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1 **Bearded pig (*Sus barbatus*) utilisation of a fragmented forest-oil palm**

2 **landscape in Sabah, Malaysian Borneo**

3 Running head: Bearded pigs in fragmented tropical landscapes

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21 **Context:** Oil palm plantations have become a dominant landscape in Southeast

22 Asia, yet we still understand relatively little about the ways wildlife are adapting to

23 fragmented mosaics of forest and oil palm. The bearded pig is of great ecological,

24 social, and conservation importance in Borneo and is declining rapidly due to habitat

25 loss and overhunting.

26 **Aims:** We sought to assess how the bearded pig is adapting to oil palm expansion

27 by investigating habitat utilisation, activity patterns, body condition, and minimum

28 group size in a mosaic composed of forest fragments and surrounding oil palm.

29 **Methods:** We conducted our study in Sabah, Malaysian Borneo, in and around the

30 Lower Kinabatangan Wildlife Sanctuary, an area consisting of secondary forest

31 fragments (ranging 1200-7400 ha) situated within an extensive oil palm matrix. We

32 modelled bearded pig habitat use in forest fragments and oil palm plantations using

33 survey data from line transects. Camera traps placed throughout the forest

34 fragments were used to assess pig activity patterns, body condition, and minimum

35 group size.

36 **Key results:** All forest transects and 80% of plantation transects showed pig

37 presence, but mean pig signs per transect were much more prevalent in forest

38 (70.00 ± 13.00 SE) than in plantations (0.91 ± 0.42 SE). Pig tracks had a positive

39 relationship with leaf cover and a negative relationship with grass cover; pig rooting

40 sites had a positive relationship with wet and moderate soils as compared to drier

41 soils. Pigs displayed very good body condition in forests across the study area,

42 aggregated in small groups (mean = 2.7 ± 0.1 SE individuals), and showed diurnal

43 activity patterns that were accentuated for groups with piglets and juveniles.

44 **Conclusions:** Our findings suggest that bearded pigs in our study area regularly

45 utilise oil palm as habitat, given their signs in most oil palm sites surveyed. However,

46 secondary forest fragments adjacent to oil palm remain the most important habitat

47 for the bearded pig, as well as many other species, and therefore must be

48 conserved.

49 **Implications:** Consistent bearded pig presence in oil palm is a potential indication of

50 successful adaptation to agricultural expansion in the study area. The good physical

51 health displayed by most pigs may result in part from year-round cross-border fruit

52 subsidies from oil palm plantations, whilst the predominance of diurnal activity

53 (especially by groups containing piglets and juveniles) may indicate a behavioural

54 response to predation or human hunting. However, the net effect of oil palm

55 expansion in the region on bearded pig populations remains unknown.

56 **Additional keywords:** activity pattern; body condition; habitat use; Lower

57 Kinabatangan; matrix; mosaic; Suidae

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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

92   response of wild pigs to oil palm expansion is understudied. The Eurasian wild boar

93   (*Sus scrofa*), perhaps the best-studied wild pig species, has been known to reach

94   high abundances in forest remnants adjacent to oil palm, likely benefitting from fruit

95   subsidies provided by plentiful, year-round fruit production in plantations (Ickes

96   2001). However, whether this pattern is consistent in other areas and with other wild

97   pig species has yet to be investigated. Given the important role played by wild pigs in

98   structuring plant communities (Ickes et al. 2001; Ickes et al. 2003; Cole et al. 2012),

99   understanding how pigs (native or introduced) are responding to tropical land use

100   change could hold major ecological implications for forest-oil palm landscapes.

101   The bearded pig (*Sus barbatus*) has great ecological, social, and conservation

102   importance in its native Sundaland (Caldecott et al. 1993). As a forest-dwelling suid

103   (Bernard et al. 2013), it is adapted to a migratory lifestyle in response to mast fruiting

104   cycles, although it can also be found in oil palm plantations (Yue et al. 2015). It is

105   also an ecosystem engineer, removing saplings to build its nests, turning over soil

106   through its rooting behaviour, and acting as a seed predator of many rainforest tree

107   species (Boogaarts 1938; Curran and Leighton 2000; Curran and Webb 2000; Linkie

108   and Sadikin 2003). Bearded pigs are known to be an important prey species for large

109   predators including the Sunda clouded leopard (*Neofelis diardi*), estuarine crocodile

110   (*Crocodylus porosus*), and reticulated python (*Python reticulatus*) (Pfeffer and

111   Caldecott 1986; Caldecott 1988; Auliya 2003; Ross et al. 2013). Additionally, the

112   bearded pig has been an important protein source for humans in Borneo for over

113   35,000 years (Medway 1958), of which it has been the primary mammalian target for

114   at least 15,000 years (Harrison 1998). The bearded pig continues to provide the

115   majority of wild meat consumed in Borneo, accounting for between 54 and 97% of

116   wild meat consumption by weight (Bennett et al. 2000; Chin 2001; Puri 2005). As a

117   result of its popularity as a game species, overhunting (exacerbated by habitat

118   fragmentation), along with habitat loss, has led to an estimated 30% decline in

119   bearded pig populations over a recent 21-year period, leading to its designation as a

120   Vulnerable species on the IUCN Red List (Kawanishi et al. 2008). Given its vital

121   ecological functions and abundant provision of protein, sustainable bearded pig

122   management should be a high conservation priority in Borneo.

123   Basic ecological research on bearded pig adaptation to forest-oil palm

124   mosaics is therefore a clear first step. We studied several aspects of bearded pig

125   natural history in a fragmented alluvial forest that serves as both an important wildlife

126   corridor and a case study for tropical landscapes characterised by interspersed

127   patches of forest and oil palm. We sought to assess how the bearded pig is adapting

128   to oil palm expansion by comparing pig habitat use between secondary forest

129   fragments and oil palm plantations, as well as collecting data in forest fragments on

130   daily and seasonal activity patterns, minimum group size, and body condition. We

131   present management implications from these findings and outline directions for

132   future research.

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134   **Materials and methods**

135   *Study area*

136   The study was conducted in the landscape surrounding Danau Girang Field Centre

137   (5.413711, 118.037646), located in the Lower Kinabatangan floodplain in eastern

138   Sabah, Malaysia. The Lower Kinabatangan Wildlife Sanctuary (LKWS) consists of

139   ten protected forest lots. The lots display a range of sizes (1200 - 7400 ha) and

140   structural connectivity, including narrow riparian corridors and small areas of

141   privately-owned forest (Abram et al. 2014). In addition to designating protections of

142   wildlife sanctuaries, the Sabah Wildlife Enactment of 1997 declared the bearded pig

143   a protected species, although hunting is allowed outside of protected areas with a

144   license. Mean annual precipitation is approximately 3460 mm, with mean monthly

145   temperatures ranging from 23-40°C (B. Goossens, unpubl. data). In drier areas, the

146   landscape is dominated by secondary lowland dipterocarp forest, with some areas of

147   riparian forest (Ancrenaz et al. 2004). Frequent inundation by flooding causes zones

148   of low-stature forest and grassland, with wetter regions encompassing areas of

149   mangrove and swamp forest (Ancrenaz et al. 2004; Estes et al. 2012). Between

150   1960 and 1995, large parts of the region were logged for hardwoods and cleared for

151   agriculture (Gillespie et al. 2012; Gaveau et al. 2014). Oil palm plantations now

152   occupy at least 48% of the floodplain (Abram et al. 2014).

