

Shifts in the demographics and behavior of bearded pigs (*Sus barbatus*) across a land-use gradient

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Funding information

Sime Darby Foundation

Abstract

Beyond broad-scale investigations of species diversity and abundance, there is little information on how land conversion in the tropics is affecting the behavior and demographics of surviving species. To fill these knowledge gaps, we explored the effects of land-use change on the ecologically important and threatened bearded pig (*Sus barbatus*) over seven years in Borneo. Random placement of camera traps across a land-use gradient of primary forest, logged forest, and oil palm plantations (32,542 trap nights) resulted in 2,303 independent capture events. Land-use was associated with changes in the age structure and activity patterns of photographed individuals, alongside large changes in abundance shown previously. The proportion of adults recorded declined from 92% in primary forests to 76% in logged forests, and 67% in plantations, likely indicating increased fecundity in secondary forests. Activity level (capture rate) did not vary, but activity patterns changed markedly, from diurnal in primary forests, crepuscular in logged forests, to nocturnal in plantations. These changes corresponded with avoidance of diurnal human activity and may also protect bearded pigs from increased thermal stress in warmer degraded forests. The percentage of adult captures that were groups rather than individuals increased five-fold from primary forests (4%) to logged forests (20%), possibly due to increased mating or in response to perceived threats from indirect human disturbance. We recommend further investigation of the demographic and behavioral effects of land-use change on keystone species as altered population structure, activity patterns, and social behavior may have knock-on effects for entire ecosystems.

KEYWORDS

activity pattern, borneo, mammal, oil palm, population structure, primary tropical forest, selective logging, social behavior

1 | INTRODUCTION

Across the tropics, the clearing of irreplaceable unlogged primary forests is leading to increasingly human-dominated landscapes

where logging and intensive permanent agriculture are widespread (Gibson et al., 2011; Lewis, Edwards, & Galbraith, 2015). Land-use change in the tropics regularly involves the degradation of forests through the selective logging of large timber trees and the replacement of native vegetation with cultivated crops. These changes exert distinct effects on species abundance and diversity (Edwards et al., 2010; Slade, Mann, & Lewis, 2011; Wearn, Carbone, Rowcliffe,

Associate Editor: Eleanor Slade. Handling Editor: Jedediah Brodie.

Bernard, & Ewers, 2016; Wearn et al., 2017). For example, there is wide consensus that land-use change, particularly clearance for agriculture, negatively affects species richness as specialist species are often unable to adapt to modified environments (Bradshaw, Sodhi, & Brook, 2009; Fitzherbert et al., 2008; Gardner et al., 2009). However, a few adaptable species are sometimes able to maintain or even increase in abundance post-disturbance (Wearn et al., 2017), and little is known about the more subtle, but potentially ecologically important, effects on those species which survive forest degradation and conversion.

Insular Southeast Asia is estimated to have lost one percent per year of its natural forests between 2000 and 2010, with Borneo suffering the largest absolute loss, approximately five million hectares (Miettinen, Shi, & Liew, 2011). Much of this change can be attributed to the growing of African oil palm (*Elaeis guineensis*), the dominant crop in Southeast Asia (Vijay, Pimm, Jenkins, & Smith, 2016), which has large impacts on biodiversity (Fitzherbert et al., 2008) and abundance (Foster et al., 2011; Turner & Foster, 2009). Wearn et al. (2017) found that the local abundance of Bornean mammals increased by 28 percent from unlogged to logged forests but declined 47 percent from forests to oil palm plantations. Mammal classes do not all fare equally, with small mammals exhibiting a far greater increase in abundance after selective logging than large mammals, whilst omnivores and invasive species also fare relatively well (Wearn et al., 2017).

Given the dramatic changes in physical structure, microclimate, and resource availability after land degradation and land conversion (Hardwick et al., 2015), it is reasonable to assume that surviving species may exhibit plastic ecological and behavioral changes (Ghazoul & McLeish, 2001; Lowry, Lill, & Wong, 2013), and that these changes may not manifest immediately in altered abundances. For example, the demography of surviving populations may be transformed under land-use scenarios by various processes, including altered reproductive rates (Servanty et al., 2011; Srinivasan, Hines, & Quader, 2015), age-specific survival (Baker & Thompson, 2007), or competitive exclusion (Holt, 1985; Polis, 1984). Land-use change may also affect the behavior of animals as they adjust to novel challenges and conditions (Halle, 2000). Such behavioral changes may indirectly influence the abundance of other species through trophic cascades (Schmitz, Beckerman, & O'Brien, 1997; Schmitz et al., 2008) and can be a mechanism by which non-lethal human disturbance affects survival (Kerbioui et al., 2009).

