Bearded pig (*Sus barbatus*) utilisation of a fragmented forest-oil palm landscape in Sabah, Malaysian Borneo

Running head: Bearded pigs in fragmented tropical landscapes

Kieran Love[A,B], David J. Kurz[C,F], Ian P. Vaughan[A], Alison Ke[C], Luke J. Evans[A,B], and Benoit Goossens[A,B,D,E,F]

[A]Organisms and Environment Division, School of Biosciences, Cardiff University, Museum Avenue, Sir Martin Evans Building, Cardiff CF10 3AX, UK.

[B]Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia.

[C]Department of Environmental Science, Policy, and Management, University of California, Berkeley, 130 Mulford Hall #3114, Berkeley, CA 94720, USA.

[D]Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia.

[E]Sustainable Places Research Institute, Cardiff University, 33 Park Place, Cardiff CF10 3BA, UK.

[F]Corresponding authors:

(Kurz) Telephone: +1 (240) 217-8107; Fax: +1 (510) 643-5438;

email: dave.kurz@gmail.com

(Goossens) Telephone: +60 (0)12 8364 005; Fax: +60 (0)88 341 528;

email: GoossensBR@cardiff.ac.uk

Context: Oil palm plantations have become a dominant landscape in Southeast Asia, yet we still understand relatively little about the ways wildlife are adapting to fragmented mosaics of forest and oil palm. The bearded pig is of great ecological, social, and conservation importance in Borneo and is declining rapidly due to habitat loss and overhunting.

Aims: We sought to assess how the bearded pig is adapting to oil palm expansion by investigating habitat utilisation, activity patterns, body condition, and minimum group size in a mosaic composed of forest fragments and surrounding oil palm.

Methods: We conducted our study in Sabah, Malaysian Borneo, in and around the Lower Kinabatangan Wildlife Sanctuary, an area consisting of secondary forest fragments (ranging 1200-7400 ha) situated within an extensive oil palm matrix. We modelled bearded pig habitat use in forest fragments and oil palm plantations using survey data from line transects. Camera traps placed throughout the forest fragments were used to assess pig activity patterns, body condition, and minimum group size.

Key results: All forest transects and 80% of plantation transects showed pig presence, but mean pig signs per transect were much more prevalent in forest (70.00 ± 13.00 SE) than in plantations (0.91 ± 0.42 SE). Pig tracks had a positive relationship with leaf cover and a negative relationship with grass cover; pig rooting sites had a positive relationship with wet and moderate soils as compared to drier soils. Pigs displayed very good body condition in forests across the study area, aggregated in small groups (mean = 2.7 ± 0.1 SE individuals), and showed diurnal activity patterns that were accentuated for groups with piglets and juveniles.

Conclusions: Our findings suggest that bearded pigs in our study area regularly utilise oil palm as habitat, given their signs in most oil palm sites surveyed. However, secondary forest fragments adjacent to oil palm remain the most important habitat for the bearded pig, as well as many other species, and therefore must be conserved.

Implications: Consistent bearded pig presence in oil palm is a potential indication of successful adaptation to agricultural expansion in the study area. The good physical health displayed by most pigs may result in part from year-round cross-border fruit subsidies from oil palm plantations, whilst the predominance of diurnal activity (especially by groups containing piglets and juveniles) may indicate a behavioural response to predation or human hunting. However, the net effect of oil palm expansion in the region on bearded pig populations remains unknown.

Additional keywords: activity pattern; body condition; habitat use; Lower Kinabatangan; matrix; mosaic; Suidae

Introduction

One of the most pressing areas of conservation research in recent years has been understanding the extent to which forest species can (or cannot) adapt to habitat loss and fragmentation caused by land use change (e.g. Fitzherbert et al. 2008; Gilroy et al. 2015; Newbold et al. 2015). This is particularly true for large parts of Southeast Asia, where oil palm (*Elaeis guineensis*) expansion is the primary driver of deforestation and subsequent wildlife loss (Koh and Wilcove 2008). Many taxa – including ants (Fayle et al. 2010), bats (Fukuda et al. 2009), beetles (Chung et al. 2000), birds (Aratrakorn et al. 2006), frogs (Konopik et al. 2015), lizards (Glor et al. 2001), moths (Chey 2006), primates (Danielsen & Heegard 1995), and small mammals (Yue et al. 2015) – exhibit declines in species richness when tropical forests are replaced by oil palm monocultures. Moreover, even when species are not lost, deforestation caused by oil palm expansion can lead to declines in wildlife abundance, loss of functional diversity, and changes in animal behaviour (Foster et al. 2011; Alfred et al. 2012; Edwards et al. 2014). However, species do not respond uniformly to oil palm expansion and forest fragmentation; species richness and abundance sometimes stay the same or even increase in oil palm as compared to forest (e.g. Liow et al. 2001; Davis & Philips 2005; Luke et al. 2014). Frequently specialist species are the ecological 'losers' that are declining in this transition due to habitat loss or modification, whilst generalist species that thrive in human-altered environments tend to be among the 'winners' (McKinney & Lockwood 1999, Fitzherbert et al. 2008).

Southeast Asia is known for its widespread and highly diverse Suidae, the majority of which are listed as vulnerable or endangered (IUCN 2016), yet the response of wild pigs to oil palm expansion is understudied. The Eurasian wild boar (*Sus scrofa*), perhaps the best-studied wild pig species, has been known to reach high abundances in forest remnants adjacent to oil palm, likely benefitting from fruit subsidies provided by plentiful, year-round fruit production in plantations (Ickes 2001). However, whether this pattern is consistent in other areas and with other wild pig species has yet to be investigated. Given the important role played by wild pigs in structuring plant communities (Ickes et al. 2001; Ickes et al. 2003; Cole et al. 2012), understanding how pigs (native or introduced) are responding to tropical land use change could hold major ecological implications for forest-oil palm landscapes.

The bearded pig (*Sus barbatus*) has great ecological, social, and conservation importance in its native Sundaland (Caldecott et al. 1993). As a forest-dwelling suid (Bernard et al. 2013), it is adapted to a migratory lifestyle in response to mast fruiting cycles, although it can also be found in oil palm plantations (Yue et al. 2015). It is also an ecosystem engineer, removing saplings to build its nests, turning over soil through its rooting behaviour, and acting as a seed predator of many rainforest tree species (Boogaarts 1938; Curran and Leighton 2000; Curran and Webb 2000; Linkie and Sadikin 2003). Bearded pigs are known to be an important prey species for large predators including the Sunda clouded leopard (*Neofelis diardi*), estuarine crocodile (*Crocodylus porosus*), and reticulated python (*Python reticulatus*) (Pfeffer and Caldecott 1986; Caldecott 1988; Auliya 2003; Ross et al. 2013). Additionally, the bearded pig has been an important protein source for humans in Borneo for over 35,000 years (Medway 1958), of which it has been the primary mammalian target for at least 15,000 years (Harrison 1998). The bearded pig continues to provide the majority of wild meat consumed in Borneo, accounting for between 54 and 97% of wild meat consumption by weight (Bennett et al. 2000; Chin 2001; Puri 2005). As a result of its popularity as a game species, overhunting (exacerbated by habitat fragmentation), along with habitat loss, has led to an estimated 30% decline in bearded pig populations over a recent 21-year period, leading to its designation as a Vulnerable species on the IUCN Red List (Kawanishi et al. 2008). Given its vital ecological functions and abundant provision of protein, sustainable bearded pig management should be a high conservation priority in Borneo.