153   *[Approximate location of Figure 1]*

154   *Data collection*

155   Bearded pig presence was assessed using line transects, and data on body

156   condition, activity patterns, and minimum group size were collected using camera

157   traps. Ten line transects (100 m long x 10 m wide) were randomly placed (minimum

158   2 km apart) in both oil palm and secondary forest sites (Fig. 1). Each transect was

159   surveyed five times by a team of 2-5 surveyors between February and April 2014.

160   One observer (K. Love) was present for all data collection, allowing for

161   standardization of protocol. Intervals between surveys ranged from 12-16 days to

162   allow sufficient time for sign accumulation. Surveyors indirectly recorded pig habitat

163   utilisation along each transect by noting the number of tracks, rooting sites, mud

164   grazes, wallowing holes, scat, and nests (Payne et al. 1985). Pig signs were cleared

165   or marked between transect surveys to prevent duplicate counts. The quantity of

166   individual signs was recorded for each sign type on each transect, and all equivalent

167   signs within 1 m^2 were used as a single sign count to standardize tallies. A Topofil

168   thread measuring device (Fremaco Devices Inc., Owen Sound, Canada) and

169   compass were used for straight surveying that ensured comparable transect

170   pathways during repeat surveys. Transects were examined with surveyors spread

171   equally across the 10 m wide transect.

172   Soil texture from each survey was categorised using a 1-5 score based on

173   moisture level (1: very wet, 5: dry and dusty). Understory density was recorded every

174   25 m of each transect using a Robel pole, which contained 47 equally partitioned 2

175   cm stripes. Density estimations were made at a height of 0.5 m above ground level,

176   and a distance of 10m between observers. Substratum composition for each transect

177   was estimated from a 2 m^2 plot placed every 25 m along transects, in which the

178   percentage of the following substrata were recorded: leaves, soil, grass, shrub and

179   stone (Fig. S1). Using ImageJ (version 1.45S) software, we calculated average

180   canopy cover by taking canopy photos at a height of 1.65 m in the middle of each

181   substrate plot. We used Google Earth (version 7.1.2.2041) to calculate the distance

182   from transect mid-sections to water sources and forest-plantation boundaries. For

183   the purpose of the study, we assumed that pigs did not cross the main river during

184   the short sampling period, as crossings are mainly reported during migratory

185   behaviour rather than during typical daily movements (Meijaard 2000).

186   *[Approximate location of Figure 2]*

187   To assess bearded pig body condition and minimum group size, we used an

188   extensive network of 110 camera trapping stations spread across the same forest

189   fragments as the line transects, although covering a much larger area than the

190   transect locations (Figs. 1, 2). Camera traps were not placed in oil palm plantations

191   due to the high risk of theft. Camera trap images of bearded pigs were collected from

192   November 2011 to December 2013 using Reconyx HC500, Hyperfire, and PC800

193   infrared digital camera traps. Each camera station was positioned 30-50 cm off the

194   ground along ridges and existing wildlife trails. Physical condition of pigs was

195   assessed following the categories of Wong et al. (2005) (Table S2). Pigs were given

196   a fat index of 1-5, with 5 being the best possible body condition. Pig age classes (i.e.

197   infant, juvenile, sub-adult and adult) and time of activity (date and time of day) were

198   documented. For photographs of pig groups taken within 1 hr of one another, we

199   considered the independent sample to be the photograph with the highest number of

200   individuals (Bernard et al. 2013, Brodie and Giordano 2013). We removed images

201   that were blurred, too dark, blocked from view, or otherwise unsuitable for assessing

202   body condition.

203

204   *Data Analysis*

205   We used generalized linear mixed effects models in the *lme4* package (Bates et al.,

206   2014) to model the number of bearded pig tracks and rooting sites as a function of

207   nine habitat variables: the percentage ground covered by leaves, soil, shrub, grass,

208   and stone, the distance to the nearest permanent water source (river, oxbows,

209   and/or tributaries) and to the nearest forest-oil palm boundary, ground fruit presence,

210   and soil texture (with textures 1 and 2 considered "wet", texture 3 considered

211   "moderate", and textures 4 and 5 considered "dry"). We used a correlation matrix to

212   ensure that all variables were relatively independent ($| r | < 0.6$). We did not model

213   wallow holes, mud grazes, scat, or nests because there were insufficient frequencies

214 of these signs to produce statistically rigorous results. These signs are known to

215 appear relatively infrequently (wallow holes, mud grazes, nests), or are difficult to

216 detect due to high decomposition rates in rainforest conditions (scat, e.g. Heise-

217 Pavlov & Meade 2012). We modelled the number of rooting sites only in forest

218 because there were also insufficient frequencies of rooting sites in oil palm. We

219 included site as a random effect to account for dependence between the transects at

220 each site, and in our models of pig tracks we included habitat type (forest or oil palm)

221 as a variable in every model to account for the strong effects of habitat type on the

222 other environmental variables. We scaled and centered all continuous variables prior

223 to analysis. We created generalized linear mixed effects models for the negative

224 binomial family, which is useful for modelling overdispersed ecological count data

225 (Lindén and Mäntyniemi, 2011). To focus modelling on the most influential variables,

226 we first compared generalized linear mixed effects models of each of the habitat

227 variables independently to a global model and a null model only containing the

228 intercept. We selected the best models to determine the strongest predictors of pig

229 tracks and rooting sites using the Akaike information criterion corrected for small

230 samples sizes (AICc) (Burnham and Anderson, 2004). We considered models with

231 ∆AICc values of at least two less than the null model as plausible models, and

232 considered the model with the lowest AICc value as our best model. Model

233 parameters were determined to be significant if the 95% confidence interval around

234 the estimate did not overlap zero. After we determined which variables had a

235 significant effect on the bearded pig signs independently, we modelled all

236 combinations of significant parameters to determine if any models containing a

237 combination of variables performed better than the single-variable models. All

238 models were run in R statistical software Version 3.2.4. (R Core Team, 2000).

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239   All other analyses were conducted using Minitab (version 17) and R (version

240   3.0.1) statistical software. Anderson darling and Shapiro-Wilk tests were used to test

241   for normally distributed pig sign and activity data. We used a two-sample t-test to test

242   for differences in the mean number of detected pig signs between forest and oil

243   palm, based on the total number of signs per transect.

