1 **Survival strategies of a frugivore, the sun bear, in a forest-oil palm landscape**

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30 **Abstract**

31   As large areas of forest are lost throughout the tropics, prime habitat of many species

32 decline and become fragmented. The island of Borneo is a prime example, with accelerated

33 clearing of forests primarily for oil palm expansion. Borneo's forests are an important stronghold

34 for the conservation of the sun bear (*Helarctos malayanus*), but it is unclear how habitat

35 reduction and fragmentation is affecting this frugivore. We used camera traps and sign surveys to

36 understand patterns of sun bear habitat use in a matrix of fragmented forests and extensive oil

37 palm development, which has existed as such for >15 years: the Lower Kinabatangan floodplain

38 in Sabah, Malaysian Borneo. Within these small forest fragments, squeezed between a major

39 river and oil palm plantations, bears exhibited selection for areas farther from human activity

40 (forest edges, river boat traffic, and buildings), and were rarely active during the day,

41 demonstrating both spatial and temporal avoidance of potential human-related threats. They

42 selected large trees to feed and rest, and also exploited adjacent plantations to feed on oil palm

43 fruits. We conclude that even relatively small forest fragments (~2,000 ha) within large

44 agricultural landscapes can be important for sun bears. Our research highlights the remarkable

45 adaptations this species has employed to persist in a drastically modified landscape.

48   **1. Introduction**

49   The island of Borneo has recorded high rates of forest loss (>30%) over the last four

50   decades (Gaveau et al. 2014). In particular, the State of Sabah (Malaysian Borneo) alone lost

51   nearly 40% of natural forest cover in that time (Gaveau et al. 2014). Agricultural expansion,

52   which has been mostly for oil palm plantations, is one of the primary drivers behind forest loss,

53   fragmentation, and degradation in the region (Koh and Wilcove 2008; Abram et al. 2014, 2016).

54   The resulting pockets of forest stand out as islands amid a sea of monoculture (Ancrenaz et al.

55   2004; Abram et al. 2014). Although these forests may not be pristine in floral and faunal

56   composition, they still may have tremendous value for biodiversity (Maddox et al. 2007; Alfred

57   et al. 2012; Estes et al. 2012; Nakashima et al. 2013; Ancrenaz et al. 2015; Abram 2016).

58   Forested landscapes in Borneo are important for the continued survival of the sun bear

59   (*Helarctos malayanus*)), a species whose range is limited to mainland Southeast Asia, Sumatra,

60   and Borneo. Being a forest-dependent species, sun bears are adversely affected by excessive

61   forest loss (Wong et al. 2013), but can survive in secondary or degraded forests provided that

62   important habitat resources such as fruiting trees are available (Wong et al. 2004; Linkie et al.

63   2007; McShea et al. 2009; Samejima et al. 2012; Fredriksson 2012; Wong and Linkie 2013;

64   Yaap et al. 2016; Wearn et al. 2017) Although sun bears consume insects (especially bees,

65   beetles, and termites), both in trees and on the ground, most studies indicate that they are

66   primarily frugivorous, unless fruits are scarce (McConkey and Galetti 1999; Augeri 2005; Cheah

67   2013; Steinmetz et al. 2013). In primary forests, the availability of sun bear food resources is tied

68   to dipterocarp mast-fruiting cycles (Wong et al. 2005; Fredriksson et al. 2006). During inter-mast

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69   periods, sun bear food sources become scarce, leading to starvation (Wong et al. 2005), greater

70   predation risk (Fredriksson 2005a), and increased human–bear conflicts (Fredriksson 2005b;

71   Wong et al. 2015).

72   With widespread deforestation and forest degradation occurring in Borneo, little is known

73   about how sun bears have been responding to the extreme changes in their habitat. Research on

74   other bear species in human-modified landscapes have shown them to be highly adaptable,

75   supplementing their diet with crops (Maddrey and Pelton 1995; Charoo et al. 2011; Northrup et

76   al. 2012; Takahata et al. 2014; Ditmer et al. 2015; Ali et al. 2017) while also attempting to

77   minimize contact with people (Nielsen et al. 2004a; Ordiz et al. 2011). However, as bears use

78   such landscapes more frequently, encounters between people and bears increase, representing

79   increased risks for both species (Nielsen et al. 2004b; Jorgenson and Sandoval-A 2005; Charoo

80   et al. 2011; Northrup et al. 2012; Scotson et al. 2014).

81   Our goal was to better understand the effects of the oil palm–forest landscape on sun

82   bears, which might serve as an indicator for other, less-studied frugivores and carnivores

83   (Ratnayeke and Van Manen 2012). We used two methods, camera trapping and sign surveys,

84   both of which have been commonly used to study populations of bears in tropical regions

85   (Akhtar et al. 2004; Ríos-Uzeda et al. 2007; Steinmetz 2011; Steinmetz et al. 2011; Ramesh et al.

86   2012; Sethy and Chauhan 2016)

87   Camera traps have become a standard tool for monitoring low-density large mammals in

88   Southeast Asian forests (Kawanishi and Sunquist 2004; Linkie et al. 2007; Ngoprasert et al.

89   2012; Rayan et al. 2012; Wong et al. 2013; Wong and Linkie 2013), and have provided valuable

90   information about mammalian use of the forest–oil palm plantation interface (Yue et al. 2015;

91   Wearn et al. 2017). Camera trap studies of sun bears have yielded density estimates (Ngoprasert

92   et al. 2012), measures of habitat use and distribution (Wong et al. 2013; Wong and Linkie 2013),

93   and assessments of activity patterns (Wong et al. 2004; Cheah 2013). Sign surveys within strip

94   transects have also been used to assess the status of sun bear populations (Augeri 2005;

95   Steinmetz et al. 2011, 2013; Ngoprasert et al. 2011; Fredriksson 2012). Sign surveys are useful

96   as a measure of bear presence, relative abundance, and habitat use (Steinmetz and Garshelis

97   2010). We employed both these methods in our study to understand the strategies used by sun

98   bears living in fragmented landscapes. Specifically, we wished to learn whether sun bears could

99   effectively utilize remnant forest surrounded by expansive oil palm plantations, and if so, we

100   sought to understand features of this habitat that they used or avoided, and aspects of their

101   behavior that enabled them to survive there.

