried out in Sabah in the early 1980s estimated the population at 300-550 individuals (Davies & Payne 1982), however this probably declined to <300 in the late 1990s (Boonratana 1997). Precise present-day Bornean banteng population and subpopulation sizes are unknown, although there is possibly one subpopulation of more than 50 individuals, the agreed minimum viable population size, present in Sabah (Gardner et al. 2016). The reduction and fragmentation of habitat and conversion to agriculture, poaching and increased risk of disease transmission from domesticated cattle, are severely threatening the Bornean banteng, with many of the remaining subpopulations confined to protected areas (Gardner et al. 2016).

Banteng form cohesive social groupings (Srikosamatara 1993), which are important aspects of their social behaviour and environment. Herd sizes of large herbivores are primarily functions of foraging strategy and anti-predator behaviour (Kie 1999), and explain, for example, increases in herd sizes in open habitat with reduced canopy cover (Gerard & Loisel 1995; Kie 1999). Additionally, herd size and dynamics, including herd formation and division, can determine the habitat selection of large herbivores, as observed by bison (*Bison bison*) (Fortin et al. 2009). This is supported by larger herds of banteng being observed in open forest (Gray 2012) and grasslands (Pudyatmoko & Djuwantoko 2006) in comparison to smaller herds observed in dense forest with continuous canopy cover, in Cambodia and Java, respectively. Herd sizes may vary in response to frequent human disturbance causing weak bonds in herds, instigating less permanent herd sizes (Pudyatmoko & Djuwantoko 2006). Herd sizes may also differ between seasons (Pudyatmoko & Djuwantoko 2006), as banteng herds often aggregate around water holes in the dry season when rainfall is limited (Nguyen 2009).

Herd sex (i.e. gender composition) provides information on ecological factors including the expression of sexual segregation, which is commonly exhibited by sexually dimorphic ungulates outside the mating season (Ruckstuhl 2007). Banteng bachelor herds of mixed ages, and banteng cow and calf groups are known to occur frequently, with mixed temporary assemblages occurring during the mating season or in large open areas (Gardner et al. 2016). Sexual segregation is more likely to occur during the birth period because the behavioural differences between males and females become more pronounced (Bon & Campan 1996; Ruckstuhl 2007); females become more asocial, timid (Copland 1974) and more dependent on water and rich food sources as a result of the additional demands of gestation and lactation (Bon & Campan 1996). No rut or calving season has been observed for *B. j. lowi* (Gardner et al. 2014), however exploring the expression of sexual segregation may allow rut or calving seasons to be observed. Research into understanding the sexual segregation of ungulates has been conducted, however the causes are still poorly understood (Ruckstuhl 2007), but could include ecological, physiological, social or foraging factors (Main et al. 1996).

Meijaard and Sheil (2008) state species with wider ecological niches, particularly herbivores, are more tolerant towards logging and may even benefit from post-logging conditions. *B. j. javanicus* occupy secondary forest formations resulting from logging and fires, however this has not been observed in *B. j. birmanicus* (Gardner et al. 2016). *B. j. lowi* thrive on the temporary abundance of pioneer species present in the early stages of post-logging regeneration when not hunted, however evidence of bark stripping by *B. j. lowi* suggests a lack of grassland forage, hunting pressure or heavy disturbance (Gardner 2015). Timber harvesting that creates open spaces may be beneficial in providing sufficient space for larger banteng herds, however energy-demanding behaviour is reduced in open areas during hot hours (Gardner 2015). Increased anthropogenic disturbance may cause herds to separate and also increase stress levels, which is likely to impact banteng breeding activity and behaviour (Gardner et al. 2014). Furthermore, *B. j. lowi* have reduced body conditions in conventionally logged forests compared to reduced-impact logging (RIL) forests (Prosser et al. 2016).

Collaborations between scientists, managers and conservationists to produce science-based wildlife management strategies is increasing and has been identified as a requirement for the effective management and conservation of ungulates (Apollonio et al. 2017). Understanding the mechanisms that influence the demography of increasingly small and isolated ungulate populations is of a conservation priority, and is essential to prevent future extinctions (Tatin et al. 2009). Bornean banteng are important ecosystem engineers, however are severely threatened and are being driven towards extinction (Gardner et al. 2016). The aims of this study were to investigate the herd demography of the Bornean banteng, specifically the herd size, sex and composition, and to explore the expression of sexual segregation in regenerating forest in Sabah. Understanding banteng herd demography will provide baseline data on their behaviour and ecology, including their vigilance (Roberts 1996), predation-risk, population density, and on habitat structure (Marino & Baldi 2014). This enhanced scientific understanding of their demography will enable the desired management and conservation of the Bornean banteng and the complex system they are incorporated within. Informative baseline data will indicate changes in the population and environment, thus will facilitate future management. As timber harvesting creates open spaces and facilitates increased growth of pioneer species that provide temporary resources, it was hypothesised that banteng herds were larger in forest with less than eight years post-logging regeneration, and that banteng herds were larger in open sites than on forest trails and logging roads. It was also hypothesised that bantengs express sexual segregation and more banteng calves were born in the dry season than in the wet season.

MATERIALS AND METHODS

Study sites

Six forest reserves in Sabah (Malaysian Borneo) were surveyed using remote infrared camera traps: Tabin Wildlife Reserve, Malua Forest Reserve, Maliau Basin Conservation Area Buffer Zones, Sipitang Forest Reserve, Sapulut Forest Reserve and Kuamut Forest Reserve (Fig. 1). (1) Tabin Wildlife Reserve (TWR; 5°14' N, 118°42' E, East Sabah) has been a totally protected area (1106 km^2) since 1989, comprising small areas of virgin jungle, surrounded by secondary forest, which consists of lowland (<500m), upland (500-1000m) and seasonal freshwater swamp dipterocarp forest, together with mangrove forest and nipah palm forest in riparian areas (Sabah Forestry Department 2005). TWR was last logged conventionally in 1989 (Sabah Forestry Department 2005), 22 years prior to this study. (2) Malua Forest Reserve (MFR; 5° 7' N, 117°39' E, central Sabah) became a Class 1 Protection forest reserve (340 km^2) in 2011 (Reynolds et al. 2011) that comprises lowland, upland and seasonal freshwater swamp dipterocarp forest. It was last logged using conventional and RIL techniques in 2007 (New Forests Ltd 2008), four years prior to the study. (3) Maliau Basin Conservation Area Buffer Zones (MBCABZ; 4°47' N, 116°53' E, South central Sabah) became a Class 1 Protection forest reserve in 1997 (Sabah Forestry Department 2005) and consists of lowland, upland and seasonal freshwater swamp dipterocarp forest, as well as scrub (0-4m) (Sabah Forestry Department 2005) and riparian fringes. The buffer zones (357 km^2) used in this study were last logged using RIL in 1997 (Sabah Forestry Department

2015), 16 years prior to the study. (4) Sipitang Forest Reserve (SPTFR; 4°45' N, 115°43' E, West Sabah) is a commercial forest (2589 km^2) that contains lowland and upland dipterocarp forest, lower montane forest (1000-2500m) (Sabah Forestry Department 2005), riparian forests and scrub which is, however, logged and severely degraded. SPTFR comprises unlogged and clear-felled areas that are converted to tree plantation. Clear-felling of commercial timbers in Sipitang is conducted at seven-year intervals. The area of Sipitang that was used in this study was most recently logged between 2010-2014 (Sabah Forest Industries 2011), three years or less to surveys. (5) Sapulut Forest Reserve (SPLFR; 4°22' N, 116°34' E, South central Sabah) is a commercial forest (2419 km^2) consisting of lowland and upland dipterocarp forest, as well as montane forest. Conventionally logged until 2003, it is currently being logged using RIL techniques or managed as plantation for timber. The years since logging in the forest compartment are between 2005-2014 (Sabah Forestry Department staff, pers. obs.). (6) Kuamut Forest Reserve (KMTFR; 5° 4' N, 117°26' E, central Sabah), is a commercial forest (1152 km^2) that contains lowland dipterocarp forest. The logging coupe permit was issued in 2006 for conventional logging in the forest compartments used in this study (R. Ong, pers. comm. 2017). Therefore, logging occurred eight years or less prior to this study. The number of years since logging activity in each forest reserve, prior to this study, determined the age of post-logging regeneration (PLR) for each forest reserve. PLR, therefore, represents the duration forest reserves have had to regenerate with no logging activity.