Increased hunting pressure is characteristic of degraded landscapes (Brodie et al., 2015; Peres, 2000) as there is greater accessibility for commercial and subsistence hunters, and the need to control crop pests (Bennett, Nyaoi, & Sompud, 2000; Luskin, Christina, Kelley, & Potts, 2014). This may lead animals to reduce their overall activity levels and bear the associated fitness costs (van Doormaal, Ohashi, Koike, & Kaji, 2015; Downes, 2008) or concentrate their activity at times of lower risk (Suselbeek et al., 2014). Temporal plasticity in response to human encroachment, typically in the form of increased nocturnality, has been well documented in medium to large mammals (Di Bitetti, Paviolo, Ferrari, De Angelo,

& Di Blanco, 2008; Gaynor, Hojnowski, Carter, & Brashares, 2018; Oberosler, Groff, Iemma, Pedrini, & Rovero, 2017; Ramesh & Downs, 2013). Human impacts can also be mediated through domesticated species. For example, free-roaming dogs are known to affect the presence and activity patterns of native mammals (Lacerda, Tomas, & Marinho-Filho, 2009; Young, Olson, Reading, Amgalanbaatar, & Berger, 2011; Zapata-Ríos & Branch, 2016) and have high abundances in oil palm plantations (Wearn et al., 2017).

In social species, grouping behavior may be affected by structural changes in human-modified landscapes. This follows theoretical work by Hancock, Milner-Gulland, and Keeling (2006), who used a genetic algorithm to decipher how regional aggregations emerge as a foraging strategy in the bearded pig. They concluded that in natural systems, nomadic foragers form aggregations when patches of rich quality food are distributed in a landscape where food is scarce, and repulsion of conspecifics as homogeneity of resources increases. In Borneo's primary forests, irregular mast fruiting of Dipterocarpaceae results in spatially and temporally heterogeneous resource availability (Curran & Leighton, 2000; Janzen, 1974; Sakai et al., 1999), whilst agricultural expansion in unprotected areas can provide a predictable long-term source of highly abundant, high energy food (Luskin, Brashares, et al., 2017). Therefore, in disturbed landscapes with consistent access to high energy crops, groups of social foragers may be less common, and smaller, than in landscapes dominated by heterogenous unlogged primary forests.

To determine how anthropogenic disturbance affects species that persist, we examined the effects of land-use change on the demography and behavior of Borneo's bearded pigs (*Sus barbatus*). Bearded pigs have declined across much of their Southeast Asian range despite some ability to survive in disturbed forests (Love et al., 2018; Meijaard & Sheil, 2008; Wearn et al., 2017). Hunting pressure is a common threat (Corlett, 2007) and these pigs can constitute up to 72% of bushmeat weight in some rural communities (Bennett et al., 2000). High local abundances are now restricted to the island of Borneo (Luskin & Ke, 2017), and the species is classified as vulnerable (Luskin et al., 2017). In Sabah, Wearn et al. (2017) estimated that bearded pig relative abundance compared to primary forest was 54% higher in selectively logged forest, but 87% lower in oil palm plantations, where they are unable to form self-sustaining populations (Love et al., 2018). The elevated abundance in logged forests may result from food subsidies from plantations, which have previously been shown to correlate with elevated wild boar (*Sus scrofa*) abundance over a kilometer into adjacent forests (Luskin, Brashares, et al., 2017).

As well as providing a window into how other large forest omnivores and herbivores may respond, bearded pigs are an important case-study due to the ecological importance of pigs in Southeast Asian forests, where they act as major seed predators (Curran & Webb, 2000; Granados, Brodie, Bernard, & O'Brien, 2017), and affect understory plant dynamics through soil rooting and nest building (Ickes, Dewalt, & Appanah, 2001; Ickes, Paciorek, & Thomas, 2005; Luskin, Ickes, Yao, & Davies, 2019; Luskin & Ke, 2017). Bearded pigs employ a wide range of spatial behaviors, from sedentary to nomadic

and from solitary to highly gregarious (Hancock et al., 2006; Luskin & Ke, 2017). This behavioral plasticity likely evolved as a response to unpredictable food availability in dipterocarp forests (Curran & Leighton, 2000) and could lead to distinct changes caused by human disturbance, such as the disappearance of large nomadic herds.

We established sites in primary forests, logged forests, and oil palm plantations to investigate the consequences of forest degradation and conversion on bearded pig demographics, activity patterns, and group behavior. We tested three main hypotheses: (1) bearded pig age structure will change across land-uses as anthropogenic disturbance impacts vital demographic rates (Brodie et al., 2015; Gamelon et al., 2011; Servanty, Gaillard, Toïgo, Brandt, & Baubet, 2009; Srinivasan et al., 2015; Toïgo, Servanty, Gaillard, Brandt, & Baubet, 2008); (2a) activity level will decrease in modified habitats (van Doormaal et al., 2015) and (2b) circadian activity patterns will shift toward nocturnality (Gaynor et al., 2018), as bearded pigs avoid increased daytime temperatures (Hardwick et al., 2015; Owen-Smith, 1998) and human disturbance (Brodie et al., 2015; Di Bitetti et al., 2008; Ohashi et al., 2013); and (3) groups of bearded pigs will be more common and contain more individuals in undisturbed primary forests due to associated navigation advantages (Biro, Sumpter, Meade, & Guilford, 2006; Couzin, Krause, Franks, & Levin, 2005; Dell'Ariccia, Dell'Omo, Wolfer, & Lipp, 2008; Nesterova et al., 2014). The final hypothesis serves as an empirical test, at the landscape level, of Hancock et al.'s (2006) modeling prediction that group formation in nomadic foragers is more advantageous when resources are randomly and patchily distributed. This research helps reveal the subtler effects of land-use change on large mammals—important functional groups in tropical forests (Terborgh et al., 2001)—and is designed to help generate management recommendations based more closely on the life-history traits of keystone species (Berger-Tal et al., 2011; Cosset, Gilroy, & Edwards, 2018).