102   **2. Materials and Methods**

103   2.1 Study site

104   Our study site was situated in the Lower Kinabatangan floodplain, in the eastern part of

105   Sabah, Malaysian Borneo. This area is dominated by oil palms, with only small forest fragments

106   remaining (Abram et al. 2014). A network of protected areas consists of seven variably sized

107   forest reserves as well as the Lower Kinabatangan Wildlife Sanctuary (LKWS), which itself

108   constitutes ten different forested areas labelled as lots (Ancrenaz et al. 2004). Forest fragments

109   that are currently protected have remained relatively unchanged since 1998 (~15 years at the

110   time of this study; Francis et al., unpublished data). We surveyed five lots (numbered 1 and 4 –

111   7), four forest reserves (Keruak, Bod Tai, Gomantong, and Pin Supu), and private lands within

112   the floodplain. Besides sun bears, large mammal species present in the landscape include the

113   Bornean orangutan (*Pongo pygmaeus*), Asian elephant (*Elephas maximus*), proboscis monkey

114   (*Nasalis larvatus*), and Sunda clouded leopard (*Neofelis diardi*).

115   2.2 Data collection

116   2.2.1 Habitat use

117   We used the detection of sun bears through camera traps as a primary measure of bear

118   habitat use in the Lower Kinabatangan. The primary goal of the camera trapping was to estimate

119   the density of Sunda clouded leopards in the region. As such, the location and method of

120   deployment was done to maximize the detections of clouded leopards; sun bear photos were non-

121   target data. We deployed Reconyx PC800 and HC500 infrared camera traps (Reconyx Inc.,

122   Holmen, Wisconsin, USA) at 77 different sites along riparian trails, forest trails, and ridgelines

123   (Figure 1). We secured camera traps to trees, 40–50 cm off the ground, with an average distance

124   of 1.22 km between adjacent sites (Ross et al. 2013). Cameras recorded the time and date of

125   every photographic capture. We checked camera sites at intervals of 30–80 days to check their

126   condition, replace batteries, and change memory cards. For each camera site, we divided the

127   sampling period into 44 weekly occasions from June 2013 until April 2014. Each occasion

128   represented a sun bear detection (1) or non-detection (0) event. We only considered independent

129   detections at each site, which we defined as photographs at least 24 hours apart.

130   We used the detection of sun bear sign as a second measure of bear habitat use. Sun bears

131   leave conspicuous and distinctive sign during foraging and resting events: claw marks on trees,

132   tree nests, ripped open logs, and broken termite nests (Fredriksson 2012; Steinmetz et al. 2013).

133   During 2012 – 2013, we searched for sign within 50 strip transects in the LKWS Lot 5 riparian

134   corridor and Lot 6 forest fragment (Figure 2). The riparian corridor is a relatively thin strip (130

135   m– 2 km width) of forest along the Kinabatangan River and connects LKWS Lot 7 and Pin Supu

136   Forest Reserve (together 3,723 ha) with the larger Lot 5 forest block and Gomantong Forest

137   Reserve (together approximately 11,900 ha; Ancrenaz et al. 2004)). Our transects were 0.25 ha in

138 size (5 x 500 m) and spaced at least 250 m apart, with 20 transects in the corridor and 30 in the

139 fragment. Every tree within the transect was closely examined for claw marks, and the ground

140 was searched for digging. On every survey, one leader trained in bear sign identification was

141 present.

142   When we found bear claw marks on trees, we further distinguished between within-year

143 and older claw marks based on our understanding of how marks age (Steinmetz and Garshelis

144 2010; Fredriksson 2012), measured the circumference at breast height (CBH) of the tree,

145 identified the tree to family (or lower taxon where possible), and recorded if there were ripped

146 open cavities or torn bark (indicating insect feeding; Fredriksson 2012). We noted if the transect

147 contained signs of human activity (cut trails, campsites, rubbish, etc.) and counted the number of

148 *Ficus sp.* trees and termite nests, both important food items for sun bears (Wong et al. 2002;

149 Fredriksson et al. 2006; Fredriksson 2012), in each transect. Also, for comparative purposes, we

150 searched an additional four 5 x 100 m (0.05 ha) transects in an area known to have abundant sun

151 bear sign. These transects were within Pin Supu Forest Reserve (Figure 2), but close (80–320 m)

152 to oil palm plantations. We selected this area after a farmer reported he had come across a sun

153 bear in oil palm plantation bordering the reserve.

154   We considered six landscape covariates, deemed as potentially important determinants of

155 sun bear habitat use: forest type, elevation, buildings, roads, intact forest edge, and water bodies.

156 For forest type data, we modified existing forest type and land use cover information from

157 2010/11 data (Abram et al. 2014). We did this by updating the forest extent vector layer, in

158 ArcMap 10.3 (Esri, Redlands, California, USA), using a 15 m resolution Landsat image from

159 2013, then extracted forest type information for the 2013 forested area. Roads included both

160 surfaced highways and certain plantation roads; buildings represented all structures visible

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161   (houses, storage areas, mills etc); and water bodies encompassed all rivers and oxbow lakes. All

162   these features were digitized from SPOT 2.5 m 2010/11 satellite imagery. For each camera trap

163   and strip transect, we measured the distance to the nearest building (hereafter building), intact

164   forest edge (hereafter forest edge), road, and water body. For camera traps, we calculated the

165   elevation and categorized the forest type as either freshwater swamp forest, mixed dipterocarp

166   forest, limestone forest, or degraded scrub forest. For strip transects, we calculated the mean

167   elevation of the start and end points of each transect.