Camera trapping

Behavioural data on the Bornean banteng was collected using non-invasive remote, passive infrared camera traps: Reconyx HC500, Reconyx PC800 and Reconyx PC850 (Reconyx Inc., WI, USA). Camera trap data originated from two different studies using 1) a grid layout and cameras positioned on an ad-hoc basis where banteng signs (tracks and dung) were located in TWR and MFR (Gardner 2015) and 2) a state-wide survey for banteng across Sabah whereby camera traps were deployed where signs of banteng were located (Gardner & Goossens unpublished). See Table 1 for the camera trapping method used in each forest reserve location. A camera trap station consisted of two Reconyx Professional Hyperfire cameras fixed to opposing trees, approximately 1-1.5m high above the ground, to maximise the chances of capturing bantengs and identifying individuals. A minimum distance of 0.5km was maintained between camera trap stations to maximise the chance of photographing banteng in the area. Camera traps detected heat and movement triggering three consecutive photographic captures at one-second intervals, with no time delay between activations. All camera trap photographs were digitally stamped with the event date, time and temperature. Camera traps operated for a minimum survey period of 90 days, and checked every 28 days to ensure functionality. Camera trapping effort, which refers to the survey duration (sum of all 24-hour operational camera trap nights), was calculated from the date the camera trap was set to the date it was retrieved for all forests. If the camera was no longer functioning, the date of the last event was used. The habitat vegetation (lowland dipterocarp, upland dipterocarp, seasonal freshwater swamp, scrub, lower montane forest and industrial tree plantation) and elevation were recorded at each camera trap station. Percentage leaf cover was extracted from photographs of the canopy, taken directly above each station using a Samsung WP10 waterproof all-weather 12.2MP x5.0 digital zoom compact camera on minimum optical zoom. Percentage leaf cover was estimated from monochrome photographs using the software Leaf Cover Calculator version 1.0 (Macdonald & Macdonald 2016). Each camera trap location was categorised into forest trail, open site or logging road, and the presence of salt licks was recorded. The distance (in metres) between each camera trap station, nearest village and forest border was extracted post-hoc using ArcGIS (version 10.1, ESRI, Redlands, USA, 2012) from Lim et al. (unpublished). Incidences of poaching, which included armed and unarmed people, shotgun cartridges, snares, carcasses, lone dogs, gaharu/sandalwood harvesters and poachers' camps, and camera trap stations stolen (two camera traps per station) was obtained from Gardner et al. (unpublished).

Herd demography

Bantengs captured on camera trap within each forest reserve were defined as subpopulations, including forests that were adjacent (MFR and KMTFR), therefore six subpopulations and their respective herd sizes were studied. Individuals were identified using a series of natural marks, including scars on the body, ear tears, horn shape and size, and natural coat colourations (Gardner & Goossens unpublished). Recognition and recaptures of solitary individuals and herds (>1 individual) by morphology and scars were recorded in each forest reserve. Herd size was estimated from the number of banteng photographed. Male and female morphological characteristics were used to calculate adult sex percentages for each event (Gardner et al. 2014). Bantengs were categorised into three broad age classes based on clear differences in body size: adult (male or female), juvenile (up to 50% smaller than adult cow) and calf (more than 50% smaller than adult cow). This classification has been applied to a banteng population in Baluran National Park, Indonesia, using direct observation (Pudyatmoko & Djuwantoko 2006). Calf births were estimated from the first date of appearance on camera and from their approximate body size. Herd composition was categorised according to eight categories: 1) male herd, 2) female herd, 3) mixed herd, 4) mixed herd including calf(s), 5) female(s) and calf(s), 6) solitary male, 7) solitary female and 8) unknown, due to low light levels or photos obscured by vegetation. Juveniles could not be reliably sexed so were disregarded when categorising the herd composition. All captures were classified according to one of two seasons: 1) wet season, which was defined as between October-March, and 2) the dry season, which was defined as between April-September for all forest reserves, due to the reduced impacts of drought and El Nino-Southern Oscillation events (Walsh 1996). Daily rainfall data (mm) collected in Danum Valley, East Sabah, provided by the South-East Asia Rainforest Research Partnership (SEARRP), was applied to all forest reserves.

Data preparation

The data set comprised discrete explanatory variables (number of bulls, cows, juveniles and calves, herd size and poaching and stolen camera trap station incidences), categorical explanatory variables (study design, herd composition, years of PLR, camera trap site, salt lick presence, season and habitat vegetation) and continuous explanatory variables (percentage encounter rates of herd compositions, temperature, rainfall, elevation, canopy cover and the distances of each camera trap station to the nearest village and forest border).

Yasuda (2004) studied medium to large sized mammals using camera traps and defined successive photographs as independent when separated by at least 30 minutes, and Phan and Gray (2010) 20 minutes for *Bos javanicus birmanicus*. Preliminary observations showed an intermission length of 90 minutes between camera trap captures accommodated a range of herd behaviours: travelling, foraging and resting. Therefore, longitudinal independence was defined by discounting any banteng individual or herd captured within 90 minutes of the previous event, unless the individual or herd was identified as different. It was assumed that the banteng's choice to join others was not constrained by availability of other banteng.

Statistical analysis

All statistical analyses were conducted using the statistical software package R (version 2.15.2, R Development Core Team 2012). As a result of the clustered, longitudinal and repeated measures data and the individual observations not being statistically independent, generalized estimating equations (GEEs) were fitted using a generalized linear model (GLM) following the protocol of Vaughan et al. (2007), using the error distribution ‘Poisson’ and Library ‘geepack’. This allowed the analysis of hierarchical and correlated data, and spatial autocorrelation to be accounted for (Højsgaard et al. 2006). GEEGLM models were used to test for differences in herd sizes between study design (grid or adhoc), forest reserve regeneration age, season, camera trap site, salt lick presence, herd sex, temperature, rainfall, habitat vegetation, elevation, canopy cover, distance to the nearest village and forest border, and poaching and stolen camera trap station incidences (Table 2). Backwards stepwise deletion was used to produce the final, most robust GEEGLM model including significant (and one marginally non-significant) explanatory terms. Pearson residuals were used to validate model output. The GEEGLM results were transformed into Odds ratios (OR), a measure of association between an environment and an outcome (Szumilas 2010), by taking the exponential. OR compared the relative odds of an outcome of interest occurring in a particular environment: OR=1; environment does not affect odds of outcome, OR>1; environment related with higher odds of outcome and OR<1; environment related with lower odds of outcome (Szumilas 2010).

One-Way Analysis of Variance (ANOVA) and Tukey Post-hoc tests were used to investigate the expression of sexual segregation by testing for differences in capture frequencies and the effect of season upon each herd sex in all forest reserves collectively. A Poisson GLM was used to test for significant differences in the number of calves born between the seasons due to the approximately equal variance to the mean and the acceptable degree of overdispersion. A Poisson generalised additive model (GAM) with a cyclic cubic spline was used to test for significant differences in the number of calves born between the months as this model accounted for the temporal autocorrelation (Table 2).