Basic ecological research on bearded pig adaptation to forest-oil palm mosaics is therefore a clear first step. We studied several aspects of bearded pig natural history in a fragmented alluvial forest that serves as both an important wildlife corridor and a case study for tropical landscapes characterised by interspersed patches of forest and oil palm. We sought to assess how the bearded pig is adapting to oil palm expansion by comparing pig habitat use between secondary forest fragments and oil palm plantations, as well as collecting data in forest fragments on daily and seasonal activity patterns, minimum group size, and body condition. We present management implications from these findings and outline directions for future research.

Materials and methods

Study area

The study was conducted in the landscape surrounding Danau Girang Field Centre (5.413711, 118.037646), located in the Lower Kinabatangan floodplain in eastern Sabah, Malaysia. The Lower Kinabatangan Wildlife Sanctuary (LKWS) consists of ten protected forest lots. The lots display a range of sizes (1200 - 7400 ha) and structural connectivity, including narrow riparian corridors and small areas of privately-owned forest (Abram et al. 2014). In addition to designating protections of wildlife sanctuaries, the Sabah Wildlife Enactment of 1997 declared the bearded pig a protected species, although hunting is allowed outside of protected areas with a license. Mean annual precipitation is approximately 3460 mm, with mean monthly temperatures ranging from 23-40°C (B. Goossens, unpubl. data). In drier areas, the landscape is dominated by secondary lowland dipterocarp forest, with some areas of riparian forest (Ancrenaz et al. 2004). Frequent inundation by flooding causes zones of low-stature forest and grassland, with wetter regions encompassing areas of mangrove and swamp forest (Ancrenaz et al. 2004; Estes et al. 2012). Between 1960 and 1995, large parts of the region were logged for hardwoods and cleared for agriculture (Gillespie et al. 2012; Gaveau et al. 2014). Oil palm plantations now occupy at least 48% of the floodplain (Abram et al. 2014).

[Approximate location of Figure 1]

Data collection

Bearded pig presence was assessed using line transects, and data on body condition, activity patterns, and minimum group size were collected using camera traps. Ten line transects (100 m long x 10 m wide) were randomly placed (minimum 2 km apart) in both oil palm and secondary forest sites (Fig. 1). Each transect was surveyed five times by a team of 2-5 surveyors between February and April 2014. One observer (K. Love) was present for all data collection, allowing for standardization of protocol. Intervals between surveys ranged from 12-16 days to allow sufficient time for sign accumulation. Surveyors indirectly recorded pig habitat utilisation along each transect by noting the number of tracks, rooting sites, mud grazes, wallowing holes, scat, and nests (Payne et al. 1985). Pig signs were cleared or marked between transect surveys to prevent duplicate counts. The quantity of individual signs was recorded for each sign type on each transect, and all equivalent signs within 1 m^2 were used as a single sign count to standardize tallies. A Topofil thread measuring device (Fremaco Devices Inc., Owen Sound, Canada) and compass were used for straight surveying that ensured comparable transect pathways during repeat surveys. Transects were examined with surveyors spread equally across the 10 m wide transect.

Soil texture from each survey was categorised using a 1-5 score based on moisture level (1: very wet, 5: dry and dusty). Understory density was recorded every 25 m of each transect using a Robel pole, which contained 47 equally partitioned 2 cm stripes. Density estimations were made at a height of 0.5 m above ground level, and a distance of 10m between observers. Substratum composition for each transect was estimated from a 2 m^2 plot placed every 25 m along transects, in which the percentage of the following substrata were recorded: leaves, soil, grass, shrub and stone (Fig. S1). Using ImageJ (version 1.45S) software, we calculated average canopy cover by taking canopy photos at a height of 1.65 m in the middle of each substrate plot. We used Google Earth (version 7.1.2.2041) to calculate the distance from transect mid-sections to water sources and forest-plantation boundaries. For the purpose of the study, we assumed that pigs did not cross the main river during the short sampling period, as crossings are mainly reported during migratory behaviour rather than during typical daily movements (Meijaard 2000).

[Approximate location of Figure 2]

To assess bearded pig body condition and minimum group size, we used an extensive network of 110 camera trapping stations spread across the same forest fragments as the line transects, although covering a much larger area than the transect locations (Figs. 1, 2). Camera traps were not placed in oil palm plantations due to the high risk of theft. Camera trap images of bearded pigs were collected from November 2011 to December 2013 using Reconyx HC500, Hyperfire, and PC800 infrared digital camera traps. Each camera station was positioned 30-50 cm off the ground along ridges and existing wildlife trails. Physical condition of pigs was assessed following the categories of Wong et al. (2005) (Table S2). Pigs were given a fat index of 1-5, with 5 being the best possible body condition. Pig age classes (i.e. infant, juvenile, sub-adult and adult) and time of activity (date and time of day) were documented. For photographs of pig groups taken within 1 hr of one another, we considered the independent sample to be the photograph with the highest number of individuals (Bernard et al. 2013, Brodie and Giordano 2013). We removed images that were blurred, too dark, blocked from view, or otherwise unsuitable for assessing body condition.

Data Analysis

We used generalized linear mixed effects models in the *lme4* package (Bates et al., 2014) to model the number of bearded pig tracks and rooting sites as a function of nine habitat variables: the percentage ground covered by leaves, soil, shrub, grass, and stone, the distance to the nearest permanent water source (river, oxbows, and/or tributaries) and to the nearest forest-oil palm boundary, ground fruit presence, and soil texture (with textures 1 and 2 considered “wet”, texture 3 considered “moderate”, and textures 4 and 5 considered “dry”). We used a correlation matrix to ensure that all variables were relatively independent ($|r| < 0.6$). We did not model wallow holes, mud grazes, scat, or nests because there were insufficient frequencies of these signs to produce statistically rigorous results. These signs are known to appear relatively infrequently (wallow holes, mud grazes, nests), or are difficult to detect due to high decomposition rates in rainforest conditions (scat, e.g. Heise-Pavlov & Meade 2012). We modelled the number of rooting sites only in forest because there were also insufficient frequencies of rooting sites in oil palm. We included site as a random effect to account for dependence between the transects at each site, and in our models of pig tracks we included habitat type (forest or oil palm) as a variable in every model to account for the strong effects of habitat type on the other environmental variables. We scaled and centered all continuous variables prior to analysis. We created generalized linear mixed effects models for the negative binomial family, which is useful for modelling overdispersed ecological count data (Lindén and Mäntyniemi, 2011). To focus modelling on the most influential variables, we first compared generalized linear mixed effects models of each of the habitat variables independently to a global model and a null model only containing the intercept. We selected the best models to determine the strongest predictors of pig tracks and rooting sites using the Akaike information criterion corrected for small samples sizes (AICc) (Burnham and Anderson, 2004). We considered models with ΔAICc values of at least two less than the null model as plausible models, and considered the model with the lowest AICc value as our best model. Model parameters were determined to be significant if the 95% confidence interval around the estimate did not overlap zero. After we determined which variables had a significant effect on the bearded pig signs independently, we modelled all combinations of significant parameters to determine if any models containing a combination of variables performed better than the single-variable models. All models were run in R statistical software Version 3.2.4. (R Core Team, 2000).