2 | METHODS

2.1 | Project site

Sampling occurred at the Stability of Altered Forest Ecosystem (SAFE) project site in Sabah, Malaysian Borneo, and encompassed three land-use categories: primary forest in protected areas, salvage logged forest concessions, and oil palm plantations (Figure S1, Ewers et al., 2011). We sampled primary forest in the Maliau Basin Conservation Area (4°49' N, 116°54' E; 1,054 km² including buffer zone) and the Brantian-Tatulit Virgin Jungle Reserve (4°40' N, 117°33' E; 22 km²). These sites typically featured well-developed canopy layers and a relatively open understory. Maliau Basin Conservation Area is primarily made up of unlogged forest and contains large numbers of trees in the family Dipterocarpaceae (mean aboveground tree biomass: 413.4 t/ha, Pfeifer et al., 2016). Despite restricted areas of low-intensity historical logging for ironwood (*Eusideroxylon zwageri*) the habitat is considered pristine and undisturbed (Ewers et al., 2011). The Brantian-Tatulit Virgin Jungle

Reserve contains similar habitat; however, some degradation from illegal logging is apparent on the southern and western borders. Borneo's lowland forests are characterized by synchronized mast fruiting events at irregular, multi-year time intervals (Janzen, 1974; Sakai et al., 1999), resulting in spatially and temporally heterogeneous distribution of food resources (Curran & Leighton, 2000).

We sampled salvage logged forests in the SAFE experimental area in the North East of the Kalabakan Forest Reserve (4°42' N, 117°34' E; 72 km²). This area has been subject to multiple rounds of unrestricted commercial logging for all large timber trees (diameter at breast height > 40cm) between 1978 and the early 2000's (Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011), leaving a structurally heterogeneous forest with few large trees and a dense understory (mean aboveground tree biomass: 42.4 t/ha, Pfeifer et al., 2016). These areas are intersected by numerous logging roads and are dominated by less productive vines, pioneer tree species, and invasive vegetation (Pfeifer et al., 2016). The altered forest structure and lower canopy cover affect microclimate, as degraded forests tend to exhibit lower humidity and warmer daytime temperatures (Hardwick et al., 2015; Luskin & Potts, 2011). Our logged forest sites were on average two kilometers from the nearest oil palm plantation (range: 1.3–2.6 km).

Two oil palm plantations beside the Kalabakan Reserve boundary represented the intensive monocultures that are characteristic of the region. The Mawang estate and adjacent Selangan Batu estate were planted in 2000 and 2006, respectively. Directly to the west of the sampling plots was a 45 km² stand of logged forest, and narrow riparian buffers of degraded forest were present within the plantation landscape. Hunting levels across all of our sites were comparatively low: Wearn et al. (2017) found hunters in just 0.03% of camera trap nights, compared to 2.7% reported elsewhere in Borneo (Brodie et al., 2015). Hunting was illegal in the plantations surveyed, the main access to the steep-sided Maliau Basin is monitored by wardens, and from mid-2013 checkpoints were installed on major access roads to the SAFE experimental area. The little evidence of hunting we saw during fieldwork was restricted to logging and plantation roads.

2.2 | Field methods

We collected data from June 2011 to March 2017. Our protocol followed the clustered hierarchical design of Wearn et al. (2017), whereby 46 plots of 1.75-ha were distributed across the landscape in 11 sampling blocks encompassing primary forest, logged forest, and oil palm (Figure S1). This equates to 13 plots of forest located in protected areas and arranged in four blocks, 24 plots of logged forests in four blocks, and 9 plots of oil palm plantations in three blocks. Following the SAFE project design, we arranged sampling plots to account for potential confounding influences from latitude, elevation, and slope (Ewers et al., 2011). Within each plot, 48 sampling points were arranged 23 m apart in a 12 × 4 rectangular grid. During a survey, we deployed cameras for at least 30 days (mean: 69, range: 30–119) at a randomly selected subset of the 48 grid points. The

number of cameras varied, with a mean of nine cameras per plot per year (range = 1–24). Plots were surveyed once per year, however, not all plots were sampled in all years: on average plots were sampled twice during the study (range 1–4).

We attached one camera trap (Reconyx HC500) to trees or posts at 30 cm above the ground and within five meters of each point. No bait or lure was used, and disturbance of surrounding vegetation was kept to a minimum. Camera traps were operated using a 10-image burst mode with no delay.

2.3 | Image processing

Camera trap image processing followed Wearn et al. (2017): adding relevant metadata to the extensible metadata platform (XMP) of each image using keyword tags in Adobe Lightroom 6.0 (Adobe Systems). All images were classified into capture events, individual or group, and processed to include information on number and age class of bearded pigs. Group size was counted subjectively based on direction of travel and the time of images (no more than 10 min apart). Size, defining features, and temporary markings such as mud patterns helped distinguish between individuals. Recorded group sizes are conservative due to the limited field of view of camera traps. The age classes, adult, subadult, and juvenile, were identified based on size and morphology, including the presence of stripes and length of beard (Luskin & Ke, 2017; Payne, Francis, & Phillipps, 1985; Phillipps & Phillipps, 2016).