RESULTS

Survey effort

During the study period (April 2011–April 2015), a total of 832 independent events of banteng were captured from 93 camera traps over 43,344 camera trap nights in six forest reserves (Table 3). Over 2,400 camera trap nights were discounted because of electronic failure and camera trap theft. A total of 30 banteng events were discounted because they were captured within 90 minutes of the previous event and violated our assumption of independence.

Herd demography

A total of 183 bantengs were identified, including 22 herds and 12 solitary bulls, with more bulls identified than cows (Table 3). The size of banteng encounters (the sighting of banteng herds or solitary individuals) in each photographic capture varied with forest reserve, and ranged from solitary individuals to herd sizes of up to 21. KMTFR had the largest encounter range of 1-21 individuals, whereas SPTFR had the smallest encounter range of 1-8 (Fig. 2). The herd composition most encountered was solitary bulls in TWR (51.4%), SPTFR (37.1%) and SPLFR (47.2%), mixed herds in MFR (48.1%) and KMTFR (30.5%), and mixed herds and solitary bulls in MBCABZ (34.0%) (Table 4). In TWR, MBCABZ, SPLFR and KMTFR, banteng encounters mainly comprised bulls, SPTFR cows, and MFR had an almost even mean adult percentage. Intra-herd comparisons revealed TWR had the highest number of bulls (69%) within herds and SPTFR the highest number of cows (52%) within herds. In all forest reserves collectively, banteng encounters comprised more bulls (58% ± 1.3) than cows (42% ± 1.3) (Fig. 3).

Banteng herd sizes

We found that forest regeneration age (ANOVA: $X^2 = 34.2$, $p < 0.001$), type of site within the forest reserve (ANOVA: $X^2 = 7.07$, $p < 0.05$), presence of salt licks (ANOVA: $X^2 = 10.2$, $p < 0.01$), habitat vegetation (ANOVA: $X^2 = 30.7$, $p < 0.001$), and the distance to the nearest forest border (ANOVA: $X^2 = 17.1$, $p < 0.001$) had significant effects upon banteng herd sizes (Table 5). Season (ANOVA: $X^2 = 3.08$, $p = 0.079$) had a marginally non-significant effect upon banteng herd size. Explanatory terms that had no significant effect upon banteng herd sizes were removed by backwards stepwise deletion in order of the most insignificant (Table 5). The final model, which included significant explanatory terms, and one marginally non-significant, had normally distributed and homogenous residuals, and was deemed robust (Model 1, Table 6).

A GEEGLM of herd sizes within each forest explained by post-logging regeneration age indicated significant negative relationships, whereby herd sizes were smaller in forest with <3 years PLR (SPTFR: OR = 0.31, SE ±1.30, $p < 0.001$), 4 years of PLR (MFR: OR = 0.68, SE ±1.09, $p < 0.001$) and 16 years of PLR (MBCABZ: OR = 0.65, SE ±1.12, $p < 0.001$) when compared to <8 years of PLR (KMTFR: OR = 2.01, SE ±1.19), the intercept (model 1, Table 6). Although herd sizes in forest with 22 years of PLR (TWR: OR = 0.83, SE ±1.15, $p = 0.1752$) were smaller than forest with <8 years of PLR (model 1, Table 6), they did not significantly differ.

Inter-forest comparisons of herd sizes and forest sites revealed that herds on logging roads were significantly larger (OR = 1.30, SE ±1.10, $p < 0.01$, model 1, Table 6) than herds in open sites, whilst herd sizes on forest trails (OR = 1.17, SE ±1.10, $p = 0.1055$) were not significantly different (model 1, Table 6). Herd sizes at sites with salt licks present were significantly larger (OR: 1.73, SE ±1.19, $p < 0.01$) than herds at sites with no salt licks present (model 1, Table 6).

The habitat vegetation had a significant effect on herd size, whereby herd sizes were larger in upland dipterocarp (OR = 2.56, SE ±1.34, $p < 0.01$) habitats when compared to lowland dipterocarp (OR = 2.01, SE ±1.19), the intercept (model 1, Table 6). Distance to the forest border had a significantly negative effect on banteng herd size, with herd sizes being significantly smaller closer to the forest border (OR = 1.00, SE ±1.00, $p < 0.001$, Fig. 4).

Sexual segregation

We observed a significant effect of banteng sex on capture frequencies when all captures from all forests were pooled (One-Way ANOVA: $F_{2,17} = 6.20$, $p < 0.05$, model 2, Table 7). We found that female herds occurred significantly less than male herds (Tukey Post-hoc test: $p < 0.05$) and mixed sex herds (Tukey Post-hoc test: $p < 0.05$). There was no significant difference between capture frequencies of male herds and mixed sex herds (Tukey Post-hoc test: $p = 0.983$). Male and mixed sex herds contributed to 40.9% and 42.3% of the camera trap events respectively, whilst females contributed only 16.8% of the events.

Survey durations were longer in TWR, MFR and MBCABZ and encompassed both wet and dry seasons, therefore only data from these forests was used to explore the effect of season on sex. Season had a significant effect on the capture frequency of female herds (One-Way ANOVA: $F_{1,5} = 19.89$, $p < 0.05$, model 3, Table 7), with more captures obtained in the dry season (72%) compared to the wet season (28%), however the seasonal effect was only marginal for male and mixed sex herds (models 4 and 5, Table 7).

We found a significant effect of sex upon herd size ($X^2 = 447$, $p < 0.001$, model 1, Table 5). A GEEGLM revealed that female herds (OR = 2.01, SE ±1.19) were significantly larger than male herds (OR = 0.54, SE ±1.12, $p < 0.001$), however were significantly smaller than mixed herds (OR = 2.35, SE ±1.09, $p < 0.001$, model 1, Table 6).

Calf births

A Poisson GLM revealed that the number of calves born during the survey period did not significantly differ between the dry and wet season (Poisson GLM: LRT = 2.28, $p = 0.1308$, model 6). However, a Poisson GAM with a cyclic cubic spline revealed a significant difference between the number of calves born between the months (Poisson GAM: Z = -20.33, $p < 0.01$, model 7). According to the month of first capture of each identified calf, births were most frequent in March and September (Fig. 5), with significantly more calf captures occurring in June and July (Fig. 6).

DISCUSSION

A total of 183 bantengs were identified in six forest reserves, including 25 calves, and herd size ranged up to 21 individuals. Forest regeneration age, type of site, presence of salt licks, sex, habitat vegetation and distance to the nearest forest border all had significant effects on banteng herd size. A significant effect of banteng sex was found on capture frequencies. The frequency of calf births was highest in March and September, and significantly more calf captures occurred in June and July.

Herd demography

A total of 183 bantengs identified in our six forest reserves is strong evidence of the Bornean banteng’s current vulnerability. The banteng encounter range of 1-21 individuals differs from 5-40 banteng estimated from villagers’ perceptions in Sabah in 1982 (Davies & Payne 1982). At the time of the survey in 1982, the estimation of 40 bantengs was thought to be an underestimate (Davies & Payne 1982), suggesting a decline in herd size over time. The forest reserves containing the highest number of identified banteng had larger herd size range and average, therefore, a declining population likely causes smaller herd sizes, as observed in a population of *B. j. birmanicus* in Vietnam (Nguyen 2009). Low population densities and restrictions to home range are causing reductions, and subsequently extinctions, in banteng populations (Pedrono et al. 2009). This is likely occurring to the Bornean banteng. Movement identified between MFR and KMTFR, which supported the largest herds, suggests that substantial and continuous forest patches are important and required for larger herds to form. Consequently, habitat reduction and fragmentation threatens the banteng population and reduces herd sizes.