168   2.2.2 Activity patterns

169   We used the time stamp on camera-trap photographs to examine the activity patterns of

170   bears. For this dataset, we also included additional data from LKWS Lot 5 (10 sites; 2011 –

171   2015) and Lot 6 (7 sites; 2010 – 2011), which were set as part of a general biodiversity survey.

172   2.2.3 Climbed tree characteristics

173   We compared features associated with claw-marked trees to a sample of trees that sun

174   bears did not climb. We randomly selected 48 claw marked trees from our strip transects as

175   targets for further investigation. We then selected another 48 unclimbed trees for comparison.

176   We chose these from transects lacking claw-marked trees: first by dividing the transect into five

177   100-m segments, and then searching each segment for a tree of suitable size for bears to climb

178   (minimum CBH $\geq$ 29 cm based on data from this study).

179   We set up 20 x 20-m plots centered on each of the 48 climbed and 48 unclimbed trees.

180   We measured the CBH and estimated the height of the focal tree using a clinometer. Within the

181   plot, we counted the number of vines present (hereafter vines). For other habitat variables, we

182   first divided each plot into four 10 x 10-m subplots. Two observers used a striped density stick to

183   quantify the percent understory density in each subplot. We used the mean of all subplots as a

184   measure of the plot understory density. We photographed the canopy directly overhead at the

185   center of each subplot and used the software "HabitApp" (Macdonald and Macdonald 2016) to

186   calculate the proportion of the color black in the photo. Larger proportions indicated greater

187   cover. We took the mean of these proportional values as the canopy cover for the plot.

188   2.3 Data analysis

189

190   2.3.1 Habitat use

191   We conducted all analysis using R (R Core Team 2015). We utilized a single season

192   occupancy model to measure sun bear habitat use (ψ) from camera trap data (MacKenzie et al.

193   2002). We examined the effects of covariates (building, forest edge, water body, elevation, road,

194   and forest type) on both ψ and detection probability (probability of a sun bear being detected

195   during an occasion given that it is present; p) using the package "unmarked" (Fiske et al. 2011).

196   In addition, we examined whether the number of trap nights a camera trap was operational in a

197   weekly sampling occasion (0-7 trap nights) had an effect on p. We used Pearson's correlation

198   coefficient (r_p) to check for multicollinearity among covariates ($r_p \geq 0.7$). We did not fit models

199   with more than one covariate for ψ and two covariates for p to avoid overfitting the model. We

200   began by fitting constant and single covariate models for both ψ and p. We fit two parameter

201   models for p by taking covariates from the best ranked single covariate models (ΔAIC $\leq$ 2) and

202   using these in combination with other covariates. The best supported models were identified

203   based on Akaike's Information Criterion (AIC) and model weight. To identify competing

204   models, we ignored models that were similar to a better ranked model but with an extra

205   parameter (Arnold 2010). We further assessed model fit through parametric bootstrap goodness

206   of fit tests using the model sum of squared errors.

207   From our strip transect detection/non-detection data, we checked if the number of

208   transects containing within-year sun bear sign and evidence of human activity differed between

209   the corridor and forest fragment using chi-squared and Fisher's exact tests, respectively. We

210   checked for differences in number of *Ficus sp.* trees, climbed tree CBH, and density of within

211   year sign between transects in the corridor and fragment using Wilcoxon-Mann-Whitney tests.

212   We used logistic regression to model the presence of within-year sun bear sign in the

213   Lower Kinabatangan. As the age of sign could only be reliably ascertained for claw marks on

214   trees, we did not include other bear signs in this analysis. We did not include data from the four

215   transects purposefully located in an area with high sign density. Our suite of covariates included

216   building, road, forest edge, water body, elevation, number of *Ficus sp.* trees in a transect

217   (hereafter *Ficus*), presence of human activity in a given transect (0 or 1), and transect location

218   (corridor or fragment). We checked for multicollinearity among covariates ($r_p \geq 0.7$). We fit

219   models with single covariates first, ranked them using AIC corrected for small sample sizes

220   (AIC$_c$), and then fitted more complex models with covariates from the top ranked models (ΔAIC$_c$

221   ≤ 2). We repeated this until we identified the best ranked models using AIC$_c$ and model weight.

222   We ignored competing models with only one additional parameter to better supported models

223   (Arnold 2010). We inspected the fit of the top ranked models visually using binned residual

224   versus fitted plots. Lastly, we used the area under the receiver operating characteristic (ROC)

225   curve to assess the predictive power of the best supported models.

226   2.3.2 Activity patterns

227   We used the R package "overlap" (Meredith and Ridout 2014) to calculate a kernel

228   density function from times at photographic capture of sun bears in the Lower Kinabatangan

229   during 2010-2015. For this analysis, we only used independent detections (one detection at a site

230   24 hour^{-1}) of bears.

231   2.3.3 Climbed tree characteristics

232   We used Wilcoxon-Mann-Whitney tests to check for differences in understory density,

233   canopy cover, tree height, vines, and CBH between climbed and non-climbed tree plots as well

234   as between trees with within-year claw marks and those without. We used logistic regression to

235   model the habitat characteristics most associated with climbed trees. We ran two groups of

236   models: one with the response being the presence or absence of claw marks on a tree and another

237   with the response being the presence or absence of within-year claw marks on a tree. We used

238   six covariates in total: CBH, tree height, canopy cover, understory density, vines, and location.

239   We checked for correlation among predictors ($r_P \geq 0.7$). We fit models sequentially with single

240   covariates first and then adding predictors from the top ranked models ($\Delta AIC_c \leq 2$). The final

241   suite of best supported models were selected and assessed similarly to the habitat use analysis.

242   **3. Results**

243

244   3.1 Habitat use

245   We obtained 583 photographs of sun bears from 11,359 camera trap nights in the lower

246   Kinabatangan. From these, only 59 represented independent detections according to our criteria

247   (192.5 trap nights/independent detection of a sun bear). We detected sun bears at 29 of 77 (38%)

248   camera trap sites.