2.4 | Data analysis

We extracted image metadata using the command line program ExifTool version 10.60 (Harvey, 2017) and conducted all cleaning and analysis in R version 3.6 (R Core Team, 2019). Capture events were considered independent if they occurred at least 30 min after the previous event. Although any interval greater than one minute is shown to significantly reduce self-dependence in camera trap studies of mammals (Yasuda, 2004), 30 min has been widely used in the literature (Burton et al., 2015; O'Brien, Kinnaird, & Wibisono, 2003; Si, Kays, & Ding, 2014; Thorn, Scott, Green, Bateman, & Cameron, 2009) and was considered a suitably conservative cutoff.

We evaluated the distribution of age classes with a Pearson's chi-squared test of independence, using the null-hypothesis that demography is independent of land-use, and post-hoc comparisons between land-uses. We assessed activity using circular, non-parametric, kernel density functions, which produce continuous measures of probability density across the 24-hr clock (Worton, 1989). Activity level estimates were obtained following Rowcliffe, Kays, Kranstauber, Carbone, and Jansen (2014) with the temporal data bootstrapped 1,000 times. This method assumes activity level is directly correlated with capture rate, which is defensible given our use of random camera locations, and estimates the proportion of time spent active as the area under the daily activity curve divided by

the theoretical maximum activity (Rowcliffe et al., 2014). Estimates for the three land-use classes were compared using the Wald chi-squared test. Circadian activity was compared using the Mardia-Watson-Wheeler test, a non-parametric test for homogeneity of variance in circular data, and the Watson's two-sample test for post-hoc pairwise comparisons. We used conditional density isopleths to further illustrate and compare peak activity periods (Oliveira-Santos, Zucco, & Agostinelli, 2013). For pairwise comparisons of circadian activity, the coefficient of overlap was assessed at isopleths of 95% and 50%, representing the activity range and activity core, respectively (Oliveira-Santos et al., 2013; Ridout & Linkie, 2009). We also considered the activity patterns of humans and free-roaming dogs (*Canis lupus familiaris*) in oil palm plantations, and the extent of overlap with bearded pigs.

For assessing group behavior, we modeled the tendency to form groups and group size together using a zero-inflated negative binomial model (ZINB) with the package "glmmTMB" (Brooks et al., 2017). "Zeros" represented individual pig capture events (alone), with additional group members above this baseline being integers. This approach was selected to account for the occurrence of excess individuals captured alone, a result of the negative bias of camera traps (i.e., not all individuals in groups pass in front of the camera), and overdispersion in the data. The number of individuals per capture event was compared across land-use categories for the zero component (i.e., likelihood of being alone, binomial with logit link) and the count component of the model (i.e., group size if not alone, negative binomial with log link). Plot number was included as a random effect in both parts of the model. To account for the effect of post-natal care of juveniles and subadults on group formation, we conducted this analysis separately for all age classes and for adults only (juveniles and subadults excluded from analysis).

3 | RESULTS

Throughout the study, cameras were deployed 731 times across 682 unique points, culminating in a total successful survey of 32,542 camera trap nights (primary: 9,842; logged: 19,596; and plantation: 3,104). We recorded 2,303 independent capture events of bearded pigs, including 1,708 solitary individuals, and 595 groups (containing 1,959 individuals). There were 1,492 independent records of humans, with the highest frequency, 22 records per 100 trap nights, observed in oil palm plantations (primary = 1.9, logged = 3.1). Free-roaming dogs were only observed in plantations ($n = 132$).

3.1 | Demographics

Recorded age structure varied across land-use types ($\chi^2 = 53.53$, $df = 4$, $p < .0001$), with post-hoc tests indicating that primary forest was different to both logged forest ($\chi^2 = 49.29$, $df = 2$, $p < .0001$) and oil palm ($\chi^2 = 34.56$, $df = 2$, $p < .0001$), but that both disturbed habitats were statistically similar ($\chi^2 = 3.16$, $df = 2$, $p = .21$). The

proportion of adults recorded declined from 92% in primary forest to 76% in logged forest and 67% in oil palm plantations (Figure 1). Conversely, the proportion of juveniles and subadults increased, with juvenile captures increasing by 157% from primary forests to logged forests and a further 26% in oil palm. Subadult captures increased approximately 300% from primary forests to logged forests and a further 65% in oil palm.