244   To characterise pig activity patterns, we pooled photographs in two different

245   ways: (i) using four intervals (0300 – 0859 h, 0900 – 1459 h, 1500 – 2059 h and

246   2100 – 0259 h) representing dawn, daytime, dusk and night (Payne et al. 1985; Ross

247   et al. 2013); and (ii) using two intervals, diurnal (0600-1759 h) and nocturnal (1800-

248   0559 h). The same values could be used throughout the year due to the small

249   variation in day length in our study area. Chi-squared tests were used to compare

250   differences in activity between time classifications. We used body condition scores

251   (Table S3) to determine average body condition for each month. As there were likely

252   pigs that were not captured in our camera trap photographs, group size estimates

253   are considered minimum group sizes and may be underestimates. However, we

254   report group sizes in line with other camera trap studies of wild pigs (Linkie and

255   Sadikin 2003, Bengsen et al. 2011).

256   *[Approximate location of Table 1]*

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258   **Results**

259   *Habitat use*

260   A total of 93 transect surveys (forest = 44, plantation = 49) across 20 transects

261   (forest = 10, plantation = 10) confirmed bearded pig presence in all transects in

262   forest and 8 of 10 transects in oil palm plantations. Pig sign was 1-2 orders of

263   magnitude more prevalent (t = 13.07, df = 18, p < 0.01) in forest than in plantation

264   transects (Table 1). When comparing the models of pig tracks and rooting sites

265   containing each habitat variable independently and a global model to a null model,

266   every model performed better than the null model; this pattern emerged because the

267   habitat variable (i.e. 'forest' or 'oil palm') had a strong, significant effect in every

268   model, with forest having significantly more pig tracks and rooting sites than oil palm.

269   In the single-variable models of pig tracks, all models had ΔAICc values of at

270   least two less than the null model because the habitat type variable was highly

271   significant in every model. The other significant variables were percentage of ground

272   covered by leaves and grass. When modelling pig tracks using the combination of

273   the two variables (with habitat type remaining as a controlling variable), the model of

274   percentage of ground covered by leaves still had the lowest AICc value (Table S5).

275   Leaf cover had a significant positive relationship with number of pig tracks (Table 2).

276   Grass cover had a significant negative effect on number of pig tracks when it was the

277   only variable in the model (Table 2).

278   In the single-variable models of pig rooting sites in forest, the only significant

279   variable was soil texture. Moderate and wet soils both had significantly more pig

280   rooting sites than dry soils (Table 2).

281   *[Approximate location of Table 2]*

282   *Minimum group size and encounter rate*

283   Camera traps documented a total of 1995 independent encounters of bearded pigs,

284   with a mean minimum group size of 2.68 individuals (± 0.1 SE, min = 1, max = 32).

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285   Pigs were recorded at all camera sites, with a total camera trap encounter rate of

286   0.63 independent photographs/100 hours.

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288   *Body condition and minimum group size*

289   From the 1995 independent encounters, 4161 individual pigs were scored to body

290   condition. The majority of pigs possessed 'Very Good' (59.4%) and 'Good' body

291   condition scores (35.6%), with relatively few pigs defined as 'Fair' (4.6%) and 'Poor'

292   (0.4%). No pigs classified as 'Very Poor' were identified. During each month of the

293   sampling period, >90% of individual pigs detected had a body condition of 'Very

294   Good' or 'Good'.

295   *[Approximate location of Figure 3]*

296   *Activity patterns*

297   Activity patterns varied significantly over the course of 24 hours (Chi-Sq. = 168.25,

298   df = 3, p < 0.01), with far fewer pig occurrences at night (Chi-Sq. = 129.87, df = 1,

299   p < 0.01). Activity was mostly diurnal, peaking early in the morning from 0600 – 0700

300   h, and again from 1700 – 1900 h (Fig. 3). Groups containing infants and juveniles (n

301   = 218) were almost exclusively active during daytime hours (Fig. 3).

302   **Discussion**

303   We show that bearded pigs are widespread in a fragmented forest-oil palm mosaic

304   landscape increasingly typical of Southeast Asia. Bearded pigs in our study region

305   appear to preferentially utilise secondary forest habitat as compared to oil palm

306   plantations. Pig habitat utilisation is positively associated with leaf cover and

307 negatively associated with grass cover. Additionally, pigs preferentially used wet and

308 moderate soil types (as compared to drier soils) for rooting behaviour. Bearded pigs

309 tended to aggregate in small groups (mean = 2.7 individuals ± 0.1 SE) and the vast

310 majority appeared to be in 'Good' or 'Very Good' physical condition (Table S3),

311 suggesting that the population of bearded pigs detected at camera traps was

312 generally healthy throughout the study period. Pigs were largely diurnal, with activity

313 peaks at dawn and dusk, and groups containing infant and juvenile pigs were even

314 more active during the day than groups without piglets and juveniles. These findings

315 provide a basic ecological foundation for future work on the adaptation of a

316 threatened large mammal species to extensive anthropogenic influences, especially

317 deforestation, habitat fragmentation, and over-hunting.

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321 *Implications of bearded pig habitat use*

322 Bearded pig signs were recorded on all forest and most oil palm transects in our

323 study area, although far more signs were documented in forest than oil palm. This

324 pattern could either reflect a difference in habitat utilisation by the pigs or a

325 difference in sign detectability. Given the strong influence of habitat and substrate

326 features in our models, it is likely that the much more abundant pig sign in forest

327 does in fact reflect a higher degree of utilisation of forest by pigs. The positive

328 relationship between leaf cover and pig tracks suggests that certain habitat features

329 within forest (e.g. trees, leaf litter) are preferred by pigs. Additionally, the negative

330   relationship between grass cover and pig tracks may help explain the lower

331   presence of pig tracks in oil palm, which contained a higher proportion of grass cover

332   than forest did (mean grass cover – oil palm: 33.9%, forest: 8.1%). Lower

333   detectability of tracks in grass could also play a role in this relationship. There is also

334   a strong possibility that bearded pigs are using forest and oil palm habitats

335   differently; for example, we did not record wallowing, mud grazing, or nest building

336   behaviours in plantations (Table 1). Furthermore, oil palm habitats may have less

337   favourable conditions for rooting behaviour, given the hotter and drier conditions as

338   compared to forest (Luskin and Potts 2011). Our models show that rooting behaviour

339   was positively associated with wet and moderate soils, which were more frequently

340   found in forest (mean soil texture – forest: 3.4, oil palm: 4.6; lower values are wetter).

341   These patterns align with other studies on wild pig habitat use showing lower levels

342   of pig sign in grassy habitats (e.g. Welander 2000) and a positive relationship

343   between rooting activity and moist soils (e.g. Mitchell et al. 2008).