All other analyses were conducted using Minitab (version 17) and R (version 3.0.1) statistical software. Anderson darling and Shapiro-Wilk tests were used to test for normally distributed pig sign and activity data. We used a two-sample t-test to test for differences in the mean number of detected pig signs between forest and oil palm, based on the total number of signs per transect.

To characterise pig activity patterns, we pooled photographs in two different ways: (i) using four intervals (0300 – 0859 h, 0900 – 1459 h, 1500 – 2059 h and 2100 – 0259 h) representing dawn, daytime, dusk and night (Payne et al. 1985; Ross et al. 2013); and (ii) using two intervals, diurnal (0600-1759 h) and nocturnal (1800-0559 h). The same values could be used throughout the year due to the small variation in day length in our study area. Chi-squared tests were used to compare differences in activity between time classifications. We used body condition scores (Table S3) to determine average body condition for each month. As there were likely pigs that were not captured in our camera trap photographs, group size estimates are considered minimum group sizes and may be underestimates. However, we report group sizes in line with other camera trap studies of wild pigs (Linkie and Sadikin 2003, Bengsen et al. 2011).

[Approximate location of Table 1]

Results

Habitat use

A total of 93 transect surveys (forest = 44, plantation = 49) across 20 transects (forest = 10, plantation = 10) confirmed bearded pig presence in all transects in forest and 8 of 10 transects in oil palm plantations. Pig sign was 1-2 orders of magnitude more prevalent (t = 13.07, df = 18, $p < 0.01$) in forest than in plantation transects (Table 1). When comparing the models of pig tracks and rooting sites containing each habitat variable independently and a global model to a null model, every model performed better than the null model; this pattern emerged because the habitat variable (i.e. 'forest' or 'oil palm') had a strong, significant effect in every model, with forest having significantly more pig tracks and rooting sites than oil palm.

In the single-variable models of pig tracks, all models had ΔAICc values of at least two less than the null model because the habitat type variable was highly significant in every model. The other significant variables were percentage of ground covered by leaves and grass. When modelling pig tracks using the combination of the two variables (with habitat type remaining as a controlling variable), the model of percentage of ground covered by leaves still had the lowest AICc value (Table S5). Leaf cover had a significant positive relationship with number of pig tracks (Table 2). Grass cover had a significant negative effect on number of pig tracks when it was the only variable in the model (Table 2).

In the single-variable models of pig rooting sites in forest, the only significant variable was soil texture. Moderate and wet soils both had significantly more pig rooting sites than dry soils (Table 2).

[Approximate location of Table 2]

Minimum group size and encounter rate

Camera traps documented a total of 1995 independent encounters of bearded pigs, with a mean minimum group size of 2.68 individuals (± 0.1 SE, min = 1, max = 32).

Pigs were recorded at all camera sites, with a total camera trap encounter rate of 0.63 independent photographs/100 hours.

Body condition and minimum group size

From the 1995 independent encounters, 4161 individual pigs were scored to body condition. The majority of pigs possessed 'Very Good' (59.4%) and 'Good' body condition scores (35.6%), with relatively few pigs defined as 'Fair' (4.6%) and 'Poor' (0.4%). No pigs classified as 'Very Poor' were identified. During each month of the sampling period, >90% of individual pigs detected had a body condition of 'Very Good' or 'Good'.

[Approximate location of Figure 3]

Activity patterns

Activity patterns varied significantly over the course of 24 hours (Chi-Sq. = 168.25, df = 3, $p < 0.01$), with far fewer pig occurrences at night (Chi-Sq. = 129.87, df = 1, $p < 0.01$). Activity was mostly diurnal, peaking early in the morning from 0600 – 0700 h, and again from 1700 – 1900 h (Fig. 3). Groups containing infants and juveniles (n = 218) were almost exclusively active during daytime hours (Fig. 3).

Discussion

We show that bearded pigs are widespread in a fragmented forest-oil palm mosaic landscape increasingly typical of Southeast Asia. Bearded pigs in our study region appear to preferentially utilise secondary forest habitat as compared to oil palm plantations. Pig habitat utilisation is positively associated with leaf cover and negatively associated with grass cover. Additionally, pigs preferentially used wet and moderate soil types (as compared to drier soils) for rooting behaviour. Bearded pigs tended to aggregate in small groups (mean = 2.7 individuals ± 0.1 SE) and the vast majority appeared to be in 'Good' or 'Very Good' physical condition (Table S3), suggesting that the population of bearded pigs detected at camera traps was generally healthy throughout the study period. Pigs were largely diurnal, with activity peaks at dawn and dusk, and groups containing infant and juvenile pigs were even more active during the day than groups without piglets and juveniles. These findings provide a basic ecological foundation for future work on the adaptation of a threatened large mammal species to extensive anthropogenic influences, especially deforestation, habitat fragmentation, and over-hunting.

Implications of bearded pig habitat use

Bearded pig signs were recorded on all forest and most oil palm transects in our study area, although far more signs were documented in forest than oil palm. This pattern could either reflect a difference in habitat utilisation by the pigs or a difference in sign detectability. Given the strong influence of habitat and substrate features in our models, it is likely that the much more abundant pig sign in forest does in fact reflect a higher degree of utilisation of forest by pigs. The positive relationship between leaf cover and pig tracks suggests that certain habitat features within forest (e.g. trees, leaf litter) are preferred by pigs. Additionally, the negative relationship between grass cover and pig tracks may help explain the lower presence of pig tracks in oil palm, which contained a higher proportion of grass cover than forest did (mean grass cover – oil palm: 33.9%, forest: 8.1%). Lower detectability of tracks in grass could also play a role in this relationship. There is also a strong possibility that bearded pigs are using forest and oil palm habitats differently; for example, we did not record wallowing, mud grazing, or nest building behaviours in plantations (Table 1). Furthermore, oil palm habitats may have less favourable conditions for rooting behaviour, given the hotter and drier conditions as compared to forest (Luskin and Potts 2011). Our models show that rooting behaviour was positively associated with wet and moderate soils, which were more frequently found in forest (mean soil texture – forest: 3.4, oil palm: 4.6; lower values are wetter). These patterns align with other studies on wild pig habitat use showing lower levels of pig sign in grassy habitats (e.g. Welander 2000) and a positive relationship between rooting activity and moist soils (e.g. Mitchell et al. 2008).