3.2 | Activity

Estimated activity levels, or proportion of time spent active, did not vary with land use ($p > .2$, Table S1) and averaged 0.514 ($SD = 0.09$) across all habitats. There was, however, an observable difference between activity patterns across land-uses ($W = 97.469$, $p < .0001$) and post-hoc tests confirmed that this was true for all pairwise comparisons (primary and logged $W = 2.155$, $p < .001$; logged and oil palm $W = 0.396$, $p < .001$; and primary and oil palm $W = 0.880$, $p < .001$). Activity core, defined by the 50% isopleth, shifted from diurnal in primary forests to crepuscular in logged forests and to nocturnal in oil palm plantations (Figure 2a-c). The overlap coefficient for core activity periods was highest between primary and logged forests (0.44), much lower between logged forests and oil palm plantations (0.13), and zero between primary forests and oil palm plantations, where there was no overlap. The pattern of decreasing circadian overlap with increasing disturbance also holds for activity range 95% isopleths, albeit at higher values (primary and logged forests = 0.76; logged forests and oil palm = 0.63; and primary forest and oil palm = 0.48). Free-roaming domestic dogs displayed diurnal activity with a large morning peak and a short peak in the early evening (Figure 2d). The overlap between dogs and pigs was very low for activity core (0.07) and activity range (0.41). Human activity in plantations was highly concentrated in the morning between 0730 h and 1100 h (Figure 2e). Human and bearded pig core activity periods

did not overlap at all, and their activity ranges overlapped minimally (0.27).

3.3 | Group behavior

The proportion of capture events containing groups increased from primary forests (all ages: 8%, adults: 4%) to logged forests (all ages: 29%, adults: 20%) and oil palm plantations (all ages: 43%, adults: 28%, Figure 3a). Pigs in logged forest were three and a half times more likely to form groups than those in primary forests ($Z = -3.98$, $p < .0001$, Table S2) and for adult pigs they were five times more likely ($Z = -1.97$, $p = .049$, Table S3). The occurrence of groups in oil palm sites was variable and did not differ significantly from either of the other land-uses (all ages $p > .99$; adults $p > .99$). There was no significant difference in group size across habitats (all ages $p > .09$; adults $p > .29$), and the median observed group size was two (range 2–21, max adult group = 17, Figure 3b). Including plot as a random effect improved model fit (all ages $\chi^2(2) = 57.78$, $p < .0001$; adults $\chi^2(2) = 28.554$, $p < .0001$).

4 | DISCUSSION

Anthropogenic disturbance was accompanied by changes to the age structure, activity patterns, and group formation of bearded pigs, a functionally important large omnivore. The proportion of juveniles recorded in images was higher in disturbed habitats, possibly indicating a greater reproductive rate. Increased selective hunting pressure has been shown to result in demographically younger populations in ungulates (Langvatn & Loison, 1999; Servanty et al., 2009), and in European wild boar, it has been linked with shifts to earlier reproduction and shorter generation time (Gamelon et al., 2011; Servanty et al., 2011; Toïgo et al., 2008). Indeed, a previous study in the same region revealed that hunting constitutes a more serious long-term threat than logging for 91% of primate and ungulate species (Brodie et al., 2015). The abundance of young individuals seen in disturbed habitats may, therefore, be a consequence of selective hunting pressure on larger adults as they carry more meat and are more detectable (Cardillo et al., 2005), or because they are more susceptible to hunting for behavioral reasons. Hunting pressure in our study was likely highest in plantations where the highest proportion of images contained hunters (0.1%, Wearn et al., 2017). Nonetheless, the sites we sampled exhibited very low hunting pressure (Wearn et al., 2017) when put into context of the wider region (Brodie et al., 2015).

Changes in the demography of capture events could also be attributed to age-specific changes in habitat use (Haraldstad & Jonsson, 1983; Sherry & Holmes, 1989); however, at our study site, all juveniles and most subadults were in groups with, and possibly dependent upon, adults. The observed demography most likely results from pigs in logged forest/plantation matrixes exhibiting higher fecundity than pigs in primary forests (e.g., Srinivasan et al., 2015) possibly due to increased resource availability or reduced

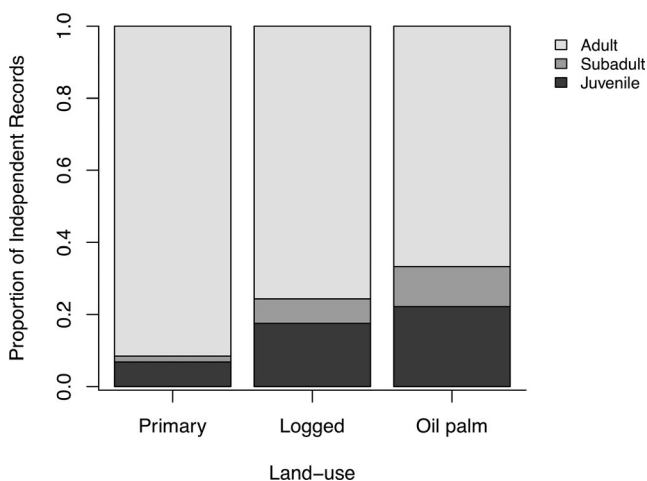


FIGURE 1 Age distribution of bearded pig images by land-use. Logged forests and oil palm plantations displayed higher proportions of juveniles and subadults than primary forests