344   Whilst our results suggest that bearded pigs are using forest more than oil

345   palm to meet many of their ecological needs, they also suggest that bearded pigs

346   may be adapting somewhat successfully to fragmented forest-oil palm landscapes,

347   an encouraging sign for conservation. The healthy body condition of pigs as well as

348   the utilisation of 80% of the oil palm sites surveyed point to the presence of some

349   resources of value to pigs in oil palm. Feral pigs take advantage of agricultural areas

350   near forest habitat in many parts of the world, often increasing in density (Caley

351   1993, Ickes 2001) and/or body size (Dexter 2003) as a result of the extra food

352   subsidies. However, there also appear to be thresholds of agricultural area relative to

353   natural habitat area at which pigs are unable to persist due to their need to access

354   forest and woodlands (Choquenot & Ruscoe 2003, Kawanishi et al. 2008). Finally, it

355 is possible that oil palm plantations may be having adverse effects on bearded pigs

356 by functioning as an "ecological trap" that decouples typical cues from true habitat

357 quality (Weldon & Haddad 2005), attracting pigs to favourable habitat features or

358 food resources and thereby making them more vulnerable to hunting for subsistence,

359 commercial sale, pest control, and/or sport, as is the case with *S. scrofa* in Sumatra

360 (Luskin et al. 2014). However, our study notes only general patterns of bearded pig

361 habitat use; further research in a variety of landscapes is needed to ascertain the net

362 effect of oil palm expansion on bearded pig habitat utilisation, behaviour, and

363 resource selection.

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367 *Body condition and fruit availability*

368 Bearded pig body size and condition is known to fluctuate dramatically in sync with

369 the abundance of resources available and the competition for those resources

370 (Wong et al. 2005, Luskin & Ke, in press). Therefore, the year-round good body

371 condition we observed could speak to significant hunting-limited pig densities

372 (as observed elsewhere, e.g. Chin 2001), abundant food availability within our study

373 landscape, or both. Bearded pig meat is easily the most preferred species of wild

374 meat in Borneo, accounting for 54-97% of the wild meat consumed in non-Muslim

375 rural areas on the island (Bennett et al. 2000, Chin 2001, Puri 2005). However, there

376 have been no studies quantifying the effects of hunting on bearded pig populations in

377 the Kinabatangan; while hunting is known to occur, it is not clear how important it is

378 in limiting bearded pig densities and thereby influencing body condition.

379   While bearded pigs feed on leaves, roots, fungi, invertebrates, small

380 vertebrate, and carrion, their cycles of body condition, growth, and breeding have

381 been mainly linked to fruit availability (Caldecott et al. 1993, Curran & Webb 2000,

382 Wong et al. 2005, Luskin & Ke in press). Oil palm fruit subsidies from plantations are

383 widespread in our study area, and *Ficus* sp. are abundant in the LKWS (Azmi 1998)

384 and are likely to be a key food source. *Ficus* sp. fruit has been described as a

385 'keystone resource' that helps sustain bearded pig populations during the extended,

386 inter-mast intervals of low productivity that characterise Southeast Asian rainforests

387 (Appanah 1985; Wong et al. 2005). However, in a human-modified, fragmented

388 landscape like our study area, it is unclear how bearded pig body condition responds

389 to periods of extended drought. The constant supply of year-round fruit from oil palm

390 plantations could mitigate the population-suppressing effects of this natural cycle for

391 bearded pigs in the Lower Kinabatangan, but the complex interactions between oil

392 palm fruit subsidies, rainforest phenological cycles, habitat fragmentation, and

393 bearded pig population dynamics have yet to be untangled.

394

395 *Behavioural implications of minimum group size and activity patterns*

396 Minimum group sizes in the LKWS averaged 2.7 (± 0.1 SE) individuals, as compared

397 to 1.9 (± 0.3 SE) reported in Kerinci Seblat National Park in Sumatra (Linkie and

398 Sadikin 2003). Given the distribution of pigs throughout most of our study area, the

399 lack of large-scale herding behaviour, and the continuous abundance of oil palm fruit

400 subsidies, pig populations of the LKWS may be largely sedentary (Caldecott et al.

401 1993). Caldecott et al. (1993) reference a bearded pig population state similar to this

402 in the *Koompassia-Burseraceae* forest in Peninsular Malaysia, characterised by

403 populations with local movements that exploit concentrated, predictable food

404 resources that allow for high breeding and growth rates. This would appear to be the

405 closest known population state corresponding to the bearded pigs in our study,

406 although further research is necessary to corroborate this hypothesis.

407   Bearded pigs without young were mostly diurnal, with the highest peaks of

408 activity at dawn (0600-0700 h) and dusk (1700-1900 h) and low levels of activity at

409 night (Fig. 3). These results accord with previous research showing that pigs tend to

410 be diurnal (Pfeffer and Caldecott 1986; Linkie and Sadikin 2003; Ross et al. 2013)

411 and avoid the hottest hours of the day (Caley 1997, Saunders and Kay 1991).

412 Additionally, bearded pigs are known to alter their activity patterns in response to

413 nocturnal clouded leopard hunting patterns (Ross et al. 2013), suggesting that their

414 diurnal tendencies may be in part a response to the clouded leopards present in the

415 LKWS. Groups of pigs including juveniles and infants were more strictly diurnal than

416 those containing only adults, with almost no activity recorded at night (Fig. 3). This

417 accentuated diurnal pattern could be due to the particular vulnerability of young pigs

418 to predation by clouded leopards; past research has shown that female bearded pigs

419 (which raise the young) respond more strongly to clouded leopard activity patterns

420 than male bearded pigs (Ross et al. 2013).

421   In addition to clouded leopard activity patterns, human hunting poses a major

422 threat to bearded pig populations in Borneo (Kawanishi et al. 2008). Bearded pig

423 hunting is extremely common in Borneo (Bennett et al. 2000; Puri 2005), and illegal

424 poaching occurs in our study area (K. Love, pers. obs.). More data on bearded pig

425 movement ecology, e.g. GPS collaring studies collecting location and accelerometer

426 data, are needed to determine to what extent this human hunting activity influences

427 bearded pig activity patterns. Tracking fine-scale pig movements in mixed

428 landscapes would build upon our results on relative habitat utilisation by illuminating

429 the role of forest fragments in bearded pig foraging and behavioural ecology. These

430 data would help determine the minimum threshold, quality, and configuration of

431 forest cover needed to ensure stable and genetically diverse bearded pig

432 populations in the Lower Kinabatangan region and other fragmented tropical

433 landscapes.

434

435 **Conclusions**

436 In a fragmented tropical forest-oil palm landscape, bearded pig signs were found in

437 all secondary forest sites and most oil palm plantation sites. This prevalence

438 throughout the mosaic, coupled with consistently high body condition scores,

439 indicates some adaptability of bearded pigs to fragmented landscapes. Oil palm

440 plantations may have some conservation value for the species by providing valuable

441 supplemental resources to primarily forest-dwelling pigs, whilst likely unable to

442 provide the habitat structure (e.g. wallowing and nest sites) needed to sustain

443 bearded pig populations in the absence of forest. Bearded pig groups, especially

444 those containing piglets and juveniles, are diurnal in the Lower Kinabatangan region,

445 possibly in response to predation or human hunting.

446   Our findings provide foundational data on bearded pig habitat use, activity

447 patterns, minimum group size, and body condition in a forest-oil palm mosaic,

448 providing a starting point for future research on how the threatened pig is adapting to

449 these important and expanding landscapes in Southeast Asia. Future work should

450 extend this study by investigating bearded pig movements through mixed

451 landscapes, migration patterns (or lack thereof) in different parts of Borneo, and

452 genetic diversity and gene flow in relation to fragmentation, as well as the effects of

453 human hunting on bearded pigs in both oil palm plantations and forest fragments.