Whilst our results suggest that bearded pigs are using forest more than oil palm to meet many of their ecological needs, they also suggest that bearded pigs may be adapting somewhat successfully to fragmented forest-oil palm landscapes, an encouraging sign for conservation. The healthy body condition of pigs as well as the utilisation of 80% of the oil palm sites surveyed point to the presence of some resources of value to pigs in oil palm. Feral pigs take advantage of agricultural areas near forest habitat in many parts of the world, often increasing in density (Caley 1993, Ickes 2001) and/or body size (Dexter 2003) as a result of the extra food subsidies. However, there also appear to be thresholds of agricultural area relative to natural habitat area at which pigs are unable to persist due to their need to access forest and woodlands (Choquenot & Ruscoe 2003, Kawanishi et al. 2008). Finally, it is possible that oil palm plantations may be having adverse effects on bearded pigs by functioning as an “ecological trap” that decouples typical cues from true habitat quality (Weldon & Haddad 2005), attracting pigs to favourable habitat features or food resources and thereby making them more vulnerable to hunting for subsistence, commercial sale, pest control, and/or sport, as is the case with *S. scrofa* in Sumatra (Luskin et al. 2014). However, our study notes only general patterns of bearded pig habitat use; further research in a variety of landscapes is needed to ascertain the net effect of oil palm expansion on bearded pig habitat utilisation, behaviour, and resource selection.

Body condition and fruit availability

Bearded pig body size and condition is known to fluctuate dramatically in sync with the abundance of resources available and the competition for those resources (Wong et al. 2005, Luskin & Ke, in press). Therefore, the year-round good body condition we observed could speak to significant hunting-limited pig densities (as observed elsewhere, e.g. Chin 2001), abundant food availability within our study landscape, or both. Bearded pig meat is easily the most preferred species of wild meat in Borneo, accounting for 54-97% of the wild meat consumed in non-Muslim rural areas on the island (Bennett et al. 2000, Chin 2001, Puri 2005). However, there have been no studies quantifying the effects of hunting on bearded pig populations in the Kinabatangan; while hunting is known to occur, it is not clear how important it is in limiting bearded pig densities and thereby influencing body condition.

While bearded pigs feed on leaves, roots, fungi, invertebrates, small vertebrate, and carrion, their cycles of body condition, growth, and breeding have been mainly linked to fruit availability (Caldecott et al. 1993, Curran & Webb 2000, Wong et al. 2005, Luskin & Ke in press). Oil palm fruit subsidies from plantations are widespread in our study area, and *Ficus* sp. are abundant in the LKWS (Azmi 1998) and are likely to be a key food source. *Ficus* sp. fruit has been described as a 'keystone resource' that helps sustain bearded pig populations during the extended, inter-mast intervals of low productivity that characterise Southeast Asian rainforests (Appanah 1985; Wong et al. 2005). However, in a human-modified, fragmented landscape like our study area, it is unclear how bearded pig body condition responds to periods of extended drought. The constant supply of year-round fruit from oil palm plantations could mitigate the population-suppressing effects of this natural cycle for bearded pigs in the Lower Kinabatangan, but the complex interactions between oil palm fruit subsidies, rainforest phenological cycles, habitat fragmentation, and bearded pig population dynamics have yet to be untangled.

Behavioural implications of minimum group size and activity patterns

Minimum group sizes in the LKWS averaged 2.7 (± 0.1 SE) individuals, as compared to 1.9 (± 0.3 SE) reported in Kerinci Seblat National Park in Sumatra (Linkie and Sadikin 2003). Given the distribution of pigs throughout most of our study area, the lack of large-scale herding behaviour, and the continuous abundance of oil palm fruit subsidies, pig populations of the LKWS may be largely sedentary (Caldecott et al.

1993). Caldecott et al. (1993) reference a bearded pig population state similar to this in the *Koompassia-Burseraceae* forest in Peninsular Malaysia, characterised by populations with local movements that exploit concentrated, predictable food resources that allow for high breeding and growth rates. This would appear to be the closest known population state corresponding to the bearded pigs in our study, although further research is necessary to corroborate this hypothesis.

Bearded pigs without young were mostly diurnal, with the highest peaks of activity at dawn (0600-0700 h) and dusk (1700-1900 h) and low levels of activity at night (Fig. 3). These results accord with previous research showing that pigs tend to be diurnal (Pfeffer and Caldecott 1986; Linkie and Sadikin 2003; Ross et al. 2013) and avoid the hottest hours of the day (Caley 1997, Saunders and Kay 1991). Additionally, bearded pigs are known to alter their activity patterns in response to nocturnal clouded leopard hunting patterns (Ross et al. 2013), suggesting that their diurnal tendencies may be in part a response to the clouded leopards present in the LKWS. Groups of pigs including juveniles and infants were more strictly diurnal than those containing only adults, with almost no activity recorded at night (Fig. 3). This accentuated diurnal pattern could be due to the particular vulnerability of young pigs to predation by clouded leopards; past research has shown that female bearded pigs (which raise the young) respond more strongly to clouded leopard activity patterns than male bearded pigs (Ross et al. 2013).

In addition to clouded leopard activity patterns, human hunting poses a major threat to bearded pig populations in Borneo (Kawanishi et al. 2008). Bearded pig hunting is extremely common in Borneo (Bennett et al. 2000; Puri 2005), and illegal poaching occurs in our study area (K. Love, pers. obs.). More data on bearded pig movement ecology, e.g. GPS collaring studies collecting location and accelerometer data, are needed to determine to what extent this human hunting activity influences bearded pig activity patterns. Tracking fine-scale pig movements in mixed landscapes would build upon our results on relative habitat utilisation by illuminating the role of forest fragments in bearded pig foraging and behavioural ecology. These data would help determine the minimum threshold, quality, and configuration of forest cover needed to ensure stable and genetically diverse bearded pig populations in the Lower Kinabatangan region and other fragmented tropical landscapes.

Conclusions

In a fragmented tropical forest-oil palm landscape, bearded pig signs were found in all secondary forest sites and most oil palm plantation sites. This prevalence throughout the mosaic, coupled with consistently high body condition scores, indicates some adaptability of bearded pigs to fragmented landscapes. Oil palm plantations may have some conservation value for the species by providing valuable supplemental resources to primarily forest-dwelling pigs, whilst likely unable to provide the habitat structure (e.g. wallowing and nest sites) needed to sustain bearded pig populations in the absence of forest. Bearded pig groups, especially those containing piglets and juveniles, are diurnal in the Lower Kinabatangan region, possibly in response to predation or human hunting.