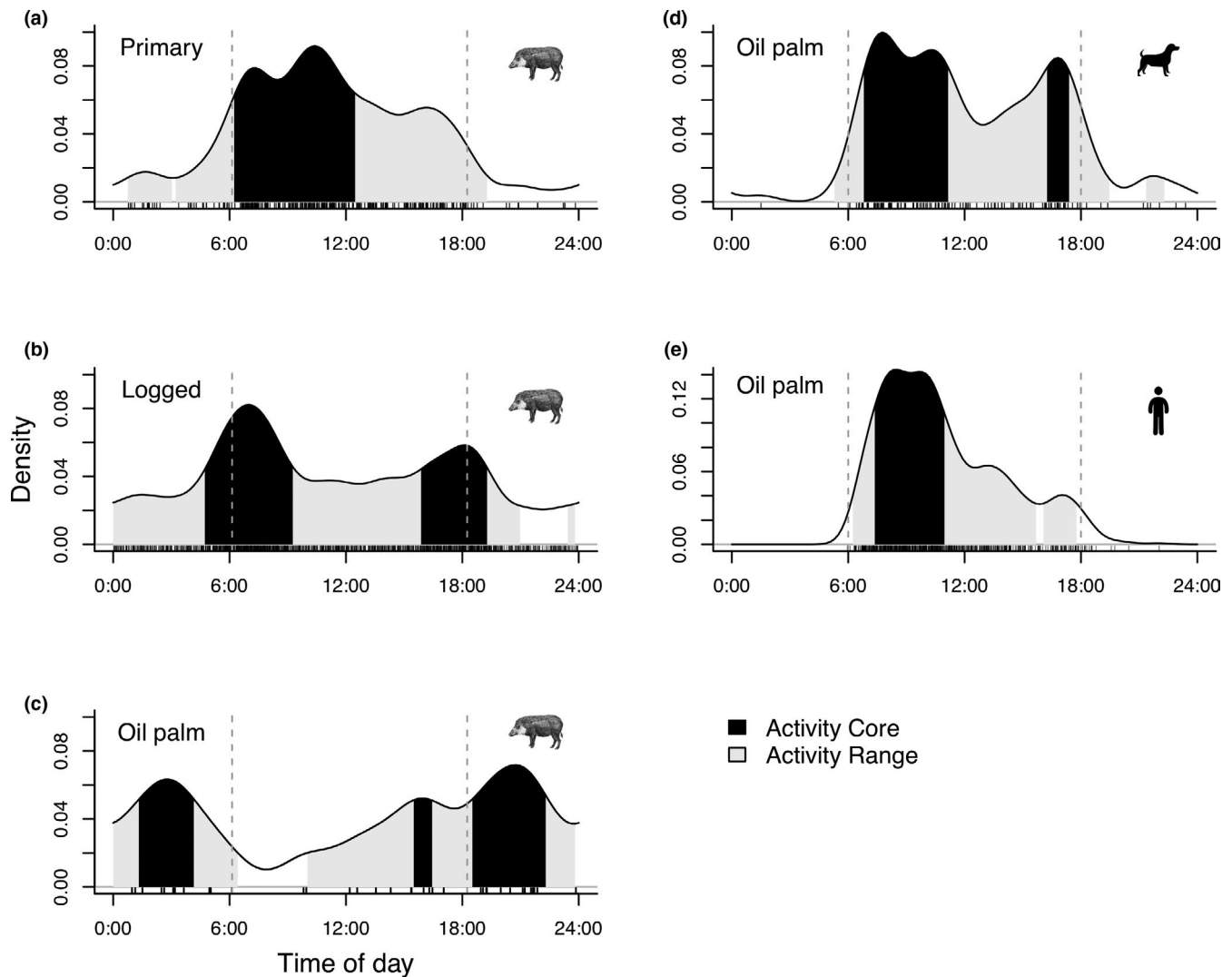


FIGURE 2 Kernel density plots illustrating the daily activity patterns of bearded pigs in (a) primary forests, (b) logged forests, (c) oil palm plantations. The final two plots show the activity patterns of two causes of disturbance in plantations: (d) free-roaming dogs and (e) humans. Black shading indicates activity core (50% isopleth) and gray shading the activity range (95% isopleth). Gray dashed lines are average sunrise and sunset

competition and predation. This hypothesis is supported by the finding that bearded pigs in the area are 54% more abundant in logged forests than in primary forests (Wearn et al., 2017) and by evidence that food subsidies from oil palm plantations can greatly enhance wild boar reproduction in logged forests up to 1.3 km away (Luskin, Brashares, et al., 2017). The distance from our logged forest sites to the nearest plantations was between 1.3 km and 2.6 km. Considering bearded pigs have longer legs than wild boar and are known to occasionally range over hundreds of kilometers (Luskin & Ke, 2017), it is probable that some individuals observed in the logged forest benefitted from this resource.

Bearded pigs are typically less mobile during intermast periods (Caldecott, Blouch, & Macdonald, 1993), and oil palm subsidies likely play an important role in degraded matrix landscapes; however, without movement data it is impossible to say how far and how often individuals in our logged forest sites traveled for these resources. Pigs photographed at our oil palm sites most likely relied on nearby

stands of logged forest and riparian buffers for nesting, reproduction, and wallowing, whilst raiding the plantation for extra resources (Love et al., 2018). The abundance of energy-rich oil palm fruit coincides with a depauperate predator community, except humans and few other mammalian herbivores (Wearn et al., 2017), potentially favorable conditions for elevated fecundity. Hence, we accept our hypothesis that land degradation affects bearded pig age structure, with greater proportions of juveniles likely resulting from increased reproductivity. Further investigation will be required to determine the vital demographic rates underlying these patterns.