SPTFR had a small number of bulls identified (10 individuals) but the highest number of bulls consistently travelling alone (six individuals). KMTFR had the highest number of bulls identified (21 individuals), and was the only forest reserve to have a bachelor herd and to contain no solitary bulls. Here, the bachelor herd was dynamic in composition, with individuals regularly leaving and new bulls joining. The reduced number of males in SPTFR is possibly affecting bull behaviour and resulting in solitary lifestyles. Moreover, the number of herds repeatedly observed in SPTFR was high, therefore the choice or chance of interacting with a herd was higher than many of the other forest reserves. Despite this, bulls in SPTFR remained solitary. KMTFR had fewer herds but they were larger, and this may have made locating and acceptance into the herd more likely.

The bachelor herd in KMTFR was observed in 26 different combinations involving 15 mature bulls, which suggest they are very tolerant and highly social, however the maximum herd size encountered comprised of only seven individuals. Additionally, due to the evidence of illegal activity encountered when surveying KMTFR, hunting and human disturbance may have caused males to form bachelor herds in order to increase vigilance and therefore survival, a behaviour that has been observed by other threatened ungulates (Averbeck et al. 2009). This dynamic bachelor herd may be an easier target for hunters, therefore considering the evidence of illegal activity encountered during this survey, is a major concern.

Banteng herd sizes

This study revealed that banteng herd size was significantly affected by the years of PLR. Forest in the onset stages of regeneration had the smallest herd size range, suggesting that regular use of heavy machinery and human disturbance may have weakened the bonds of association between individuals within herds. This may have resulted in smaller herds that are less permanent and prone to splitting more frequently (Pudyatmoko & Djuwantoko 2006). Logging increases the abundance of pioneer species (Imai et al. 2012), including grasses, vines and shrubs favourable to banteng (Ridge unpublished), and regenerating vegetation benefits banteng body condition and breeding (Gardner et al. 2014; Prosser et al. 2016), which is likely to have influenced the larger herds observed in forest with <8 years of PLR. Reduced disturbance from heavy machinery in the years following logging activity may have helped herds re-form and allowed herds to aggregate more frequently. With MFR and KMTFR being adjacent and banteng movement between these forest reserves identified, is evidence that banteng individuals have had access to two forests and therefore a larger range of PLR. This would have provided increased optimal conditions to allow larger herds to form. Forest with 22 years of PLR would have increased closed areas that reduce ambient temperatures and thermal stress (Gardner et al. unpublished), and reduce conflict between dominant individuals and vulnerability to poaching. This likely contributed to the larger banteng herds observed in forest with 22 years of PLR. Although, the overall effects of deforestation, heavy machinery and human presence may have raised banteng stress levels to negatively affect breeding, and possibly increased mortality (Gardner et al. 2014).

Herd sizes not significantly differing between open sites and dense forest contrasts with *B. j. javanicus* in Baluran National Park (Pudyatmoko & Djuwantoko 2006). Gerard and Loisel (1995) states that large herbivores, including roe deer (*Capreolus capreolus*) and Alaskan moose (*Alces alces*), generally have larger herds in open habitats with less canopy cover, when there is minimal disturbance. Our results, therefore, suggest that Bornean banteng are not analogous to the majority of large herbivores or even to other banteng subspecies. Bornean banteng have been observed to forage in open grasslands and socialise in open spaces (Gardner et al. 2014), however disturbance is likely altering this behaviour and reducing herd size. Larger banteng herd sizes in upland compared to lowland dipterocarp forest suggests banteng are being forced to higher habitats for space and forage, likely a result of habitat destruction, fragmentation and human disturbance.

Larger herds on logging roads than in open sites suggest they provide sufficient space for larger aggregations and the opportunity to travel as a larger unit. Furthermore, bantengs forage along internal abandoned logging roads due to the increased regeneration of pioneer species over time would support this result (Gardner 2015). Moreover, logging roads provide easy access to the previously cultivated areas that provide secondary growth which banteng benefit from (Pedrono et al. 2009). Thus, more individuals will be attracted to the available forage causing larger herds to be vulnerable to human conflict on logging roads.

Larger herds were observed in sites with salt licks than when no salt licks were present. This result suggests that banteng may well be deficient in sodium and need this additional source, which is supported by a small-scaled diet-supplementation survey in Sabah that captured banteng at sites with mineral blocks and loose salt (Phillips unpublished), together with Davies and Payne (1982) and Matsubayashi et al. (2007) who state banteng require and frequently visit salt licks. It may be advantageous to implement salt licks for monitoring herds; however, it may make them more vulnerable to poaching.

Smaller herd sizes occurring closer to the forest border shows they are influenced by human disturbance in the vicinity and that forest reserves must be substantial enough for banteng to express their natural demography. In contrast to the findings of Nguyen (2009), season marginally did not have a significant influence on banteng herd size. This may imply that enough water sources were available in the study sites for the banteng to not aggregate or the conditions in the wet and dry seasons were not distinct enough to have an effect.

Although the incidences of poaching and stolen camera trap stations did not have a significant difference on banteng herd size, Gardner et al. (unpublished) identified illegal activity in all forest reserves, which is likely affecting their stress levels and therefore possibly breeding, together with increasing their vulnerability.

Sexual segregation

Bachelor herds were observed as frequently as mixed sex herds, therefore bulls segregated from cows, thus showing that sexual segregation is a required behaviour and that this study provides evidence to support this theory. Although one or several of the proposed factors (ecological, physiological, social or foraging) may cause males to segregate, they may not affect females as strongly or at all, due to female herds occurring significantly less than bachelor herds. In addition, it is possible that females forced bulls to leave mixed sex herds, either due to differences in the previously stated factors, or because of birthing. Female herds being significantly larger than male herds implies that females remain in herds however males are possibly forced out. This is possible as Bornean cows and calves have been observed to assert authority, and younger bulls do force older bulls from herds in Java and Burma (Gardner et al. 2014).

Female herds were captured significantly more during the dry compared to the wet seasons, indicating that a possible calving period is more likely to occur during the dry season. Female ungulates are more likely to segregate from males during the birth period because of behavioural and nutritional differences, and more specifically to locate suitable birthing places and to give birth (Bon and Campan 1996; Ruckstuhl 2007). Evidence of a female banteng actively segregating itself in preparation for the birthing period was observed (S1). In contrast, no significant difference in the capture of male herds between seasons suggests that males do not experience the same pressures as females for niche habitat or nutritional requirements, and that they do not have a need to segregate from females during gestation.

Calf births

No evidence was found to suggest that births were elevated in either the wet or the dry season, which indicates that females experience gestation through both seasons. It is possible that both seasons provided optimal environmental conditions for breeding and therefore season was not a constraining factor, or because of the season classification. More calves born in March and September and significantly higher calf captures in June and July suggests a possible calving season. More calf captures in the months following March was due to calves taking approximately 2.5-3 months to be categorised as juvenile. This increase in calf capture would be expected after September, however two calves born in September in TWR were born at the end of camera trapping in this forest. Increased calf births in March and captures through to June is supported by the calving season of *B. j. javanicus* between April-June in Baluran National Park (Pudyatmoko & Djuwantoko 2006). The very presence of calves indicates the potential for a population expansion, however this area of Bornean banteng ecology requires further research.