249   The best ranked single season occupancy model included ψ as constant and *p* as a

250   function of forest edge and building (Table 1). The parametric bootstrap goodness of fit test

251   using the model sum of squared errors suggested a good fit for this model (P = 0.37). Our best

252   estimate of ψ was 0.74 (SE = 0.12). Detection of sun bears on camera traps increased farther

253   from buildings and farther from the forest edge (i.e., more interior; Figure 3). Our best estimate

254   of *p* was 0.03 (SE = 0.01) at the mean distance to building (2.08 km) and forest edge (0.61 km).

255   The probability of detecting a sun bear throughout the entire survey (all 44 weekly occasions;

256   *p**) was 77.6% at the mean covariate values.

257   We detected sun bear sign (96.8% claw-marked trees, 3.2% ripped open logs, n = 94) in

258   31 of 50 strip transects. In both the corridor and fragment, a large proportion of transects

259   contained sign (60% and 70%, respectively). All ripped-open logs (insect feeding) were within

260   the fragment transects. Of the 91 claw-marked trees that we observed, about half (48.4%) were

261   judged to have been made within 1 year. The density of within-year bear claw marks was higher

262   in the fragment (median = 4 ha^{-1}, SD = 6.33 ha^{-1}) than the corridor (median = 0 ha^{-1}, SD = 3.0 ha$^-$

263   ^{1}), but this difference was not significant (P = 0.17). All four transects in the Pin Supu Forest

264   Reserve contained bear sign, and sign density was extremely high (median = 100 ha^{-1}, SD = 60.0

265   ha^{-1}).

266   Six tree families made up 67% of the total climbed trees found on sign survey transects:

267   Sterculiaceae, Lamiaceae, Lauraceae, Euphorbiaceae, Rubiaceae, and Tiliaceae. Climbed trees in

268   the corridor were smaller ($\bar{x}$ = 132.1 cm, SD = 75.1 cm) than trees in the fragment ($\bar{x}$ = 145.5

269   cm, SD = 107.2 cm) but this difference was not significant (P = 0.94). About a quarter (26.4%)

270   of the climbed trees had torn bark or holes that were noticeable, consistent with sign of insect

271   feeding by a bear. In terms of other potential bear food sources, we located 71 *Ficus sp.* trees and

12

272   4 termite mounds within transects. A larger number of *Ficus sp.* trees per transect were in the

273   corridor ($\bar{x}$ = 2.55, SD = 3.86) than in the fragment ($\bar{x}$ = 0.6, SD = 0.81; P = 0.03). All termite

274   mounds were within the fragment. Corridor transects were more disturbed (59.3% contained

275   human signs) than fragment transects (40.7%; P = 0.004).

276   Building, elevation, and water were significant predictors of within-year sun bear sign

277   (Table 2). Greater distances from buildings and water, and higher elevations were associated

278   with higher detection of within-year claw marks (Figure 4). All competing models had moderate

279   predictive power (61–72%). Binned residual versus fitted plots of competing models displayed

280   an acceptable fit.

281   3.2 Activity patterns

282   We obtained 953 photographs of sun bears during 2010–2015, of which 116 were

283   independent detections according to our criteria. On trails and ridgelines, bears were largely

284   crepuscular with sustained nocturnal activity (Figure 5). Sun bear activity peaked at around 2000

285   and again at 0400 hours, with a low activity during daylight, especially between 0800 and 1600

286   hours.

287   3.3 Climbed tree characteristics

288   Considering bear claw marks of all ages, we found that understory density and number of

289   vines around climbed trees was less than around unclimbed trees (Table 3). Climbed trees were

290   also taller and had a larger CBH (Table 3). When considering only trees climbed by bears that

291   year, we detected similar selections by bears for tress with less understory density that were taller

292   and that had a larger CBH (Table 4).

293 The best supported model explaining climbed tree selection contained the covariates

294 understory density and height (Table 5). Tree height was positively associated with climbed trees

295 while understory density seemed to have a negative impact on tree climbing (Figure 6). The

296 binned residual versus fitted plots showed good fit, and the model had high predictive power

297 (89.2%). For models focused on just within-year marks, the probability of climbing increased

298 significantly (76%; best supported model) if the tree was within the fragment (Table 6). Tree

299 height and understory density were also significant covariates of within-year climbing. All top

300 ranked models explaining within-year climbing fit decently, and had good predictive power (76-

301 78.5%).

302 **4. Discussion**

303 Camera-trap detection rates of sun bears was moderately high in the Lower Kinabatangan

304 (1 bear detection every 192.5 camera trap nights) compared to other locations across mainland

305 Southeast Asia (Steinmetz 2011). One caveat of our study was that our camera traps were placed

306 solely on wildlife trails and ridgelines, limiting our inference to just these habitat features. Our

307 study suggested sun bears used many portions (74%) of the riparian trails, forest trails, and

308 ridgelines in the landscape. This high perceived use was likely due to the long survey period in

309 our study, enabling the accumulation of detections of a fairly wide-ranging species. In addition,

310 the sites were not closed (bears could have been present in the vicinity of a camera trap during

311 some weeks but not others) and the small area of forest left in the Lower Kinabatangan probably

312 confined bears to a limited space, hence they would use a large part of the remaining forest.

313 However, the lack of closure does not affect inferences about habitat use (MacKenzie et al.

314 2018). Therefore, we presume that the comparatively high habitat use estimate was the result of

315 the circumstances of the species and study, rather than a high density of bears.

316   We observed a decline in the probability of detecting bears closer to buildings, the forest

317   edge, and water bodies, all used frequently by people. Although our estimate of habitat use was

318   high, the intensity of use was drastically affected by a sensitivity towards human presence. This

319   has been observed elsewhere in the sun bear's range (Augeri 2005; Nazeri et al. 2012, 2014;

320   Wong and Linkie 2013). In contrast, forest streams not used intensively by people were reported

321   to attract sun bears (Nazeri et al. 2014). Our study clearly shows that sun bear habitat use in the

322   Lower Kinabatangan is driven by an avoidance to anthropogenic disturbance or threats.

323   Elevation appeared to be an additional predictor of sun bear habitat use, as reflected by

324   within-year sign, even though the difference in minimum and maximum elevations of our strip

325   transects was only 17 m. We suspect that bears were not actively selecting slightly higher

326   elevations, but rather habitat features associated with these elevations. Lower lying patches of

327   habitat become inundated and hold water more frequently, which may restrict sun bear use

328   directly and also may impact the composition of tree species and understory (Abram et al. 2014).