Our results indicate that bearded pigs sustain similar activity levels across land-use types but have considerably altered the circadian timing of their activity. In primary forests where individuals are buffered from temperature extremes and contact with humans, they are active throughout the daylight hours with the greatest peak occurring in the late morning. In logged forest, however, they exhibit a distinctly crepuscular pattern. This is perhaps explained by

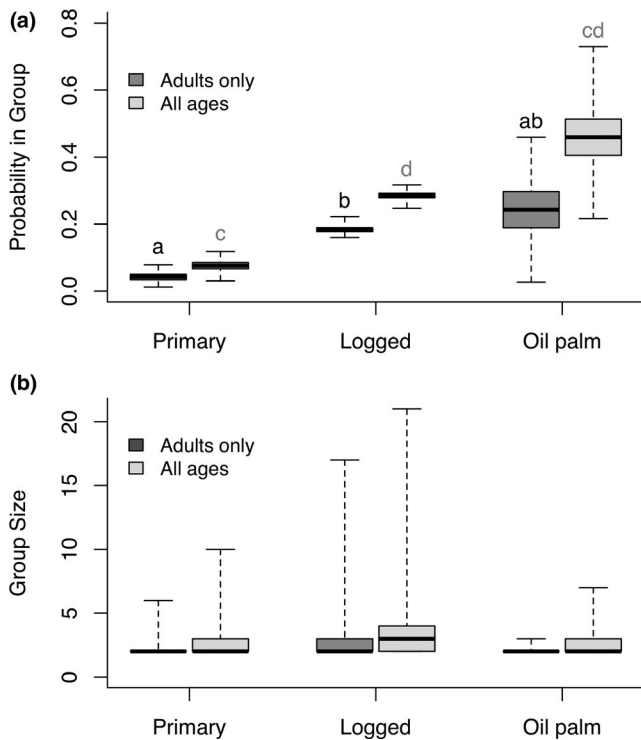


FIGURE 3 Group behavior of bearded pigs across land-uses. (a) Tendency to form groups was higher in logged forests than primary forests and was highly variable in oil palm sites. This pattern remains when considering only adult pigs. Group data were bootstrapped 1,000 times to produce a range of means. (b) When in groups, the number of individuals present does not vary appreciably by land-use. Solid black lines indicate medians, boxes incorporate 25% of the data either side of this value, and dashed whiskers show the entire range. Lower-case letters indicate significant differences, with significantly different means not sharing letters

avoidance of high midday temperatures in the low canopy cover, less sheltered logged forests, where temperatures can average nearly 3°C warmer (Hardwick et al., 2015; Owen-Smith, 1998). Additionally, it may be an adjustment to minimize conflict with humans, who typically have greater access to these habitats (Brodie et al., 2015; Lewis et al., 2015).

In oil palm plantations, the majority of bearded pig observations occurred during nocturnal hours and probably represented foraging raids from nearby forests. Even more so than logged forests, oil palm plantations display higher mean daytime temperatures, larger daily temperature variation, and lower humidity than unlogged forests (Hardwick et al., 2015; Luskin & Potts, 2011). However, considering the marked lack of early morning activity when microclimates remain favorable, these activity shifts probably reflect avoidance of oil palm workers who were typically very active between 07:00 h and 12:00 h. Bearded pigs likely also avoid free-roaming dogs, which were only observed at oil palm sites, and whose core activity patterns overlapped minimally with bearded pigs. Dog activity closely matched that of humans; however, the presence of an evening activity peak exclusive to dogs indicates that their presence may be exacerbating the disturbance effects. Indeed, dogs often elicit stronger

stress responses in wild animals than humans (Lord, Waas, Innes, & Whittingham, 2001; MacArthur, Johnston, & Geist, 1979), predate many local species (Young et al., 2011), and have caused temporal activity shifts in several other native forest mammals (Gerber, Karpanty, & Randrianantenaina, 2012; Zapata-Ríos & Branch, 2016). Bearded pigs may be particularly sensitive to dogs due to a long history of using dogs for hunting in Borneo (Corlett, 2007).

Love et al. (2018) found that groups of bearded pigs with juveniles may reduce their predation risk from nocturnal predators by shifting their activity diurnally. Therefore, the greater proportion of juveniles seen in riskier oil palm habitats than in primary forests was unexpected. The benefit of the resource surplus in plantations may override any elevated mortality risks associated with using this habitat, or the behavioral changes we observed may sufficiently mitigate the risks. Globally, there is growing evidence for increased animal nocturnality in response to anthropogenic disturbance (Gaynor et al., 2018). For example, Ohashi et al. (2013) found that wild boar in Japan became increasingly nocturnal in response to direct hunting and indirect anthropogenic disturbance. Our results support these previous observations and provide evidence of significant behavioral changes in human-modified landscapes. The temporal plasticity demonstrated by bearded pigs may help them adapt to human disturbance, although the long-term effect of these shifts is yet to be investigated. Species that are temporally constrained, by morphology or ecology, may suffer greater fitness costs from disturbance (van Doormaal et al., 2015).