Methodology limitations

Camera traps are a useful tool for wildlife behavioural studies, and are increasingly being used to improve species conservation (Caravaggi et al. 2017). It is, however, important to acknowledge their limitations. Dark photographs and vegetation obstruction made banteng identification impossible for some encounters. Camera trap placement has major influences on group size estimates. This study's camera trap height and location were specifically chosen to capture banteng. It was acknowledged that trails and logging roads had dense vegetation surrounding camera trap stations making banteng more likely to travel between the two cameras in order to remain within the herd. It is, however, important to state that bantengs are not inhibited by thick thorny vegetation, and can penetrate dense vegetation either side of trails and logging roads. When undisturbed, banteng show tendencies to follow their own trails, which was factored into the camera trap sensor area when positioning cameras. Open sites had far less vegetation to obstruct view, and when temperature decreased in open sites the range of the camera sensor had a tendency to extend. Despite the limitations of camera trapping, this survey method has been identified as superior when compared to the use of signs for detecting banteng (Gardner 2015). Camera trapping has provided conservation-relevant behavioural data of the Bornean banteng, and will act as baseline for future ecological studies aiming to assess the Bornean banteng demography.

Conclusion

This study has supplemented the limited knowledge and understanding of Bornean banteng ecology. The identification of the Bornean banteng subpopulations and their respective herd sizes in Sabah has provided evidence of their vulnerability. This study presents baseline data of the Bornean banteng which can assist in producing appropriate management procedures that will work towards their conservation. Future land management must acknowledge the extent of habitat reduction and fragmentation, and thus ensure substantial and continuous forest patches, to allow large banteng herds to form, particularly away from forest borders, and to reduce their disturbance and stress levels. Forest management should consider the stages of PLR and habitat vegetation in each forest reserve, ensuring the availability of <8 and 22+ years of PLR, and suitable lowland and upland dipterocarp forest respectively, to maximise herd sizes. Bantengs have adapted to habitat modifications by utilising logging roads, therefore forest management should include restricted human access and constant monitoring. Bachelor herds being observed as frequently as mixed sex herds, and a significantly higher capture frequency of female herds in the dry season, showed a strong indication of sexual segregation. Future research to understand banteng sexual segregation should be conducted to enhance understanding of banteng ecology and behaviour. The number of calves born did not significantly differ between seasons; however, frequency was highest in March and September, and significantly more calf captures occurred in June and July, thus forest disturbance should be minimal during these months. The current banteng demography should be compared to the results of future research and monitoring in these six forest reserves, to enhance understanding and to stimulate any necessary protection measures. Incidences of illegal activity, including poaching, occurred in all forest reserves, therefore anti-poaching patrols should be conducted. This enhanced scientific understanding of Bornean banteng demography can facilitate in science-based wildlife and forest management strategies to allow banteng re-population and their long-term existence.

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Figures and Tables

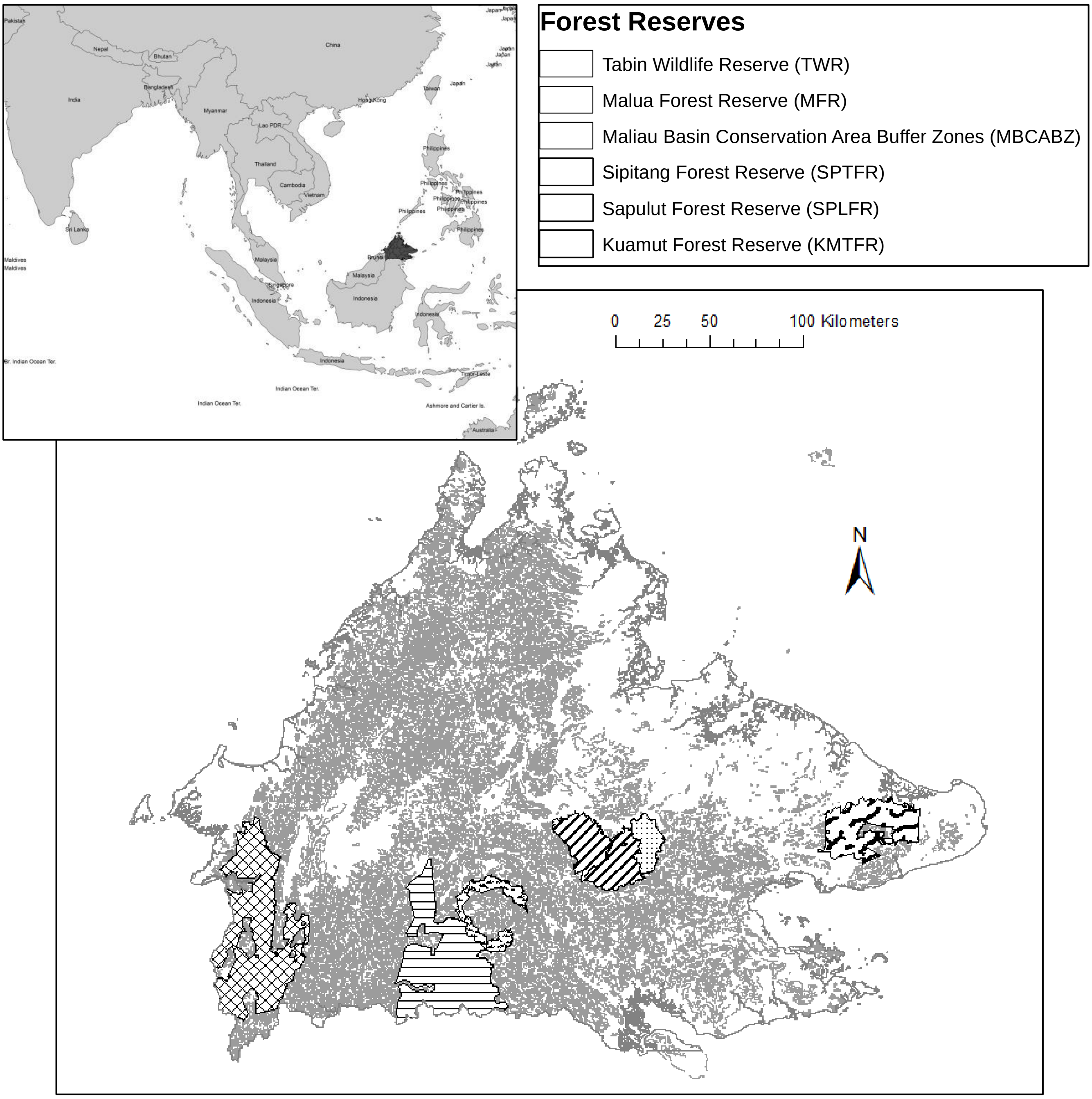

Fig. 1. The location of Sabah, Malaysian Borneo (inset), and a map showing the six study sites in Sabah. In central Sabah are Kuamut Forest Reserve and Malua Forest Reserve, South central are Maliau Basin Conservation Area Buffer Zones and Sapulut Forest Reserve, West is Sipitang and East is Tabin Wildlife Reserve.