329   Sun bears have been recorded venturing past the forest edge to feed in oil palm

330   plantations (Normua et al. 2004; Cheah 2013; Yue et al. 2015; Wearn et al. 2017; Guharajan et

331   al. 2017). As the camera trap survey was not targeted directly at sun bears, we did not have

332   cameras placed within oil palm plantations, but sign surveys (see below) and reports from

333   farmers in the area (Guharajan et al. 2017), indicated that at least some sun bears fed in

334   plantations. Poachers use tree platforms and snares to hunt at the forest–oil palm interface (R.

335   Guharajan and S. Payar, pers. obs.). It is thus risky for bears to use trails crossing into the

336   agricultural lands. In addition, we do not know if lack of use of these trails during daylight hours

337   was indicative of their general activity pattern in the area, or just an avoidance of trails at times

338   when humans might have been present. Sun bears have been observed to be active mainly during

339   non-daylight hours in human-disturbed habitats (Mohd-Azlan 2006; Cheah 2013) but diurnal

340   where human disturbance was low (Fredriksson 2012). In a different forest reserve in Sabah,

341   radiocollared sun bears were diurnally-active in the forest, but bears were photographed on trails

342   mainly during crepuscular-nocturnal hours (Wong et al. 2004).

343   Based on sign density, bears used the narrow riparian corridor (Lot 5), but they appeared

344   to make greater use of the larger forest fragment directly across the river (Lot 6; Figure 2; Table

345   S1). We found a higher density of *Ficus sp.* trees, an important food source and possible

346   attractant, within corridor transects; however, even with a greater potential density of food in the

347   corridor, sun bears showed an apparent wariness to the proximity of human disturbance, which

348   occurred on both sides of the narrow corridor. Although the Lot 6 fragment is also relatively

349   small (2,673 ha; Ancrenaz et al. 2004), it may provide more insulation from these anthropogenic

350   disturbances.

351   The sign we observed, primarily claw-marked trees, was a more definitive indication than

352   camera-trap photos that the forest patches provided resources to sustain bears, not just cover to

353   pass through. Sun bears climb trees to feed on fruits and insects, for refuge while resting, and

354   possibly to cool off from the hot and humid weather. Accordingly, their selection for larger trees

355   may have provided (1) a higher density of fruits than smaller trees, (2) more cavities for insects

356   like stingless bees (*Trigona* spp.), (3) larger branches for resting, and (4) better access for bears

357   to get above the surrounding canopy where there might be breeze. Conversely, Powell (2011)

358   found no selection by sun bears for taller trees in a more intact and diverse forest in Sumatra,

359   possibly because this forest offered a greater abundance and diversity of fruiting trees, so bears

360   could afford to seek a diet of assorted fruits (as shown empirically by Steinmetz et al. 2013). We

361   also found that sun bears tended to climb trees surrounded by a sparser understory. The sparser

362   understory below these climbed trees is likely a reflection of a less-disturbed and more shaded

363   forest, rather than selection by sun bears for open understory per se.

364   We found exceedingly high sun bear sign density in a patch of forest within Pin Supu

365   Forest Reserve (110 within-year sign ha^{-1}; 135 all-aged sign ha^{-1}), near where a farmer reported

366   seeing bears foraging in oil palm. Elsewhere, others have reported sun bear sign densities of 4.9

367   – 8.8 all aged sign ha^{-1} in primary and commercial forests of central Sabah (Teo 2013), 40 – 45

368   all-aged sign ha^{-1} in prime habitat in Indonesian Borneo (Augeri 2005; Fredriksson 2012) and

369   only 9 within-year sign ha^{-1} in prime habitat in western Thailand (Steinmetz et al. 2011). The

370   high sign density in the small patch of Pin Supu Forest Reserve (~ 2,000 ha) suggests that bears

371   may have used it as a frequent refuge between feeding bouts into the plantations. Nighttime

372   feeding forays from the forest into oil palm plantations have been observed among radiocollared

373   bears at another site in Sabah (Normua et al. 2004) and Peninsular Malaysia (Cheah 2013).

374   Likewise, camera-trap photos elsewhere in Sabah showed that sun bears used both oil palm

375   plantations and the adjacent forest (Yue et al. 2015; Wearn et al. 2017). The high use of small

376   forest patches, like Pin Supu, Lot 5 and Lot 6, signify their importance for sun bears in the

377   Lower Kinabatangan.

378   **5. Conclusions**

379   Sun bears exhibited a clear avoidance, in both space and time, of humans in the Lower

380   Kinabatangan. This strategy is undoubtedly beneficial when living in a landscape dominated by

381   people and agricultural activities, where encounters with humans could be deadly. This strategy

382   also aids in the utilization of an important food resource: oil palm fruits. Sun bears do feed on

383   this easily available and abundant food source (Normua et al. 2004; Cheah 2013) but oil palm

384   workers and farmers in our study area hardly encountered bears, likely because the bears only

17

385　used these plantations at night (Guharajan et al. 2017). This highlights how this extremely

386　adaptable frugivore is able to make use of beneficial resources in a degraded and potentially

387　dangerous landscape. Encouragingly, camera-trapped sun bears in the lower Kinabatangan did

388　not exhibit any gunshot wounds or snare-related injuries, unlike those from a similar landscape

389　in Peninsular Malaysia (Cheah 2013). However, discoveries of disemboweled sun bear carcasses

390　with missing paws in the landscape (L. Liman, WWF-Malaysia, pers. comm., T. Eriksson, pers.

