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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.

46 **Keywords:** Borneo, Sabah, Lower Kinabatangan, oil palm, fragmentation, *Helarctos malayanus*,
47 habitat use

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

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

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 ($\Delta AIC \leq 2$) 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⁻¹),
263 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

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 trees 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

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.

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414 **7. Data availability**

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

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