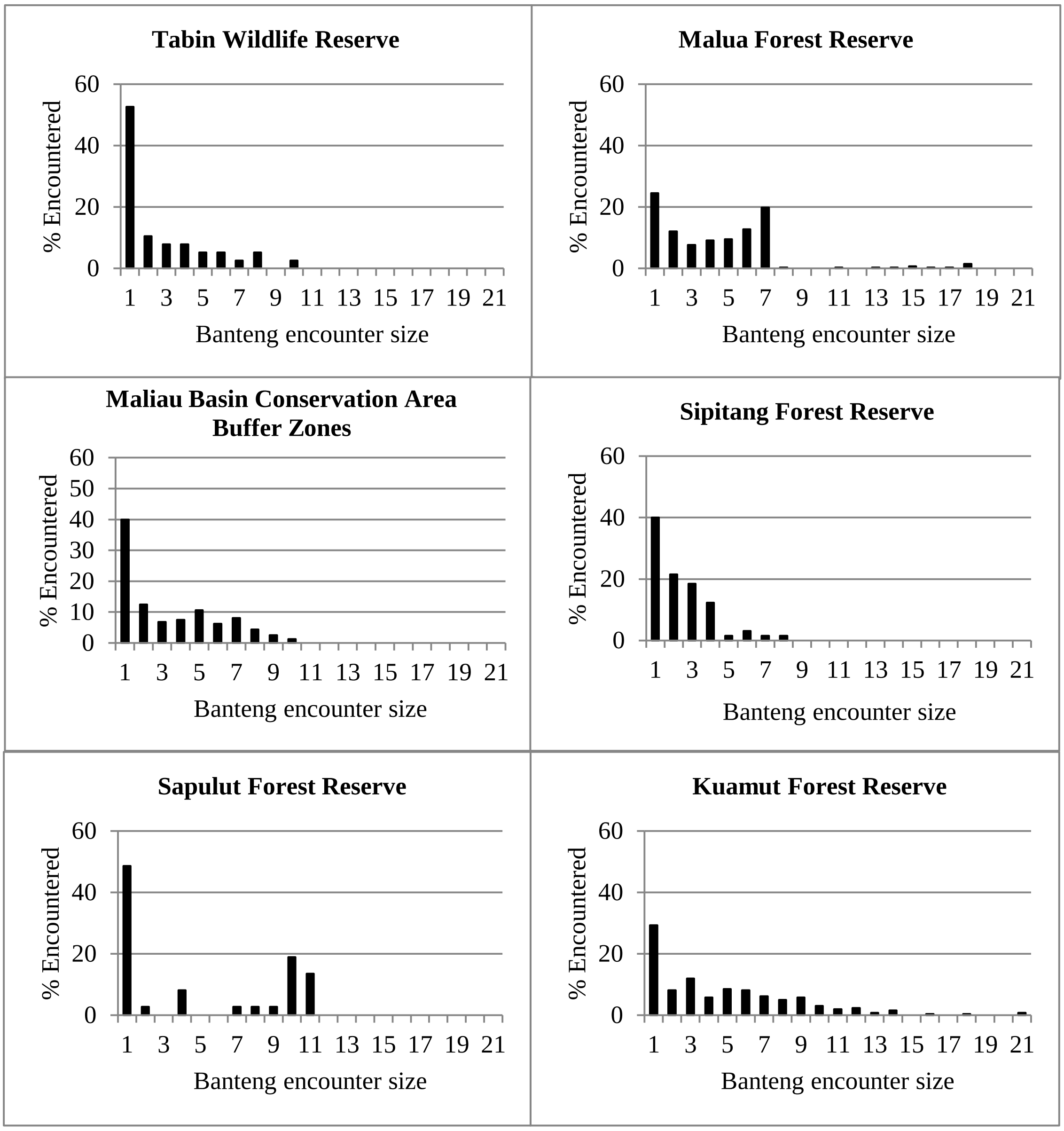

Fig. 2. Banteng encounters expressed as a percentage of all events captured by camera traps within each forest reserve.

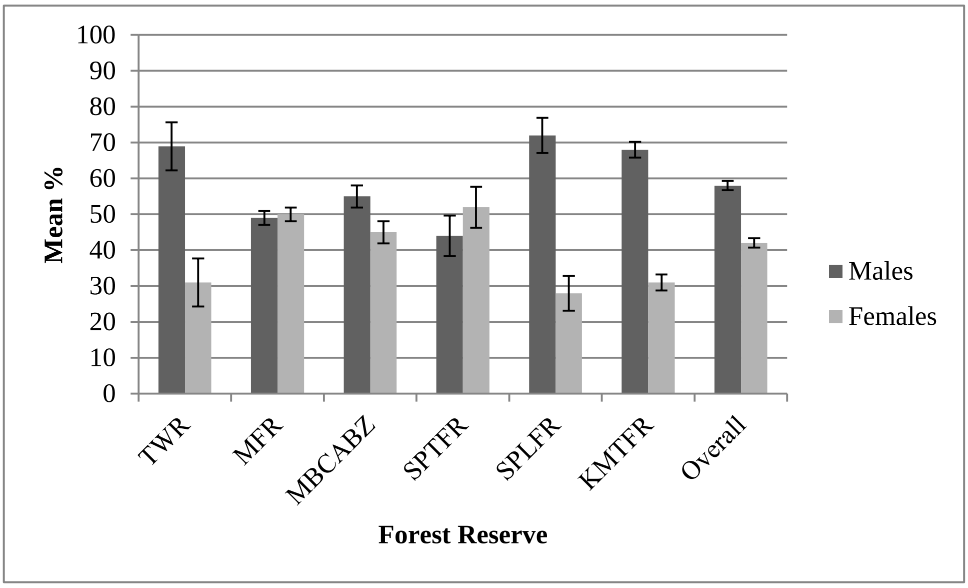

Fig. 3. Mean percentage of males and females in banteng encounters in each forest reserve. TWR: Tabin Wildlife Reserve, MFR: Malua Forest Reserve, MBCABZ: Maliau Basin Conservation Area Buffer Zones, SPTFR: Sipitang Forest Reserve, SPLFR: Sapulut Forest Reserve, and KMTFR: Kuamut Forest Reserve. Standard error of the mean included.

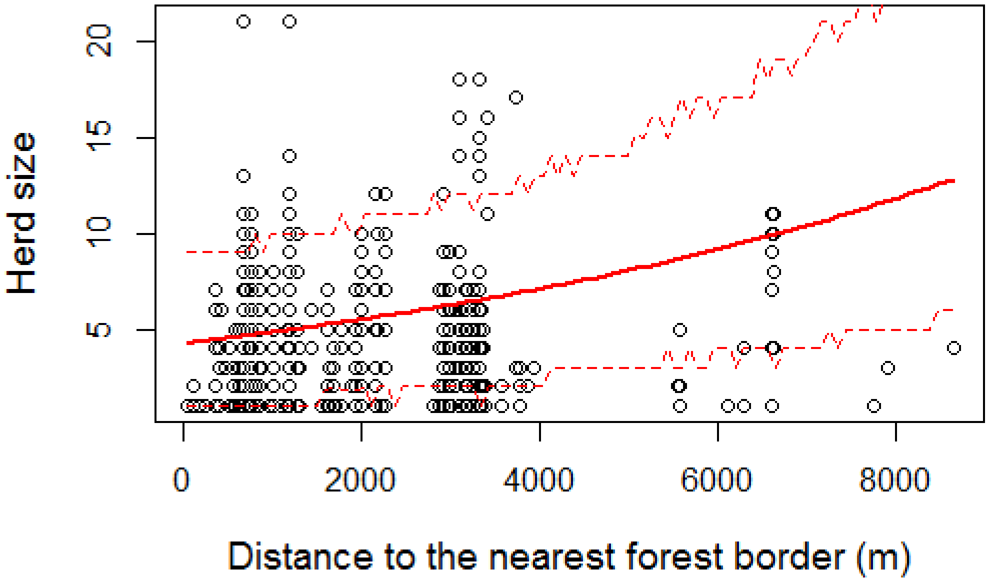

Fig. 4. Prediction plot of herd sizes at varying distances to the nearest forest border (in metres). Dashed lines represent prediction intervals.