454 Understanding at finer scales how individual resources and microhabitats within

455 forest and oil palm are utilized for different purposes (e.g. thermoregulation, predator

456 avoidance, food acquisition) by bearded pigs will provide a more detailed picture of

457 their ecological requirements and conservation needs. In the meantime, given that

458 our results suggest that pigs preferentially utilise forest habitat much more than oil

459 palm, protection of secondary forest fragments adjacent to oil palm plantations

460 should be a major conservation priority in order to ensure healthy bearded pig

461 populations in the Lower Kinabatangan.

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475

476   **Conflict of Interest Statement**

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483

484   **References**

485   Abram, N. K., Xofis, P., Tzanopoulos, J., MacMillan, D. C., Ancrenaz, M., Chung, R.,

486   Peter, L., Ong, R., Lackman, I., Goossens, B., Ambu, L., and Knight, A. T.

487   (2014). Synergies for improving oil palm production and forest conservation in

488   floodplain landscapes. *PLoS ONE* **9**, e95388.

489   Alfred, R., Ahmad, A. H., Payne, J., Williams, C., Ambu, L. N., How, P. M., and

490   Goossens, B. (2012). Home range and ranging behaviour of Bornean

491   elephant (*Elephas maximus borneensis*) females. *PLoS ONE* **7**, e31400

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

493 (2004). Determination of ape distribution and population size using ground

494 and aerial surveys: a case study with orang-utans in lower Kinabatangan,

495 Sabah, Malaysia. *Animal Conservation* **7**, 375-385.

496 Appanah, S. (1985). General flowering in the climax rain forests of South-east Asia.

497 *Journal of Tropical Ecology* **1**, 225-240.

498 Aratrakorn, S., Thunhikorn, S., and Donald, P. F. (2006). Changes in bird

499 communities following conversion of lowland forest to oil palm and rubber

500 plantations in southern Thailand. *Bird Conservation International* **16**, 71-82.

501 Auliya, M. (2003). A reticulated python (*Python reticulatus*) preys on an adult

502 Sulawesi pig (*Sus celebensis*). *Asian Wild Pig News* **3,** 11-12.

503 Azmi, R. (1998). Natural vegetation of the Kinabatangan floodplain. Part 1:

504 background and preliminary checklist. (WWF-Malaysia: Kota Kinabalu.)

505 Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-

506 Effects Models Using lme4. Journal of Statistical Software, **67**, 1-48.

507 <doi:10.18637/jss.v067.i01>.

508 Bengsen, A. J., Leung, L. K.-P., Lapidge, S. J., and Gordon, I. J. (2011). Using a

509 general index approach to analyze camera-trap abundance indices.

510 *The Journal of Wildlife Management* **75**, 1222-1227.

511 Bennett, E. L., Nyaoi, A. J., and Sompud, J. (2000). Saving Borneo's bacon: the

512 sustainability of hunting in Sarawak and Sabah. In 'Hunting for Sustainability

513 in Tropical Forests'. (Eds J. G. Robinson and E. L. Bennett.) pp. 305-324.

514 (Columbia University Press: New York.)

515 Bernard, H., Ahmad, A. H., Brodie, J., Giordano, A. J., Lakim, M., Amat, R., Koh,

516 S.P.H., Khee, L.S., Tuuga, A., Malim, P. T., Lim-Hasegawa, D., Wai, Y.S.,

517 and

518   Sinun, W. (2013). Camera-trapping survey of mammals in and around Imbak

519   Canyon Conservation Area in Sabah, Malaysian Borneo. *The Raffles Bulletin*

520   *of Zoology* **61**, 861-870.

521 Boogaarts, M. (1938). Nangoeih's. In 'De Nederlandsch-Indische Jager 1'. (Ed. M.

522   Boogaarts.) pp. 305, 308. [Freely translated from Dutch by Erik Meijaard]

523   Caldecott, J. O. (1988). Hunting and wildlife management in Sarawak. (IUCN:

524   Gland and Cambridge.)

525 Brodie, J. F., and Giordano, A. (2013). Lack of trophic release with large mammal

526   predators and prey in Borneo. *Biological Conservation* **163,** 58-67.

527 Burnham, K. P., and Anderson, D. R. (2004). Multimodel inference: understanding

528   AIC and BIC in model selection. *Sociological Methods & Research* **33,**

529   261-304.

530 Caldecott, J. O., Blouch, R. A., and Macdonald, A. A. (1993). The bearded pig (*Sus*

531   *barbatus*). In 'Pigs, Peccaries and Hippos: Status Survey and Conservation

532   Action Plan'. (Ed. W. L. Oliver.) pp. 136-145. (IUCN: Gland.)

533 Chey, V. K. (2006). Impacts of forest conversion on biodiversity as indicated by

534   moths. *Malayan Nature Journal* **57**, 383-418.

535 Chin, C. (2001). Pig in the pot: comments on Sus barbatus in the hunting lifestyle of

536   the Penan in Sarawak (Borneo). *Asian Wild Pig News* **1**, 10-12. Chung, A. Y.

537   C., Eggleton, P., Speight, M. R., Hammond, P. M., and Chey, V. K. (2000).

538   The diversity of beetle assemblages in different habitat types in Sabah,

539   Malaysia. *Bulletin of Entomological Research* **90**, 475-496.

540 Cole, R. J., Litton, C. M., Koontz, M. J., and Loh, R. K. (2012). Vegetation recovery

541   16 years after feral pig removal from a wet Hawaiian forest. *Biotropica* **44**,

542   463-471. Curran, L. M. and Leighton, M. (2000). Vertebrate responses to

543   spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae.

544   *Ecological Monographs* **70**, 101–128.

545   Curran, L.M. and C.O. Webb. (2000). Experimental tests of the spatiotemporal scale

546   of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs*

547   **70**, 129–148.

548   Danielsen, F., and Heegaard, M. (1995). Impact of logging and plantation

549   development on species diversity: a case study from Sumatra. In

550   'Management of Tropical Forests: Towards an Integrated Perspective'. (Ed.

551   Ø. Sandbukt.) pp. 73-92. (University of Oslo – Centre for Development and

552   the Environment: Oslo.)

553   Davis, A. L. V., and Philips, T. K. (2005). Effect of deforestation on a southwest

554   Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery

555   of Ankasa conservation area. *Environmental Entomology* **34**, 1081-1088.

556   Edwards, F. A., Edwards, D. P., Larsen, T. H., Hsu, W. W., Benedick, S., Chung, A.,

557   Khen, Wilcove, D. S., and Hamer, K. C. (2014). Does logging and forest

558   conversion to oil palm agriculture alter functional diversity in a biodiversity

559   hotspot? *Animal Conservation* **17**, 163-173.