391　comm.) suggest that poaching of this species does occur, though the extent is still not clear. Our

392　research indicates that sun bears can survive in a landscape like the Lower Kinabatangan for at

393　least 15 years, provided there are pockets of connected forests: even small fragments that can

394　serve as refuges and core areas. Additionally, 12 other carnivores were detected by the camera

395　traps in the forest fragments where we worked, demonstrating the importance of saving even

396　small forest remnants (Evans et al. 2016). Likewise, sun bears and other threatened species have

397　been observed at reasonably high rates (via camera-trapping) in riparian forest fragments in

398　Indonesia (Yaap et al. 2016). Whereas there are obviously severe negative impacts of widespread

399　land conversion and fragmentation on this forest-dependent species, our results offer hope that

400　conservation of forest fragments within the agricultural landscape enables this species, and

401　others like it, to persist. We believe that the most pressing conservation action needed for sun

402　bears in the Lower Kinabatangan is not to do with habitat or food resources, but protection from

403　human-caused mortality, primarily poaching.

404　**6. Acknowledgements**

408 International Association for Bear Research and Management, Association of Zoos and

409 Aquariums, Columbus Zoo and Aquarium, Wildlife Reserves Singapore, Hauser Bears and the

410 Bell Museum of Natural History. The camera trapping work was funded by Sime Darby

411 Foundation and Point Defiance Zoo and Aquarium. Funders had no role in study design, data

412 collection, analysis and interpretation, or decision to publish. We thank two anonymous

413 reviewers for helpful comments on an earlier draft.

414 **7. Data availability**

415 The datasets used in this study are available upon request from the corresponding author.

416 **8. References**

417 Abram NK (2016) Trade-offs between ecosystem protection and oil palm development. Royal
418 Institution of Chartered Surveyors

419 Abram NK, MacMillan DC, Xofis P, et al (2016) Identifying where REDD+ financially out-
420 competes oil palm in floodplain landscapes using a fine-scale approach. PLOS ONE
421 11:e0156481. doi: 10.1371/journal.pone.0156481

422 Abram NK, Xofis P, Tzanopoulos J, et al (2014) Synergies for improving oil palm production
423 and forest conservation in floodplain landscapes. PLoS ONE 9:e95388. doi:
424 10.1371/journal.pone.0095388

425 Akhtar N, Singh Bargali H, Chauhan NPS (2004) Sloth bear habitat use in disturbed and
426 unprotected areas of Madhya Pradesh, India. Ursus 15:203–211. doi: 10.2192/1537-
427 6176(2004)015<0203:SBHUID>2.0.CO;2

428 Alfred, R., Ahmad, A.H., Payne, J., Williams, C., Ambu, L.N., How, P.M., Goossens, B., 2012.
429 Home range and ranging behaviour of Bornean elephant (*Elephas maximus borneensis*)
430 females. PLoS ONE 7, e31400. doi:10.1371/journal.pone.0031400

431 Ali A, Zhou Z, Waseem M, et al (2017) An assessment of food habits and altitudinal distribution
432 of the Asiatic black bear (*Ursus thibetanus*) in the Western Himalayas, Pakistan. J Nat
433 Hist 51:689–701. doi: 10.1080/00222933.2017.1303097

434 Ancrenaz M, Goossens B, Gimenez O, et al (2004) Determination of ape distribution and
435 population size using ground and aerial surveys: a case study with orang-utans in lower
436 Kinabatangan, Sabah, Malaysia. Anim Conserv 7:375–385. doi:
437 10.1017/S136794300400157X

438 Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N.K.,
439   Meijaard, E., 2015. Of Pongo, palms and perceptions: a multidisciplinary assessment of
440   Bornean orang-utans *Pongo pygmaeus* in an oil palm context. Oryx 49, 465–472.
441   doi:10.1017/S0030605313001270

442 Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information
443   Criterion. J Wildl Manag 74:1175–1178. doi: 10.2193/2009-367

444 Augeri DM (2005) On the biogeographic ecology of the Malayan sun bear. PhD dissertation,
445   University of Cambridge

446 Charoo SA, Sharma LK, Sathyakumar S (2011) Asiatic black bear–human interactions around
447   Dachigam National Park, Kashmir, India. Ursus 22:106–113. doi: 10.2192/URSUS-D-
448   10-00021.1

449 Cheah, C.P.I., 2013. The ecology of Malayan sun bears (*Helarctos malayanus*) at the Krau
450   Wildlife Reserve, Pahang, Malaysia and adjacent plantations (PhD dissertation).
451   Universiti Putra Malaysia.

452 Ditmer, M.A., Garshelis, D.L., Noyce, K.V., Haveles, A.W., Fieberg, J.R., 2015. Are American
453   black bears in an agricultural landscape being sustained by crops? J. Mammal. 97, 54-67.
454   doi:10.1093/jmammal/gyv153

455 Estes JG, Othman N, Ismail S, et al (2012) Quantity and configuration of available elephant
456   habitat and related conservation concerns in the Lower Kinabatangan floodplain of
457   Sabah, Malaysia. PLoS ONE 7:e44601. doi: 10.1371/journal.pone.0044601

458 Evans MN, Vickers SH, Abu-Bakar MS, Goossens B (2016) Small carnivores of the Lower
459   Kinabatangan Wildlife Sanctuary, Sabah, Borneo, including a new locality for the otter
460   civet Cynogale bennettii. Small Carniv Conserv 54:26–38

461 Fiske I, Chandler R, others (2011) unmarked: An R package for fitting hierarchical models of
462   wildlife occurrence and abundance. J Stat Softw 43:1–23

463 Fredriksson, G.M., 2012. Effects of El-Nino and large-scale forest fires on the ecology and
464   conservation of Malayan sun bears (*Helarctos malayanus*) in East Kalimantan,
465   Indonesian Borneo (PhD dissertation). Universiteit van Amsterdam.