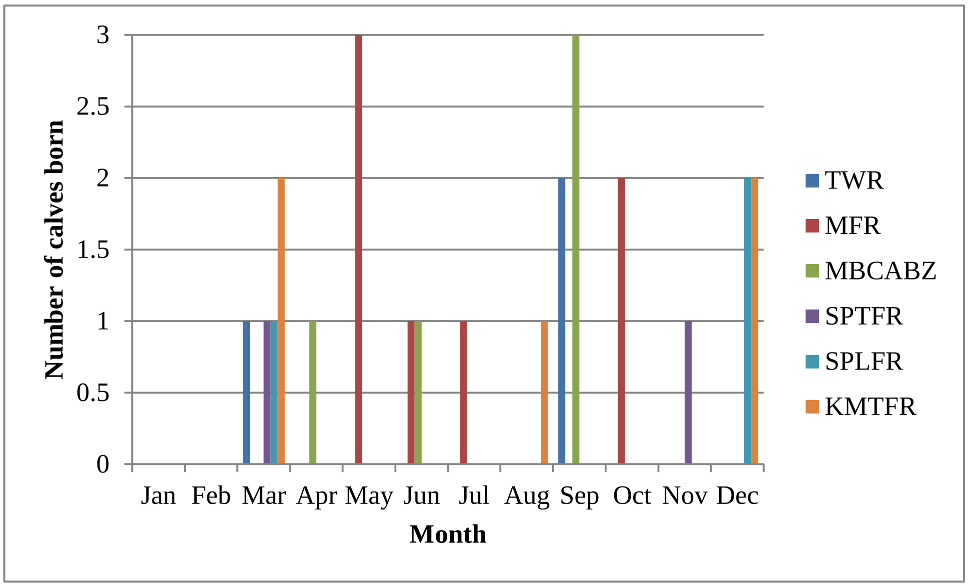

Fig. 5. Frequency of calves born over the survey period in each forest reserve (month & years – month & years) according to the month of the first capture of each identified calf and cow and calf approximate body size. TWR: Tabin Wildlife Reserve, MFR: Malua Forest Reserve, MBCABZ: Maliau Basin Conservation Area Buffer Zones, SPTFR: Sipitang Forest Reserve, SPLFR: Sapulut Forest Reserve and KMTFR: Kuamut Forest Reserve.

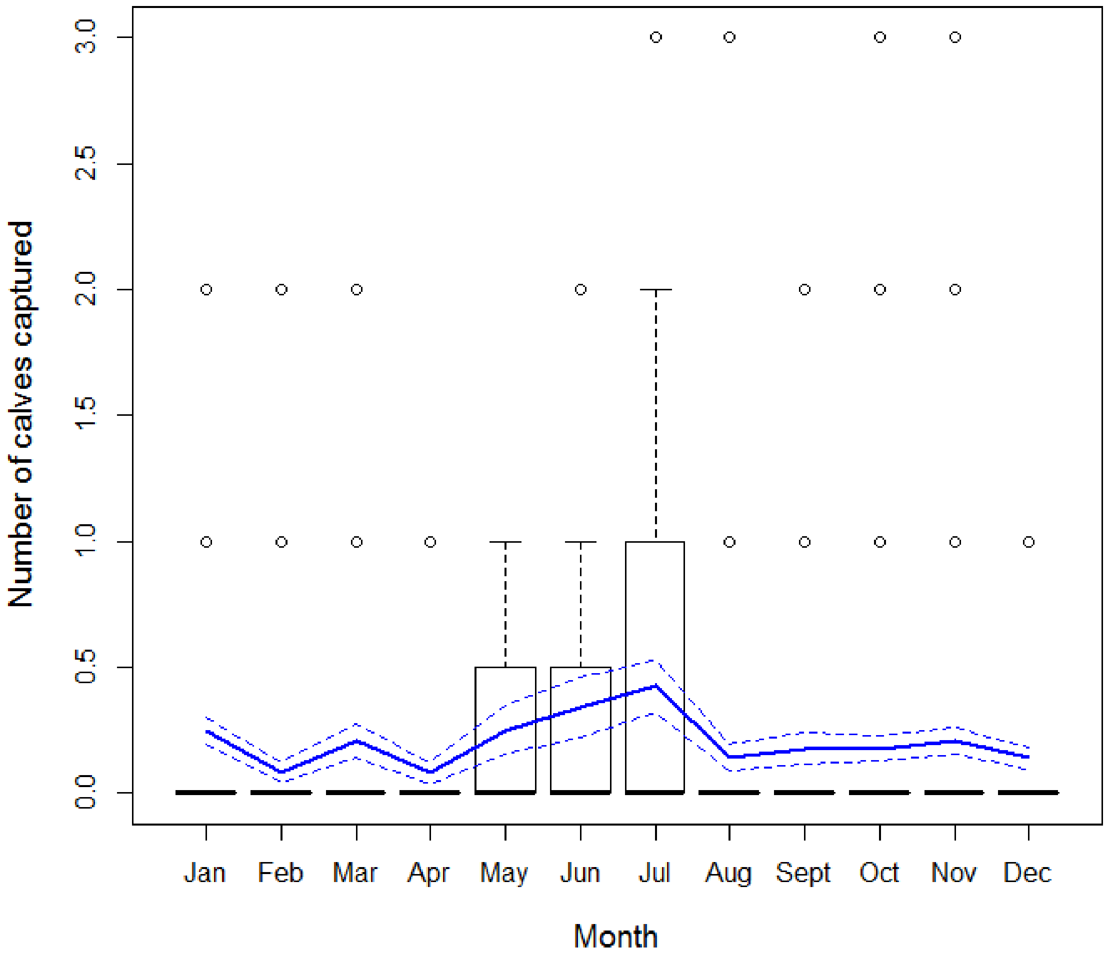

Fig. 6. Prediction plot of the average number of calves captured over the survey period in each forest reserve (month & years – month & years). Dashed lines represent the standard error of the mean.

Table 1. The location of each survey, the camera trap model used, sampling method (Grids or ad-hoc), the survey period and the study.

Location	Camera trap model	Sampling method	Camera distances	Survey period	Study
Tabin Wildlife Reserve	Reconyx HC500, PC800	Grid 1 - 2.5km x 2.5km	0.5km	2011.05.10 – 2011.09.18	Gardner (2015)
		Grid 2 - 2.5 km x 2.5km	0.5km	2011.08.20 – 2012.02.15	Gardner (2015)
		Grid 3 - 3km x 3km	0.5km	2012.03.15 – 2012.07.13	Gardner (2015)
		Grid 4 - 3km x 3km	0.5km	2012.08.06 – 2012.10.22	Gardner (2015)
		Ad-hoc: cameras 0.5km apart	0.5km	2012.02.22 – 2012.03.21	Gardner (2015)
Malua Forest Reserve	Reconyx HC500, PC800	Grid 5: 3x3km	0.5km	2011.04.25 – 2011.08.02	Gardner (2015)
		Grid 6: 3x3km	0.5km	2013.07.17 – 2013.10.17	Gardner (2015)
		Grid 7: 3x3km	0.5km	2013.07.21 – 2013.10.21	Gardner (2015)
		Ad-hoc: cameras 0.5km apart	0.5km	2011.03.29 – 2014.06.08	Gardner (2015)
Maliau Basin Conservation Area Buffer Zones	Reconyx HC500, PC800, PC850	Ad-hoc: cameras 0.5km apart	1km	2013.06.21 – 2014.10.12	Gardner & Goossens (unpublished)
Sipitang Forest Reserve	Reconyx HC500, PC800	Ad-hoc: cameras 0.5km apart	1km	2013.09.22 – 2014.03.25	Gardner & Goossens (unpublished)
Sapulut Forest Reserve	Reconyx HC500, PC800	Ad-hoc: cameras 0.5km apart	1km	2013.11.24 – 2014.04.17	Gardner & Goossens (unpublished)
Kuamut Forest Reserve	Reconyx HC500, PC800	Ad-hoc: cameras 0.5km apart	1km	2014.09.25 – 2015.04.08	Gardner & Goossens (unpublished)

Table 2. The questions investigated (response term ~ explanatory term), and their respective statistical test and model number. Explanatory terms: study design (grid or adhoc), forest regeneration age (years of post-logging regeneration), season, site (camera trap location), salt lick (presence), sex (herd sex), temperature, rainfall, habitat vegetation, elevation, canopy cover, distance_village (distance to the nearest village), distance_forest (distance to the nearest forest border), poaching, stolen camera stations and month.