560   Estes, J. G., Othman, N., Ismail, S., Ancrenaz, M., Goossens, B., Ambu, L. N.,

561   Estes, A. B., and Palmiotto, P. A. (2012). Quantity and configuration of

562   available elephant habitat and related conservation concerns in the lower

563   Kinabatangan Floodplain of Sabah, Malaysia. *PLoS ONE* **7**, e44601.

564 Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y. C., Eggleton,

565 P., and Foster, W. A. (2010). Oil palm expansion into rain forest greatly

566 reduces ant biodiversity in canopy, epiphytes, and leaf litter. *Basic and*

567 *Applied Ecology* **11**, 337-345.

568 Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P.

569 F., and Phalan, B. (2008). How will oil palm expansion affect biodiversity?

570 *Trends in Ecology and Evolution* **23**, 538-545.

571 Foster, W. A., Snaddon, J. L., Turner, E. C., Fayle, T. M., Cockerill, T. D., Ellwood,

572 M. D. F., Broad, G. R., Chung, A. Y. C., Eggleton, P., Khen, C. V., and Yusah,

573 K. M. (2011). Establishing the evidence base for maintaining biodiversity and

574 ecosystem function in the oil palm landscapes of South East Asia.

575 *Philosophical Transactions of the Royal Society B* **366**, 3277-3291.

576 Fukuda, D., Tisen, O. B., Momose, K., and Sakai, S. (2009). Bat diversity in the

577 vegetation mosaic around a lowland dipterocarp forest of Borneo. *The Raffles*

578 *Bulletin of Zoology* **57**, 213-221.

579 Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K.,

580 Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N., and Meijaard, E. (2014).

581 Four decades of forest persistence, clearance and logging on Borneo. *PLoS*

582 *ONE* **9**, e101654.

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

584   Scroggie, M. P. (2012). Conservation of amphibians in Borneo: relative value

585   of secondary tropical forest and non-forest habitats. *Biological Conservation*

586   **152**, 136-144.

587 Gilroy, J. J., Prescott, G. W., Cardenas, J. S., Castañeda, P. G. P., Sánchez, A.,

588   Rojas-Murcia, L. E., Uribe, C. A. M., Haugaasen, T., and Edwards, D. P.

589   (2015). Minimizing the biodiversity impact of Neotropical oil palm

590   development. *Global Change Biology* **21**, 1531-1540.

591 Glor, R. E., Flecker, A. S., Benard, M. F., and Power, A. G. (2001). Lizard diversity

592   and agricultural disturbance in a Caribbean forest landscape. *Biodiversity and*

593   *Conservation* **10**, 711-723.

594 Harrison, T. (1998). Vertebrate faunal remains from the Madai caves (MAD 1/28),

595   Sabah, East Malaysia. *Bulletin of the Indo-Pacific Prehistory Association* **17**,

596   85-92.

597 Ickes, K. (2001). Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland

598   dipterocarp rain forest of peninsular Malaysia. *Biotropica* **33**, 682-690.

599 Ickes, K., Dewalt, S. J., and Appanah, S. (2001). Effects of native pigs (*Sus scrofa*)

600   on woody understorey vegetation in a Malaysian lowland rain forest. *Journal*

601   *of Tropical Ecology* **17**, 191-206.

602 Ickes, K., Dewalt, S. J., and Thomas, S. C. (2003). Resprouting of woody saplings

603   following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology*

604   **91,** 222-233.

605 International Union for Conservation of Nature (IUCN). 2016. IUCN Red List of

606   Threatened Species. www.iucnredlist.org. Accessed on 4 August, 2015.

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

608   Threatened Species. E.T41772A10559190.

609   http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41772A10559190.en.

610   Accessed on 9 October, 2016.

611 Koh, L.P. and Wilcove, D. S. (2008). Is oil palm agriculture really destroying tropical

612   biodiversity? *Conservation Letters* **1**, 60-64.

613 Konopik, O., Steffan-Dewenter, I., and Grafe, T. U. (2015). Effects of logging and oil

614   palm expansion on stream frog communities on Borneo, Southeast Asia.

615   *Biotropica* **47**, 636-643.

616 Lindén, A., and Mäntyniemi, S. (2011). Using the negative binomial distribution to

617   model overdispersion in ecological count data. *Ecology* **92**, 1414-1421.

618 Linkie, M., and Sadikin, L. (2003). The bearded pig in Kerinci Seblat National Park,

619   Sumatra. *Asian Wild Pig News* **3**, 3-9.

620 Liow, L. H., Sodhi, N. S., and Elmqvist, T. (2001). Bee diversity along a disturbance

621   gradient in tropical lowland forests of south-east Asia. *Journal of Applied*

622   *Ecology* **38**, 180-192.

623 Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., and Davies, R. G. (2014).

624   Functional structure of ant and termite assemblages in old growth forest,

625   logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and*

626   *Conservation* **23**, 2817-2832.

627 Luskin, M. S., Christina, E. D., Kelley, L. C., and Potts, M. D. (2014). Modern hunting

628   practices and wild meat trade in the oil palm plantation-dominated landscapes

629   of Sumatra, Indonesia. *Human Ecology* **42**, 35-45.

630 Luskin, M. S., and Potts, M. D. (2011). Microclimate and habitat heterogeneity

631   through the oil palm lifecycle. *Basic and Applied Ecology* **12**, 540-551.

632   MacKenzie, D. I., and Bailey, L. L. (2004). Assessing the fit of site-occupancy

633   models. *Journal of Agricultural, Biological, and Environmental Statistics* **9**,

634   300–318.

635   MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and

636   Langtimm, C. A. (2002). Estimating site occupancy rates when detection

637   probabilities are less than one. *Ecology* **83**, 2248–2255.

638   MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines,

639   J. E. (2006). 'Occupancy Estimation and Modeling – Inferring Patterns and

640   Dynamics of Species Occurrence.' (Academic Press: London.)

641   Medway, L. (1958). Food bone in Niah Cave excavations. *Sarawak Museum Journal*

642   **8**, 627-636.

643   McKinney, M. L., & Lockwood, J. L. (1999) Biotic homogenization: a few winners

644   replacing many losers in the next mass extinction. *Trends in Ecology &*

645   *Evolution* **14, 450-453.**

646   Meijaard, E. (2000). Bearded pig (*Sus barbatus*): Ecology, conservation status, and

647   research methodology. Background document for the electronic conference

648   on bearded pig research, and recommendations for a collaborative research

649   programme. (WWF-Indonesia, CIFOR, and Ecosense Consultants:

650   Bogor.)

651   Mitchell, J., Dorney, W., Mayer, R., and McIlroy, J. (2008). Spatial and temporal

652   patterns of feral pig diggings in rainforests of north Queensland. *Wildlife*

653   *Research* **34,** 597-602.

654   Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A.,

655   Börger, L., Bennet, D. J., Choimes, A., Collen, B., Day, J., De Palma, A.,

656   Díaz, S., Cheverria-Londoño, S., Edgard, M. J., Feldman, A., Garon, M.,

657   Harrison, M. L. K., Alhusseini, T., Ingram, D. J., Itsecu, Y., Kattge, J., Kemp,

658   V., Kirkpatrick, L., Kleyer, M., Correia, D. L. P., Martin, C. D., Meiri, S.,

659   Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D. W., Robinson, A.,

660   Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M.,

661   Scharlemann, J. P. W., and Purvis, A. (2015). Global effects of land use on

662   local terrestrial biodiversity. *Nature* **520**, 45-50.