Our findings provide foundational data on bearded pig habitat use, activity patterns, minimum group size, and body condition in a forest-oil palm mosaic, providing a starting point for future research on how the threatened pig is adapting to these important and expanding landscapes in Southeast Asia. Future work should extend this study by investigating bearded pig movements through mixed landscapes, migration patterns (or lack thereof) in different parts of Borneo, and genetic diversity and gene flow in relation to fragmentation, as well as the effects of human hunting on bearded pigs in both oil palm plantations and forest fragments. Understanding at finer scales how individual resources and microhabitats within forest and oil palm are utilized for different purposes (e.g. thermoregulation, predator avoidance, food acquisition) by bearded pigs will provide a more detailed picture of their ecological requirements and conservation needs. In the meantime, given that our results suggest that pigs preferentially utilise forest habitat much more than oil palm, protection of secondary forest fragments adjacent to oil palm plantations should be a major conservation priority in order to ensure healthy bearded pig populations in the Lower Kinabatangan.

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Conflict of Interest Statement

Funding for the research included funds from the Sime Darby Foundation, the main philanthropic arm of Sime Darby Berhad, a multinational conglomerate that owns oil palm plantations. However, no representatives of any of the funding sources were involved in the study design, execution, analysis, or interpretation of results.

References

Abram, N. K., Xofis, P., Tzanopoulos, J., MacMillan, D. C., Ancrenaz, M., Chung, R., Peter, L., Ong, R., Lackman, I., Goossens, B., Ambu, L., and Knight, A. T. (2014). Synergies for improving oil palm production and forest conservation in floodplain landscapes. *PLoS ONE* **9**, e95388.

Alfred, R., Ahmad, A. H., Payne, J., Williams, C., Ambu, L. N., How, P. M., and Goossens, B. (2012). Home range and ranging behaviour of Bornean elephant (*Elephas maximus borneensis*) females. *PLoS ONE* **7**, e31400

Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A., and Lackman-Ancrenaz, I.

(2004). Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation* **7**, 375-385.

Appanah, S. (1985). General flowering in the climax rain forests of South-east Asia. *Journal of Tropical Ecology* **1**, 225-240.

Aratrakorn, S., Thunhikorn, S., and Donald, P. F. (2006). Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. *Bird Conservation International* **16**, 71-82.

Auliya, M. (2003). A reticulated python (*Python reticulatus*) preys on an adult Sulawesi pig (*Sus celebensis*). *Asian Wild Pig News* **3,** 11-12.

Azmi, R. (1998). Natural vegetation of the Kinabatangan floodplain. Part 1: background and preliminary checklist. (WWF-Malaysia: Kota Kinabalu.)

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, **67**, 1-48. <doi:10.18637/jss.v067.i01>.

Bengsen, A. J., Leung, L. K.-P., Lapidge, S. J., and Gordon, I. J. (2011). Using a general index approach to analyze camera-trap abundance indices. *The Journal of Wildlife Management* **75**, 1222-1227.

Bennett, E. L., Nyaoi, A. J., and Sompud, J. (2000). Saving Borneo's bacon: the sustainability of hunting in Sarawak and Sabah. In 'Hunting for Sustainability in Tropical Forests'. (Eds J. G. Robinson and E. L. Bennett.) pp. 305-324. (Columbia University Press: New York.)

Bernard, H., Ahmad, A. H., Brodie, J., Giordano, A. J., Lakim, M., Amat, R., Koh, S.P.H., Khee, L.S., Tuuga, A., Malim, P. T., Lim-Hasegawa, D., Wai, Y.S., and

Sinun, W. (2013). Camera-trapping survey of mammals in and around Imbak Canyon Conservation Area in Sabah, Malaysian Borneo. *The Raffles Bulletin of Zoology* **61**, 861-870.

Boogaarts, M. (1938). Nangoeih's. In 'De Nederlandsch-Indische Jager 1'. (Ed. M. Boogaarts.) pp. 305, 308. [Freely translated from Dutch by Erik Meijaard] Caldecott, J. O. (1988). Hunting and wildlife management in Sarawak. (IUCN: Gland and Cambridge.)

Brodie, J. F., and Giordano, A. (2013). Lack of trophic release with large mammal predators and prey in Borneo. *Biological Conservation* **163,** 58-67.

Burnham, K. P., and Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33,** 261-304.

Caldecott, J. O., Blouch, R. A., and Macdonald, A. A. (1993). The bearded pig (*Sus barbatus*). In 'Pigs, Peccaries and Hippos: Status Survey and Conservation Action Plan'. (Ed. W. L. Oliver.) pp. 136-145. (IUCN: Gland.)

Chey, V. K. (2006). Impacts of forest conversion on biodiversity as indicated by moths. *Malayan Nature Journal* **57**, 383-418.

Chin, C. (2001). Pig in the pot: comments on Sus barbatus in the hunting lifestyle of the Penan in Sarawak (Borneo). *Asian Wild Pig News* **1**, 10-12. Chung, A. Y. C., Eggleton, P., Speight, M. R., Hammond, P. M., and Chey, V. K. (2000). The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. *Bulletin of Entomological Research* **90**, 475-496.

Cole, R. J., Litton, C. M., Koontz, M. J., and Loh, R. K. (2012). Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. *Biotropica* **44**, 463-471. Curran, L. M. and Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* **70**, 101–128.

Curran, L.M. and C.O. Webb. (2000). Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs* **70**, 129–148.

Danielsen, F., and Heegaard, M. (1995). Impact of logging and plantation development on species diversity: a case study from Sumatra. In 'Management of Tropical Forests: Towards an Integrated Perspective'. (Ed. Ø. Sandbukt.) pp. 73-92. (University of Oslo – Centre for Development and the Environment: Oslo.)

Davis, A. L. V., and Philips, T. K. (2005). Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa conservation area. *Environmental Entomology* **34**, 1081-1088.

Edwards, F. A., Edwards, D. P., Larsen, T. H., Hsu, W. W., Benedick, S., Chung, A., Khen, Wilcove, D. S., and Hamer, K. C. (2014). Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation* **17**, 163-173.

Estes, J. G., Othman, N., Ismail, S., Ancrenaz, M., Goossens, B., Ambu, L. N., Estes, A. B., and Palmiotto, P. A. (2012). Quantity and configuration of available elephant habitat and related conservation concerns in the lower Kinabatangan Floodplain of Sabah, Malaysia. *PLoS ONE* **7**, e44601.

Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y. C., Eggleton, P., and Foster, W. A. (2010). Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes, and leaf litter. *Basic and Applied Ecology* **11**, 337-345.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., and Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution* **23**, 538-545.