466 Fredriksson GM (2005a) Predation on sun bears by reticulated python in East Kalimantan,
467   Indonesian Borneo. Raffles Bull Zool 53:165–168

468 Fredriksson GM (2005b) Human-sun bear conflicts in East Kalimantan, Indonesian Borneo.
469   Ursus 16:130–137

470 Fredriksson, G.M., Wich, S.A., Trisno, 2006. Frugivory in sun bears (*Helarctos malayanus*) is
471   linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia.
472   Biol. J. Linn. Soc. 89, 489–508.

473   Gaveau DLA, Sloan S, Molidena E, et al (2014) Four decades of forest persistence, clearance
474   and logging on Borneo. PLoS ONE 9:e101654. doi: 10.1371/journal.pone.0101654

475   Guharajan R, Abram NK, Magguna MA, et al (2017) Does the Vulnerable sun bear *Helarctos*
476   *malayanus* damage crops and threaten people in oil palm plantations? Oryx 1–9. doi:
477   10.1017/S0030605317001089

478   Jorgenson JP, Sandoval-A S (2005) Andean bear management needs and interactions with
479   humans in Colombia. Ursus 16:108–116. doi: 10.2192/1537-
480   6176(2005)016[0108:ABMNAI]2.0.CO;2

481   Kawanishi K, Sunquist ME (2004) Conservation status of tigers in a primary rainforest of
482   Peninsular Malaysia. Biol Conserv 120:329–344. doi: 10.1016/j.biocon.2004.03.005

483   Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity?: Oil
484   palm agriculture and tropical biodiversity. Conserv Lett 1:60–64. doi: 10.1111/j.1755-
485   263X.2008.00011.x

486   Linkie M, Dinata Y, Nugroho A, Haidir IA (2007) Estimating occupancy of a data deficient
487   mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region,
488   Sumatra. Biol Conserv 137:20–27. doi: 10.1016/j.biocon.2007.01.016

489   Macdonald, G., Macdonald, H., 2016. HabitApp. Available at:
490   http://www.scrufster.com/habitapp/

491   MacKenzie DI, Nichols JD, Lachman GB, et al (2002) Estimating site occupancy rates when
492   detection probabilities are less than one. Ecology 83:2248–2255

493   MacKenzie DI, Nichols JD, Royle JA, et al (2018) Occupancy estimation and modeling:
494   inferring patterns and dynamics of species occurrence. Academic Press, London

495   Maddox, T., Priatna, D., Gemita, E., Salampessy, A., 2007. The conservation of tigers and other
496   wildlife in oil palm plantations, Jambi Province, Sumatra, Indonesia (October 2007).
497   Unpublished report. Zoological Society of London.

498   Maddrey RC, Pelton MR (1995) Black bear damage to agricultural crops in coastal North
499   Carolina. In: Proceedings of the Annual Conference of Southeastern Associated Fish and
500   Wildlife Agencies. pp 570–579

501   McConkey KIM, Galetti M (1999) Seed dispersal by the sun bear Helarctos malayanus in
502   Central Borneo. J Trop Ecol 15:237–241

503   McShea WJ, Stewart C, Peterson L, et al (2009) The importance of secondary forest blocks for
504   terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. Biol
505   Conserv 142:3108–3119. doi: 10.1016/j.biocon.2009.08.009

506   Meredith, M., Ridout, M.S., 2014. overlap: Estimates of coefficient of overlapping for animal
507   activity patterns. Available at: https://CRAN.R-project.org/package=overlap

508 Mohd-Azlan J (2006) Mammal diversity and conservation in a secondary forest in Peninsular
509   Malaysia. Biodivers Conserv 15:1013–1025. doi: 10.1007/s10531-004-3953-0

510 Nakashima, Y., Nakabayashi, M., Sukor, J.A., 2013. Space use, habitat selection, and day-beds
511   of the common palm civet (*Paradoxurus hermaphroditus*) in human-modified habitats in
512   Sabah, Borneo. J. Mammal. 94, 1169–1178. doi:10.1644/12-MAMM-A-140.1

513 Nazeri, M., Jusoff, K., Madani, N., Mahmud, A.R., Bahman, A.R., Kumar, L., 2012. Predictive
514   modeling and mapping of Malayan sun bear (*Helarctos malayanus*) Distribution Using
515   Maximum Entropy. PLoS ONE 7, e48104. doi:10.1371/journal.pone.0048104

516 Nazeri M, Kumar L, Jusoff K, Bahaman AR (2014) Modeling the potential distribution of sun
517   bear in Krau wildlife reserve, Malaysia. Ecol Inform 20:27–32. doi:
518   10.1016/j.ecoinf.2014.01.006

519 Ngoprasert D, Reed DH, Steinmetz R, Gale GA (2012) Density estimation of Asian bears using
520   photographic capture–recapture sampling based on chest marks. Ursus 23:117–133. doi:
521   10.2192/URSUS-D-11-00009.1

522 Ngoprasert D, Steinmetz R, Reed DH, et al (2011) Influence of fruit on habitat selection of Asian
523   bears in a tropical forest. J Wildl Manag 75:588–595. doi: 10.1002/jwmg.83

524 Nielsen SE, Boyce MS, Stenhouse GB (2004a) Grizzly bears and forestry I. Selection of
525   clearcuts by grizzly bears in west-central Alberta, Canada. For Ecol Manag 199:51–65.
526   doi: 10.1016/j.foreco.2004.04.014

527 Nielsen SE, Herrero S, Boyce MS, et al (2004b) Modelling the spatial distribution of human-
528   caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biol Conserv
529   120:101–113. doi: 10.1016/j.biocon.2004.02.020

530 Normua F, Higashi S, Ambu L, Mohamed M (2004) Notes on oil palm plantation use and
531   seasonal spatial relationships of sun bears in Sabah, Malaysia. Ursus 15:227–231

532 Northrup JM, Stenhouse GB, Boyce MS (2012) Agricultural lands as ecological traps for grizzly
533   bears. Anim Conserv 15:369–377. doi: 10.1111/j.1469-1795.2012.00525.x

534 Ordiz A, Støen O-G, Delibes M, Swenson JE (2011) Predators or prey? Spatio-temporal
535   discrimination of human-derived risk by brown bears. Oecologia 166:59–67. doi:
536   10.1007/s00442-011-1920-5

537 Powell, V., 2011. Resource use and habitat utilization of Malayan sun bear (Helarctos
538   malayanus) in Harapan Rainforest, Sumatra (End of Project Report). Unpublished report.
539   International Association for Bear Research and Management.