663 Payne, J., and Francis, C. M. (1985). 'A Field Guide to the Mammals of

664   Borneo.' (The Sabah Society: Kota Kinabalu.)

665 Pfeffer, P. and Caldecott, J. (1986). The bearded pig (*Sus barbatus*) in East

666   Kalimantan and Sarawak. *Journal of the Malaysian Branch of the Royal*

667   *Asiatic Society* **59**, 81-100.

668 Puri, R. K. (2005). 'Deadly Dances in the Bornean Rainforest: Hunting Knowledge of

669   the Penan Benalui.' (KTLV Press: Leiden.)

670 Ross, J., Hearn, A. J., Johnson, P. J., and Macdonald, D.W. (2013). Activity patterns

671   and temporal avoidance by prey in response to Sunda clouded leopard

672   predation risk. *Journal of Zoology* **290**, 96-106.

673 Saunders, G., and Kay, B. (1991). Movements of feral pigs (*Sus scrofa*) at Sunny

674   Corner, New South Wales. *Wildlife Research* **18**, 49-61.

675 Welander, J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting

676   in a mosaic landscape. *Journal of Zoology* 252: 263-271.

677 Weldon, A. J., & Haddad, N. M. (2005). The effect of patch shape on indigo

678   buntings: evidence for an ecological trap. *Ecology* **86**, 1422-1431.

679 Wong, S. T., Servheen, C., Ambu, L., and Norhayati, A. (2005). Impacts of fruit

680   production cycles on Malayan sun bears and bearded pigs in lowland tropical

681   forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology* **21**, 627–639.

682 Yue, S., Brodie, J. F., Zipkin, E. F., and Bernard, H. (2015). Oil palm plantations fail

683   to support mammal diversity. *Ecological Applications* **25**, 2285-2292.

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688 **Figure Legends**

689 **Figure 1.** Transect positions for forest transects (red flags) and oil palm plantation

690 transects (blue flags) sites within the Lower Kinabatangan Wildlife Sanctuary and

691 surrounding region. The blue boundaries represent permanent water sources. The

692 green lines correspond to the forest regions.

693 **Figure 2.** The camera trap stations within the Lower Kinabatangan Wildlife

694 Sanctuary (LKWS) and surrounding areas. Illustrated are twenty corridor sites

695 (yellow icons) and 75 forest patch sites (purple icons). The blue outlines display the

696 Kinabatangan River and neighbouring oxbow lakes. The green markings show forest

697 areas of LKWS. The grey lines show privately owned forest areas and yellow lines

698 display degraded forest within plantation fragments.

699 **Figure 3.** The activity patterns of bearded pigs throughout an average day, based on

700 the percentage of independent camera trap detections (min. 1 hr apart) occurring at

701 various times of day. The solid line displays the diurnal activity pattern of the entire

702   population (n = 1995), whereas the checked line illustrates the more strictly diurnal

703   activity patterns of groups containing juveniles and piglets (n = 221).

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711   **Figure 1.**
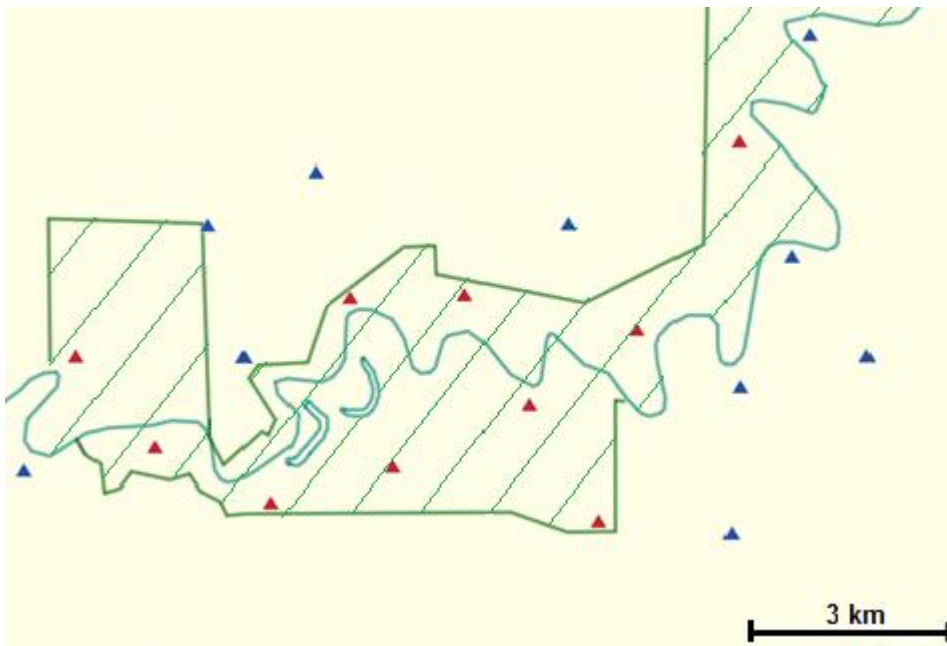
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727 **Figure 2.**
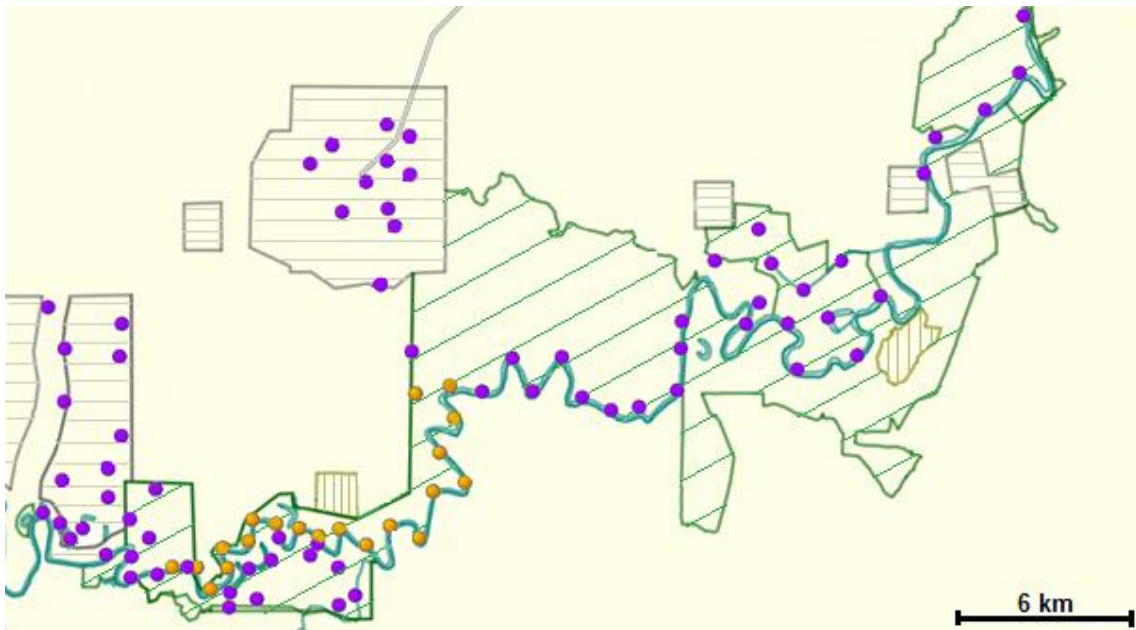
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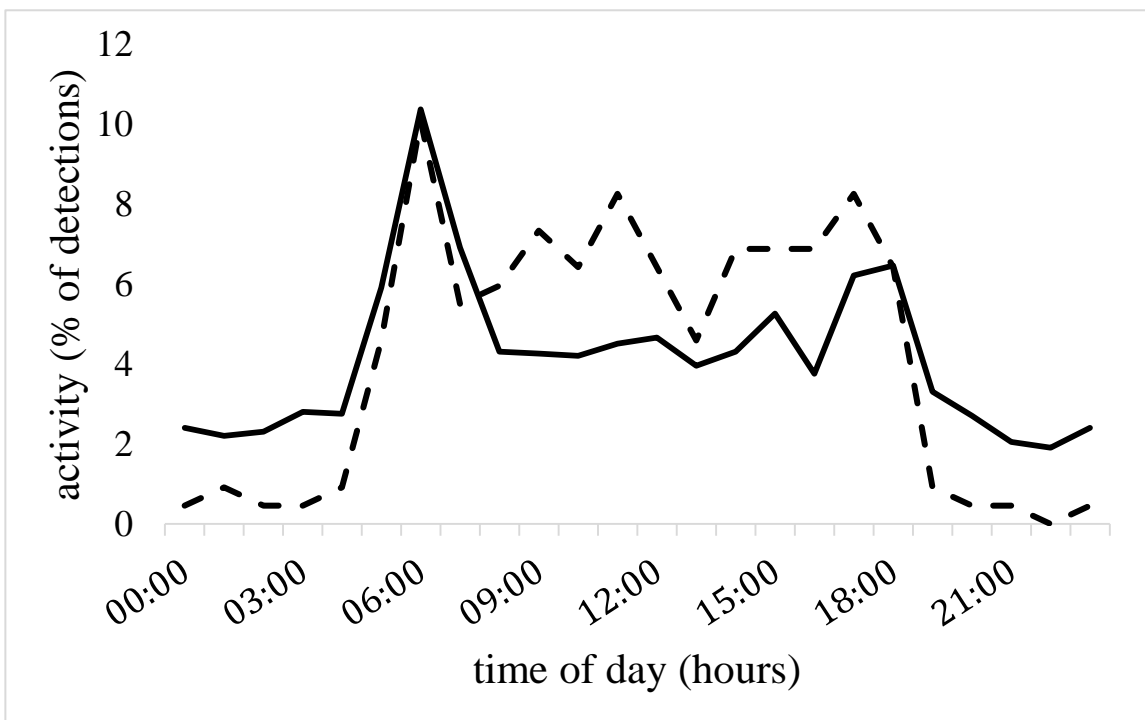
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744 **Figure 3.**