Question	Statistical Test	Model Number
Herd size ~ Study design + regeneration age + season + site + salt lick + sex + temperature + rainfall + habitat vegetation + elevation + canopy cover + distance_village + distance_forest + poaching + stolen camera stations	GEEGLM, transformed into OR	1
Capture frequencies ~ Sex	ANOVA & Tukey Post-hoc tests	2
Herd sex ~ Season	ANOVA & Tukey Post-hoc tests	3, 4, 5
Number of calves ~ Season	Poisson GLM	6
Number of calves ~ Month	Poisson GAM	7

Table 3. Total number of camera trap (CT) stations, number of CT stations that captured banteng, total number of CT nights (operational for 24-hour), the number of independent events (banteng individual or herd not captured within 90 minutes of the previous event, unless the individual or herd was identified as different), herds (>1 individual), solitary bulls and identified banteng for each forest reserve.

							No. of identified banteng				
Forest Reserve	**Total no. CT stations**	**No. CT stations that captured banteng**	**Total no. of CT nights**	**No. of independent events**	**No. of herds**	**No. of solitary bulls**	**Total**	**Bulls**	**Cows**	**Juveniles**	**Calves**
Tabin Wildlife Reserve	129	23	13,942	38	3	2	27	12	10	2	3
Malua Forest Reserve	148	26	14,859	273	4	1	40	16	13	4	7
Maliau Basin Conservation Area Buffer Zones	26	14	5,162	160	6	2	35	13	15	2	5
Sipitang Forest Reserve	30	11	3,620	65	5	6	29	10	13	4	2
Sapulut Forest Reserve	30	7	2,480	37	1	1	14	6	5	0	3
Kuamut Forest Reserve	30	12	3,281	259	3	0	38	21	9	3	5

Table 4. Percentage encounter rates of herd composition according to each forest reserve. TWR: Tabin Wildlife Reserve, MFR: Malua Forest Reserve, MBCABZ: Maliau Basin Conservation Area Buffer Zones, SPTFR: Sipitang Forest Reserve, SPLFR: Sapulut Forest Reserve and KMTFR: Kuamut Forest Reserve.

	TWR	**MFR**	**MBCABZ**	**SPTFR**	**SPLFR**	**KMTFR**
All Male	3	4	2	2	0	21
All Female	0	3	5	24	0	4
Mixed	26	48	34	16	22	30
Mixed + Calf	3	18	13	3	28	13
Female + Calf	11	2	2	3	0	1
Solitary Male	51	17	34	37	47	27
Solitary Female	6	8	10	15	3	4

Table 5. Summary of backwards stepwise deletion of explanatory terms from GEEGLM models explaining banteng herd size. The final, most robust GEEGLM model with only significant (and marginally non-significant) explanatory terms included forest regeneration age (years of post-logging regeneration), site (camera trap location), salt lick presence, sex (herd sex), habitat vegetation, distance_forest (distance to the nearest forest border) and season. Explanatory terms were removed in the order of most insignificant: canopy cover, rainfall, temperature, poaching, stolen camera stations, study design, distance_village (distance to the nearest village) and elevation. The significance of the relationship (P value) denoted by: **.** = < 0.1 marginally non-significant, * = < 0.05, ** = < 0.01, *** = < 0.001 high significance.

Response term	**Explanatory terms**	**X^2**	**Df**	**P value**	**Significance**
Herd size	Regeneration age	34.2	5,829	2.2e-06	***
	Site	7.07	2,829	0.029	*
	Salt lick	10.2	1,829	0.0014	**
	Sex	447	3,829	<2e-16	***
	Habitat vegetation	30.7	5,829	1.1e-05	***
	Distance_forest	17.1	1,829	3.6e-05	***
	Season	3.08	1,829	0.079	**.**
	Elevation	1.12	1,829	0.29	
	Distance_village	1.28	1,829	0.26	
	Study design	1.07	1,829	0.3	
	Stolen camera stations	0.923	1,829	0.34	
	Poaching	0.289	1,829	0.59	
	Temperature	0.413	1,829	0.52	
	Rainfall	0.11	1,829	0.74	
	Canopy cover	0.0861	1,829	0.77	

Table 6. Summary of the final, most robust GEEGLM model including the different factors of the terms regeneration age (years of post-logging regeneration (PLR)), site (camera trap location), salt lick presence, sex (herd sex), habitat vegetation, distance_forest (distance to the nearest forest border) and season. GEEGLM model estimates were converted to Odds Ratio, which is a measure of association between an environment and an outcome. Intercept included <8 years PLR (Kuamut Forest Reserve), open site, absent salt lick, female herd sex, lowland dipterocarp forest and dry season. SPTFR: Sipitang Forest Reserve, MFR: Malua Forest Reserve, MBCABZ: Maliau Basin Conservation Area Buffer Zones and TWR: Tabin Wildlife Reserve. The significance of the relationship (P value) denoted by: **.** = < 0.1 marginally non-significant, * = < 0.05, ** = < 0.01, *** = < 0.001 high significance.

Model No.	**Response term**	**Explanatory term**	**Factor**	**GEEGLM coefficient**	**Odds Ratio Estimate**	**Odds Ratio Standard Error**	**P value**	**Significance**
1	Herd Size		Intercept	0.7000	2.013752707	1.191246217	6.30e-05	***
		Regeneration age	<3 years PLR (SPTFR)	-1.1700	0.310366941	1.296930087	6.30e-06	***
			4 years PLR (MFR)	-0.3840	0.681131427	1.094830985	2.30e-05	***
			16 years PLR (MBCABZ)	-0.4260	0.653116342	1.120752125	0.0002	***
			22 years PLR (TWR)	-0.1850	0.831104284	1.145681894	0.1752	
		Site	Trail	0.1540	1.166490887	1.099548895	0.1055	
			Logging	0.2590	1.295633805	1.102521688	0.0078	**
		Salt lick	Present	0.5480	1.729789976	1.186490749	0.0014	**
		Sex	Male	-0.6230	0.536333023	1.121873438	5.70e-08	***
			Mixed	0.8580	2.358439095	1.094612041	< 2e-16	***
		Habitat vegetation	Seasonal freshwater swamp	-0.0419	0.958965672	1.257342039	0.8549	
			Scrub	0.1670	1.181754265	1.291752728	0.5138	
			Upland dipterocarp	0.9400	2.559981418	1.335091729	0.0011	**

	Lower montane forest	0.0193	1.019487449	1.421908524	0.9564	
	Industrial tree plantation	0.2480	1.281459932	1.347161788	0.4061	
Distance_forest	N/A	0.0001	1.000116007	1.000028100	3.60e-05	***
Season	Wet	0.0708	1.073366531	1.041227182	0.0795	.

Table 7. Summary of One-Way ANOVA determining any significant differences in the capture frequency of each herd sex: male, female and mixed in all forest reserves, together with the effect of season on these. The significance of the relationship (P value) denoted by: **.** = < 0.1 marginally non-significant, and * = < 0.05 high significance.

Model No.	**Model Description**	**Term**	**F value**	**Df**	**P value**	**Significance**
2	Capture frequency	Sex	6.20	2, 17	0.0109	*
3	Female banteng	Season	19.89	1, 5	0.0112	*
4	Male banteng	Season	5.24	1, 5	0.0840	**.**
5	Mixed sex	Season	6.51	1, 5	0.0632	**.**

Supplementary Information

S1. Female banteng actively segregating itself in preparation for the birthing period (top image), followed by the same female banteng and her new-born calf (bottom image) on the same day (06.04.2014) in Maliau Basin Conservation Area Buffer Zones. This identified female banteng was observed regularly in a mixed herd of six individuals before and after the birth.