540 R Core Team (2015) R: A language and environment for statistical computing. R Foundation for
541   Statistical Computing, Vienna, Austria

Ramesh T, Kalle R, Sankar K, Qureshi Q (2012) Factors affecting habitat patch use by sloth bears in Mudumalai Tiger Reserve, Western Ghats, India. Ursus 23:78–85. doi: 10.2192/URSUS-D-11-00006.1

Ratnayeke S, Van Manen FT (2012) Assessing sloth bears as surrogates for carnivore conservation in Sri Lanka. Ursus 23:206–217

Rayan, D.M., Mohamad, S.W., Dorward, L., Aziz, S.A., Clements, G.R., Christopher, W.C.T., Traeholt, C., Magintan, D., 2012. Estimating the population density of the Asian tapir (*Tapirus indicus*) in a selectively logged forest in Peninsular Malaysia. Integr. Zool. 7, 373–380. doi:10.1111/j.1749-4877.2012.00321.x

Ríos-Uzeda B, Gómez H, Wallace RB (2007) A preliminary density estimate for Andean bear using camera-trapping methods. Ursus 18:124–128. doi: 10.2192/1537-6176(2007)18[124:APDEFA]2.0.CO;2

Ross J, Hearn AJ, Johnson PJ, Macdonald DW (2013) Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk: Activity of Sunda clouded leopards and their prey. J Zool 290:96–106. doi: 10.1111/jzo.12018

Samejima H, Ong RC, Lagan P, Kitayama K (2012) Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. 270:248–256

Scotson L, Vannachomchan K, Sharp T (2014) More valuable dead than deterred? Crop-raiding bears in Lao PDR. Wildl Soc Bull 38:783–790. doi: 10.1002/wsb.466

Sethy J, Chauhan NS (2016) Status and distribution of Malayan sun bear in Namdapha Tiger Reserve, Arunachal Pradesh, India. Int J Conserv Sci 7:533–552

Steinmetz, R., 2011. Ecology and distribution of sympatric Asiatic black bears and sun bears in the seasonally dry forests of Southeast Asia, in: W. McShea, S. Davies, and N. Bhumpakphan (eds). The Ecology and Conservation of Seasonally Dry Forests in Asia. Smithsonian Institution Press, Washington, D.C., pp. 249–273.

Steinmetz R, Garshelis DL (2010) Estimating ages of bear claw marks in Southeast Asian tropical forests as an aid to population monitoring. Ursus 21:143–153

Steinmetz R, Garshelis DL, Chutipong W, Seuaturien N (2013) Foraging ecology and coexistence of Asiatic black bears and sun bears in a seasonal tropical forest in Southeast Asia. J Mammal 94:1–18. doi: 10.1644/11-MAMM-A-351.1

Steinmetz R, Garshelis DL, Chutipong W, Seuaturien N (2011) The Shared Preference Niche of Sympatric Asiatic Black Bears and Sun Bears in a Tropical Forest Mosaic. PLoS ONE 6:e14509. doi: 10.1371/journal.pone.0014509

Takahata C, Nielsen SE, Takii A, Izumiyama S (2014) Habitat selection of a large carnivore along human-wildlife boundaries in a highly modified landscape. PLoS ONE 9:e86181. doi: 10.1371/journal.pone.0086181

578   Teo, S.D., 2013. Habitat use by Malayan sun bears (*Helarctos malayanus*) in the lowland
579   rainforests of Sabah, Malaysian Borneo (MSc thesis). National Pingtung University of
580   Science and Technology.

581   Wearn OR, Rowcliffe JM, Carbone C, et al (2017) Mammalian species abundance across a
582   gradient of tropical land-use intensity: A hierarchical multi-species modelling approach.
583   Biol Conserv 212:162–171. doi: 10.1016/j.biocon.2017.05.007

584   Wong ST, Servheen C, Ambu L, Norhayati A (2005) Impacts of fruit production cycles on
585   Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian
586   Borneo. J Trop Ecol 21:627–639. doi: 10.1017/S0266467405002622

587   Wong, S.T., Servheen, C.W., Ambu, L., 2004. Home range, movement and activity patterns, and
588   bedding sites of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo.
589   Biol. Conserv. 119, 169–181. doi:10.1016/j.biocon.2003.10.029

590   Wong ST, Servheen CW, Ambu LN (2002) Food habits of Malayan sun bears in lowland
591   tropical forests of Borneo. Ursus 13:127–136

592   Wong W-M, Leader-Williams N, Linkie M (2013) Quantifying changes in sun bear distribution
593   and their forest habitat in Sumatra: Sun bear population trends and deforestation in
594   Sumatra. Anim Conserv 16:216–223. doi: 10.1111/j.1469-1795.2012.00587.x

595   Wong W-M, Leader-Williams N, Linkie M (2015) Managing human-sun bear conflict in
596   Sumatran agroforest systems. Hum Ecol 43:255–266. doi: 10.1007/s10745-015-9729-1

597   Wong W-M, Linkie M (2013) Managing sun bears in a changing tropical landscape. Divers
598   Distrib 19:700–709. doi: 10.1111/ddi.12020

599   Yaap B, Magrach A, Clements GR, et al (2016) Large mammal use of linear remnant forests in
600   an industrial pulpwood plantation in Sumatra, Indonesia. Trop Conserv Sci
601   9:194008291668352. doi: 10.1177/1940082916683523

602   Yue S, Brodie JF, Zipkin EF, Bernard H (2015) Oil palm plantations fail to support mammal
603   diversity. Ecol Appl 25:2285–2292

604