Foster, W. A., Snaddon, J. L., Turner, E. C., Fayle, T. M., Cockerill, T. D., Ellwood, M. D. F., Broad, G. R., Chung, A. Y. C., Eggleton, P., Khen, C. V., and Yusah, K. M. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B* **366**, 3277-3291.

Fukuda, D., Tisen, O. B., Momose, K., and Sakai, S. (2009). Bat diversity in the vegetation mosaic around a lowland dipterocarp forest of Borneo. *The Raffles Bulletin of Zoology* **57**, 213-221.

Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N., and Meijaard, E. (2014). Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE* **9**, e101654.

Gillespie, G. R., Ahmad, E., Elahan, B., Evans, A., Ancrenaz, M., Goossens, B., and

Scroggie, M. P. (2012). Conservation of amphibians in Borneo: relative value of secondary tropical forest and non-forest habitats. *Biological Conservation* **152**, 136-144.

Gilroy, J. J., Prescott, G. W., Cardenas, J. S., Castañeda, P. G. P., Sánchez, A., Rojas-Murcia, L. E., Uribe, C. A. M., Haugaasen, T., and Edwards, D. P. (2015). Minimizing the biodiversity impact of Neotropical oil palm development. *Global Change Biology* **21**, 1531-1540.

Glor, R. E., Flecker, A. S., Benard, M. F., and Power, A. G. (2001). Lizard diversity and agricultural disturbance in a Caribbean forest landscape. *Biodiversity and Conservation* **10**, 711-723.

Harrison, T. (1998). Vertebrate faunal remains from the Madai caves (MAD 1/28), Sabah, East Malaysia. *Bulletin of the Indo-Pacific Prehistory Association* **17**, 85-92.

Ickes, K. (2001). Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of peninsular Malaysia. *Biotropica* **33**, 682-690.

Ickes, K., Dewalt, S. J., and Appanah, S. (2001). Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology* **17**, 191-206.

Ickes, K., Dewalt, S. J., and Thomas, S. C. (2003). Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology* **91,** 222-233.

International Union for Conservation of Nature (IUCN). 2016. IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed on 4 August, 2015.

Kawanishi, K., Gumal, M. and Oliver, W. (2008). *Sus barbatus.* The IUCN Red List of Threatened Species. E.T41772A10559190.

http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41772A10559190.en. Accessed on 9 October, 2016.

Koh, L.P. and Wilcove, D. S. (2008). Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters* **1**, 60-64.

Konopik, O., Steffan-Dewenter, I., and Grafe, T. U. (2015). Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. *Biotropica* **47**, 636-643.

Lindén, A., and Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology* **92**, 1414-1421.

Linkie, M., and Sadikin, L. (2003). The bearded pig in Kerinci Seblat National Park, Sumatra. *Asian Wild Pig News* **3**, 3-9.

Liow, L. H., Sodhi, N. S., and Elmqvist, T. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology* **38**, 180-192.

Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., and Davies, R. G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation* **23**, 2817-2832.

Luskin, M. S., Christina, E. D., Kelley, L. C., and Potts, M. D. (2014). Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Human Ecology* **42**, 35-45.

Luskin, M. S., and Potts, M. D. (2011). Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology* **12**, 540-551.

MacKenzie, D. I., and Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* **9**, 300–318.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2006). 'Occupancy Estimation and Modeling – Inferring Patterns and Dynamics of Species Occurrence.' (Academic Press: London.)

Medway, L. (1958). Food bone in Niah Cave excavations. *Sarawak Museum Journal* **8**, 627-636.

McKinney, M. L., & Lockwood, J. L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14, 450-453.**

Meijaard, E. (2000). Bearded pig (*Sus barbatus*): Ecology, conservation status, and research methodology. Background document for the electronic conference on bearded pig research, and recommendations for a collaborative research programme. (WWF-Indonesia, CIFOR, and Ecosense Consultants: Bogor.)

Mitchell, J., Dorney, W., Mayer, R., and McIlroy, J. (2008). Spatial and temporal patterns of feral pig diggings in rainforests of north Queensland. *Wildlife Research* **34,** 597-602.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennet, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Cheverria-Londoño, S., Edgard, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J., Itsecu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D. L. P., Martin, C. D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D. W., Robinson, A., Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J. P. W., and Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45-50.

Payne, J., and Francis, C. M. (1985). 'A Field Guide to the Mammals of Borneo.' (The Sabah Society: Kota Kinabalu.)

Pfeffer, P. and Caldecott, J. (1986). The bearded pig (*Sus barbatus*) in East Kalimantan and Sarawak. *Journal of the Malaysian Branch of the Royal Asiatic Society* **59**, 81-100.

Puri, R. K. (2005). 'Deadly Dances in the Bornean Rainforest: Hunting Knowledge of the Penan Benalui.' (KTLV Press: Leiden.)

Ross, J., Hearn, A. J., Johnson, P. J., and Macdonald, D.W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* **290**, 96-106.

Saunders, G., and Kay, B. (1991). Movements of feral pigs (*Sus scrofa*) at Sunny Corner, New South Wales. *Wildlife Research* **18**, 49-61.

Welander, J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology* 252: 263-271.

Weldon, A. J., & Haddad, N. M. (2005). The effect of patch shape on indigo buntings: evidence for an ecological trap. *Ecology* **86**, 1422-1431.

Wong, S. T., Servheen, C., Ambu, L., and Norhayati, A. (2005). Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology* **21**, 627–639.

Yue, S., Brodie, J. F., Zipkin, E. F., and Bernard, H. (2015). Oil palm plantations fail to support mammal diversity. *Ecological Applications* **25**, 2285-2292.

Figure Legends

Figure 1. Transect positions for forest transects (red flags) and oil palm plantation transects (blue flags) sites within the Lower Kinabatangan Wildlife Sanctuary and surrounding region. The blue boundaries represent permanent water sources. The green lines correspond to the forest regions.

Figure 2. The camera trap stations within the Lower Kinabatangan Wildlife Sanctuary (LKWS) and surrounding areas. Illustrated are twenty corridor sites (yellow icons) and 75 forest patch sites (purple icons). The blue outlines display the Kinabatangan River and neighbouring oxbow lakes. The green markings show forest areas of LKWS. The grey lines show privately owned forest areas and yellow lines display degraded forest within plantation fragments.

Figure 3. The activity patterns of bearded pigs throughout an average day, based on the percentage of independent camera trap detections (min. 1 hr apart) occurring at various times of day. The solid line displays the diurnal activity pattern of the entire

population (n = 1995), whereas the checked line illustrates the more strictly diurnal activity patterns of groups containing juveniles and piglets (n = 221).

Figure 1.