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757 **Table 1.** Summary table displaying the mean number of signs detected (± SE) during

758 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)

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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	

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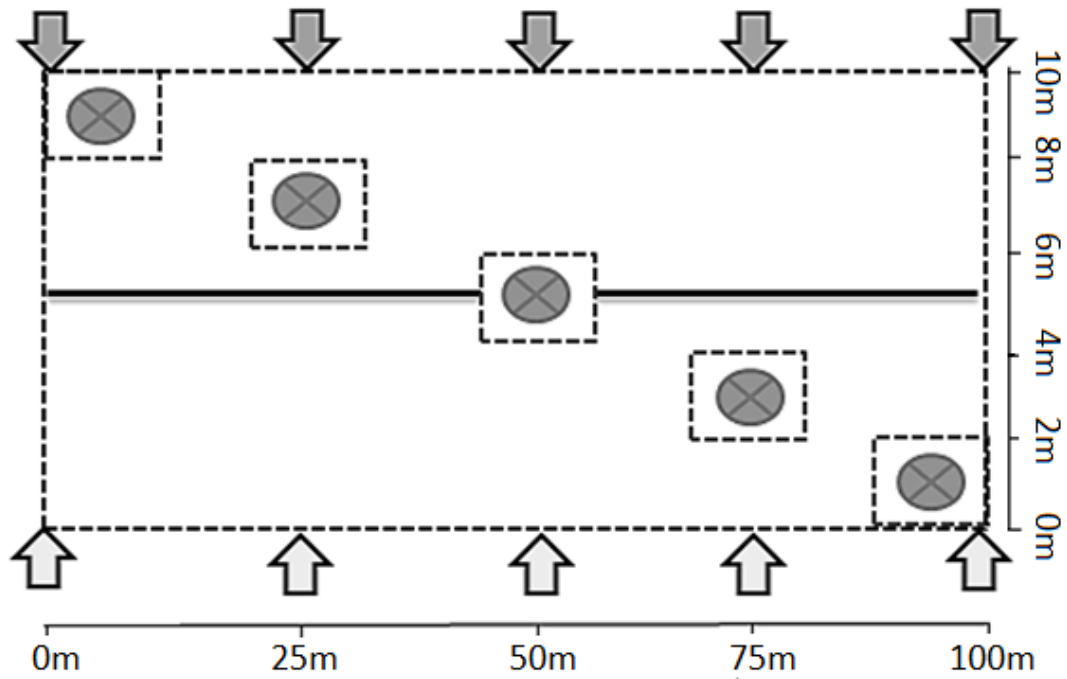
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806 **Table S1.** Example photographs of pig sign used for detecting pig habitat use on

807 transects.

Sign	Example
Track	

Scat	
Nest	
Rooting site	
Wallowing hole	
Mud graze	

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818 **Table S2.** Visual factors used to determine bearded pig body condition from camera

819 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

820 Bones include the scapulae, vertebral columns, ribs and hipbones

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825 **Table S3.** Example photographs used for categorising body condition of pigs from

826 camera photos.

Category	Example
Very good	

Good	
Fair	
Poor	

Very poor	 (Wong et al. 2005)

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

Age	Example

Infant	
Juvenile	
Sub-adult	
Adult	

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858 **Table S5.** The null and competing generalized linear mixed effects models

859 investigating the effects of the identified influential parameters on pig tracks and

860 rooting sites. All models of pig tracks include habitat type as a controlling variable.

861 The models are ranked based on the differences in the cumulative corrected

862 Akaike's Information Criteria (AICc). Table includes the number of estimated

863 parameters (K), the AICc, the difference in AICc with the top model (Delta_AICc), the

864 weight of each model (AICcWt), and the -2log-likelihood output (LL).

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	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

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