We reject our hypothesis, based on the model predictions of Hancock et al. (2006), that groups will be more prevalent in primary forests. Bearded pigs in logged forests exhibited a greater tendency to form groups than those in more resource heterogeneous primary forests, and this pattern held when considering only adults. Group formation was highly variable in oil palm plantations and not distinct from either of the other land-uses. We anticipated that the more patchy resource availability of Dipterocarp primary forests would result in group formation becoming more prevalent due to the many-wrongs principle, whereby the ability to find scattered food sources is improved due to group interactions and cohesion diminishing the effect of individual navigation error (Bergman & Donner, 1964; Hamilton, 1967; Simons, 2004; Wallraff, 1978). This principle implies that the formation of groups would be more advantageous where rich food patches occur irregularly in a low resource landscape, as opposed to the stable and predictable resources of vast oil palm plantations.

Considering all age classes, the higher grouping tendency in logged forests may have simply resulted from increased density (Hancock et al., 2006; Wearn et al., 2017) combined with the post-natal care of younger pigs that were more prevalent in these habitats. This pattern held when considering only adults, a possible consequence of increased mating behavior or antipredator advantages (e.g., Sorato, Gullett, Griffith, & Russell, 2012). Natural predators of bearded pigs include reticulated pythons, salt-water crocodiles, and the rare Sunda clouded leopard (Corlett, 2011; Hearn et al., 2016; Ross, Hearn, Johnson, & Macdonald, 2013); however,

“safety in numbers” antipredator behavior can also occur in response to human disturbance stimuli (Frid & Dill, 2002). Despite a greater range being observed in logged forests, there was no statistically significant variation in group size across the land-use gradient. The observed median group size of two is likely an underestimate due to the negative bias of camera traps (i.e., not all individuals in groups are always captured). Over a relatively large spatial and temporal extent, including at least three mast fruiting events (Ghazoul, 2016), we detected none of the characteristic large aggregations of bearded pigs (Caldecott, 1988; Luskin, Brashares, et al., 2017), potentially indicating a significant decline in mass herding behavior with increasing habitat modification over time. Habitat fragmentation and the proliferation of vast oil palm plantations may have disrupted the potential, and the benefit, of forming large nomadic aggregations.

Our study employed a large data set to demonstrate that land-use change affects bearded pigs in myriad ways and furthers our understanding of the ecology of these understudied and ecologically important forest nomads. Alongside the elevated abundance in logged forests and depleted abundance in plantations shown previously (Wearn et al., 2017), we provide clear evidence that land degradation imposes many subtle but pervasive effects on this species. We observed significant impacts of logging and intensive agriculture on bearded pig age structure and behavior that potentially form the first steps toward population declines seen in parts of their range (Luskin, Brashares, et al., 2017). Future research will need to address whether the observed patterns hold in different locations and under different scenarios of hunting and human activity. Our results should direct attention toward the altered ecosystem dynamics which may result from changes in activity patterns, demographics, and social behavior of an ecosystem engineer like the bearded pig. These changes could have implications for the survival of other species, akin to the habitat changes observed following elevated wild boar reproduction near plantations (Luskin, Brashares, et al., 2017; Luskin et al., 2019). Even though generalist species might persist in degraded habitats, non-lethal changes to behavior and demography may significantly alter ecosystem function under continued land development scenarios (Post, Peterson, Stenseth, & McLaren, 1999; Schmitz et al., 2008).

A significant knowledge gap to be reconciled is how the spatio-temporal distribution of food in plantations affects some of the observed changes via shifts in diet and ranging behavior. For example, the potential co-occurrence of abundant fruit and human-induced mortality in oil palm plantations could drive an ecological trap with the potential to cause wide-ranging population declines (e.g., Lamb, Mowat, McLellan, Nielsen, & Boutin, 2017). Future investigations into the movement behavior of bearded pigs will be particularly useful for improving our understanding of their ecology and behavior, especially in response to land-use intensity and the altered resource distribution resulting from extensive oil palm agriculture. A thorough survey of hunting practices in the area would also help clarify the contribution of this threat to observed trends (e.g., Luskin et al., 2014). Behavior and demography must be considered when contemplating species long-term resilience in human-modified landscapes

(Cosset et al., 2018) and for improving the effectiveness of conservation initiatives (Berger-Tal et al., 2011).

ACKNOWLEDGMENTS

We would like to thank Yayasan Sabah, Maliau Basin Management Committee and the Sabah Biodiversity Council for permission to conduct this research. Many thanks to Sui Heon, Ryan Gray, SAFE research assistants and staff, Derek Shapiro, and David Orme for their assistance. We are grateful for the valuable comments from Matthew Luskin and two anonymous reviewers. This study was supported by funding from the Sime Darby Foundation and represents a contribution to Imperial College London's Grand Challenges in Ecosystems and the Environment Initiative.

DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there are no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from Zenodo at <http://doi.org/10.5281/zenodo.2599732> (Davison, Wearn, Chapman, & Ewers, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Davison CW, Chapman PM, Wearn OR, Bernard H, Ewers RM. Shifts in the demographics and behavior of bearded pigs (*Sus barbatus*) across a land-use gradient. *Biotropica*. 2019;00:1–11. <https://doi.org/10.1111/btp.12724>