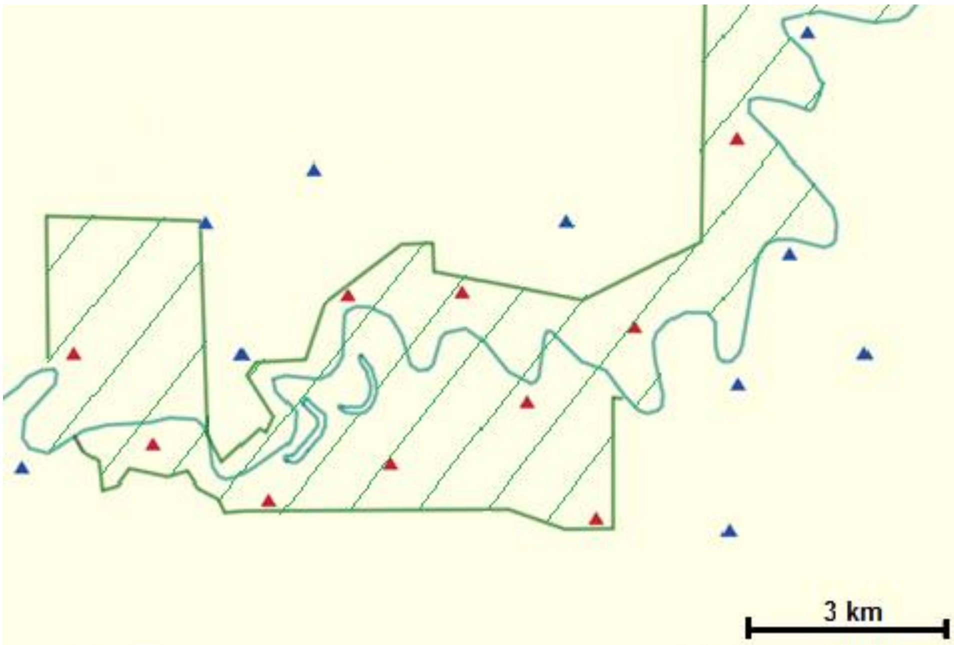


Figure 2.

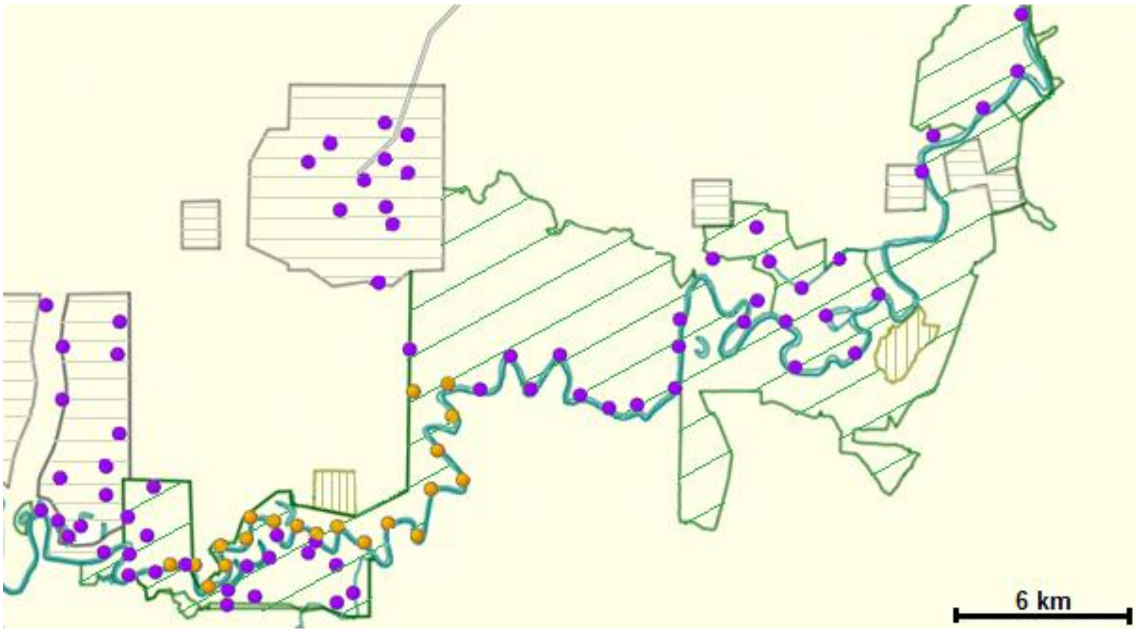
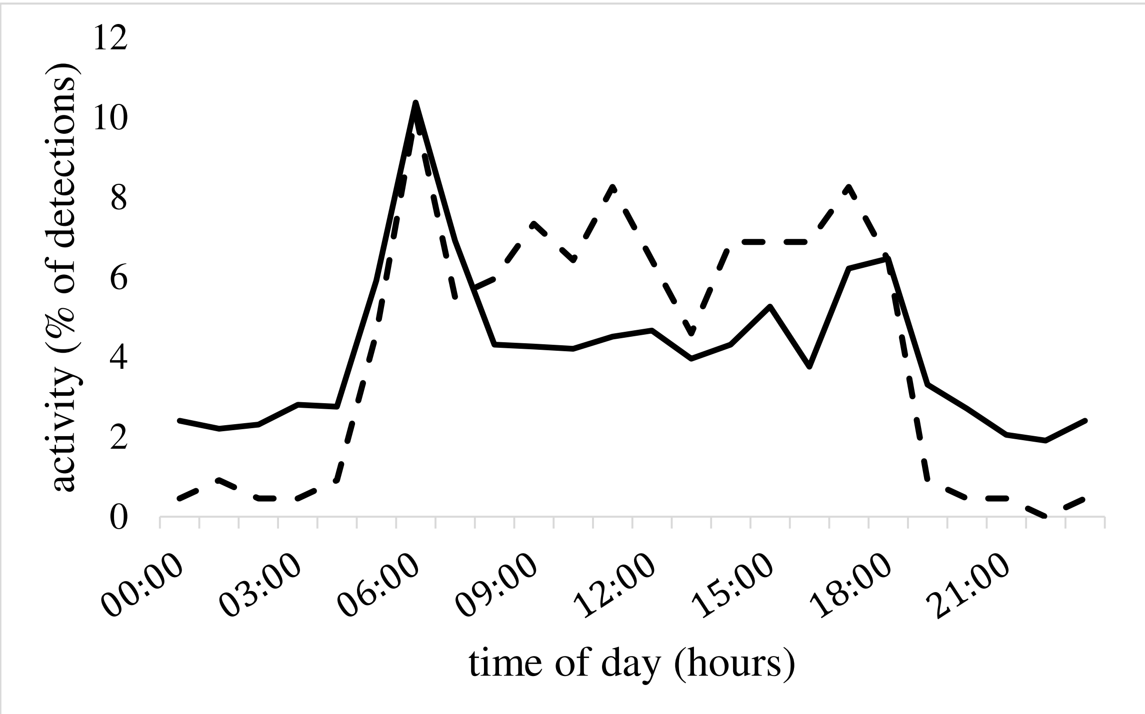


Figure 3.



activity (% of detections)
0
2
4
6
8
10
12
00:00
03:00
06:00
09:00
12:00
15:00
18:00
21:00
time of day (hours)

Table 1. Summary table displaying the mean number of signs detected (± SE) during transect surveys in forest and plantation habitats.

Habitat	Mean tracks	Mean rooting sites	Mean mud grazes	Mean wallowing holes	Mean scat	Mean nest	Mean total sign
Forest	58.57 (±9.41)	9.02 (±3.97)	2.39 (±2.00)	0.02 (±0.03)	0.00 (±0.00)	0.02 (±0.02)	70.00 (±13.00)
Plantation	0.65 (±0.18)	0.27 (±0.30)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.91 (±0.42)

Table 2: Parameter estimates, Standard errors, z-values, p-values, and AICc values of generalized linear mixed effects models using all combinations of predetermined influential variables to predict number of pig tracks and rooting sites. All models of pig tracks contain habitat type as a controlling variable, which had a highly significant effect in every model. Moderate and wet soil textures are compared to the dry soil texture. Significant parameters are in bold.

Model	Parameters	Estimate	Std. Error	z value	Pr(>|z|)	AICc
Pig Tracks						
Leaves	**Leaves**	0.43	0.15	2.86	0.004	548.29
Leaves + Grass	Leaves	0.32	0.18	1.83	0.067	549.31
	Grass	-0.17	0.15	-1.14	0.254	
Grass	**Grass**	-0.32	0.13	-2.43	0.015	550.27
Rooting Sites						
Soil Texture	**Moderate - Dry**	1.39	0.36	3.81	0.0001	238.07
	Wet - Dry	1.90	0.55	3.48	0.0005	

Supplementary Material

Figure S1. A 10 x 100m line transect displaying the habitat analysis layout. The black dashed rectangular box displays the transect area whilst the solid black bar represents the transect midline. The five smaller checked boxes represent the $2m^2$ plots where the substrate composition was estimated. Crossed circles signify five points where canopy cover photos were taken. The grey arrows symbolise five sections where person 1 stood and measured the understory density, whilst the white arrows indicate where person 2 stood and held the Robel pole.

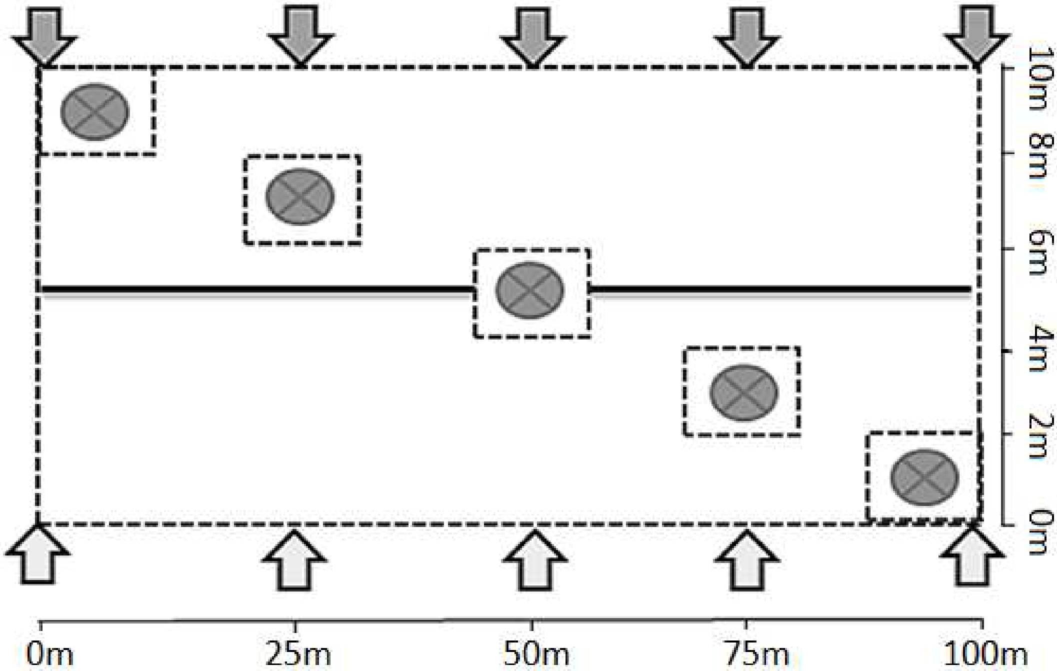
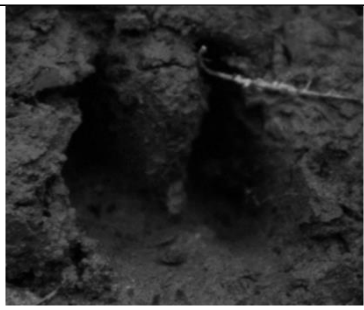


Table S1. Example photographs of pig sign used for detecting pig habitat use on transects.

Sign	**Example**
Track	

Scat	
Nest	
Rooting site	
Wallowing hole	
Mud graze	

Table S2. Visual factors used to determine bearded pig body condition from camera trap images (used with permission from Wong et al. 2005).

Index	Category	Fur condition	Neck size	Body fat and muscle	Bones
5	Very good	Sleek, dense	Thick	Fat, muscular	Not visible
4	Good	Sleek, dense	Thick	Little fat, Muscular	Not visible

3	Fair	Dense	Medium	Lacking in fat, muscular	Slightly visible
2	Poor	Dull	Narrow	Lacking in fat, slim	Visible, less protruding bones
1	Very poor	Dull, sparse	Narrow	Lacking in fat, little muscle	Protruding

Bones include the scapulae, vertebral columns, ribs and hipbones

Table S3. Example photographs used for categorising body condition of pigs from camera photos.

Category	**Example**
Very good	

Good	
Fair	
Poor	

Very poor	 (Wong et al. 2005)

Table S4. Example photographs used for categorising age of pigs from camera trap photos.

Age	**Example**

Infant	
Juvenile	
Sub-adult	
Adult	

Table S5. The null and competing generalized linear mixed effects models investigating the effects of the identified influential parameters on pig tracks and rooting sites. All models of pig tracks include habitat type as a controlling variable. The models are ranked based on the differences in the cumulative corrected Akaike's Information Criteria (AICc). Table includes the number of estimated parameters (K), the AICc, the difference in AICc with the top model (Delta_AICc), the weight of each model (AICcWt), and the -2log-likelihood output (LL).

	K	AICc	Delta_AICc	AICcWt	LL
Pig Tracks					
Leaves	5	548.29	0	0.51	-268.80
Leaves + Grass	6	549.31	1.02	0.30	-268.17
Grass	5	550.27	1.97	0.19	-269.79
Null	3	603.76	55.47	0.00	-298.75
Rooting Sites					
Soil Texture	5	238.07	0	1.00	-113.24
Null	3	250.45	12.38	0	-121.92