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1 **Responses of Sunda clouded leopard population density to anthropogenic**
2 **disturbance and refining estimates of their conservation status in Sabah**

3

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20

21 **Keywords:** Sunda clouded leopard; *Neofelis diardi*; selective logging, forest management;
22 population density; spatially explicit capture recapture

23

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25

26

27 **Abstract**

28

29 Extensive areas of the world's tropical forests have been, and continue to be, disturbed as a
30 result of selective timber extraction. While such anthropogenic disturbance typically
31 results in the loss of biodiversity, many species persist, and their conservation in
32 production landscapes could be enhanced by a greater understanding of how biodiversity
33 responds to forest management practices. We conducted intensive camera trap surveys of
34 eight protected forest areas in Sabah, Malaysian Borneo, and developed estimates of Sunda
35 clouded leopard population density from spatially explicit capture-recapture analyses of
36 detection data to investigate how their abundance varies across the landscape and in
37 response to anthropogenic disturbance. Estimates of population density from six forest
38 areas ranged from 1.39 to 3.10 individuals per 100 km². Our study provides the first
39 evidence that Sunda clouded leopard population density is negatively impacted by hunting
40 pressure and forest fragmentation, and that among selectively logged forests, time since
41 logging is positively associated with abundance. We argue that these negative
42 anthropogenic impacts could be mitigated with improved logging practices, such as by
43 reducing the access of poachers by effective gating and destruction of road access points,
44 and by the deployment of anti-poaching patrols. By calculating a weighted mean
45 population density estimate from estimates developed in this paper and from the literature,
46 and by extrapolating this value to an estimate of current available habitat, we estimated
47 there are 754 (95% posterior Interval 325–1337) Sunda clouded leopard individuals in
48 Sabah.

49

50 **Introduction**

51

52 While still containing some of the largest contiguous tracts of forested land in Southeast
53 Asia, the rainforests of Borneo are experiencing amongst the highest global levels of forest
54 degradation and loss, principally as a result of selective timber extraction and subsequent
55 conversion to oil palm, *Elaeis guineensis*, plantations (Gaveau et al., 2014, 2016; Cushman
56 et al., 2017). The intricate ecological responses to selective logging of Borneo's forests
57 remain unclear for most species, yet several studies have indicated that many can persist
58 after such management, with only a minority of species studied so far exhibiting markedly
59 reduced post logging densities (e.g., Meijaard et al., 2005; Costantini et al., 2016). In
60 comparison, the conversion of these forests to oil palm production has been shown to
61 result in a very substantial reduction in biodiversity and functional diversity (Fitzherbert et
62 al., 2008; Yue et al., 2015), a pattern mirrored region-wide (Wilcove et al., 2013). Thus,
63 while logged forest undoubtedly has lower intrinsic value to biodiversity conservation than
64 pristine forest, it is becoming increasingly clear that further gains to conservation could be
65 achieved if management of production forests was improved to minimise negative impacts
66 on biodiversity (Meijaard and Scheil, 2008). However, such an optimisation approach,
67 based on an understanding of how biodiversity responds to forest management practices
68 and other anthropogenic disturbances, is currently lacking for many species, and
69 remedying this knowledge gap remains a priority.

70

71 The Sunda clouded leopard *Neofelis diardi*, is a medium-sized felid, endemic to the islands
72 of Borneo - where it is the terrestrial apex predator - and Sumatra. This species is currently
73 listed as Vulnerable on the IUCN Red List as a result of a presumed small and declining
74 population size (Hearn et al., 2016a). Assessment of its conservation status and
75 development of effective conservation actions, however, are hindered by a lack of
76 understanding regarding their abundance, distribution and responses to anthropogenic

77 disturbance (Hearn et al., 2016b). Records of Sunda clouded leopards inhabiting a diverse
78 range of forest types, including both pristine and selectively logged forests (e.g., Brodie &
79 Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013, 2016; Sollmann et al., 2014;
80 McCarthy et al., 2015; Hearn et al., 2016a), indicate that they exhibit some capacity to
81 tolerate anthropogenic disturbance. Brodie et al. (2015a), however, showed that Sunda
82 clouded leopard local scale abundance was lower in logged forest sites compared to
83 unlogged sites. In addition, the movements of Sunda clouded leopards from a fragmented
84 landscape were shown to be positively and strongly associated with forest, including
85 highly disturbed forest types, but negatively associated with a range of non-forest
86 vegetation (Hearn, 2016), thus confirming earlier predictions that forest loss and
87 conversion to oil palm plantations present one of this felid's greatest threats (Rabinowitz et
88 al., 1987; Hearn et al., 2016a,b). Indeed, the increasing prevalence of vast tracts of oil
89 palm plantations throughout this species' range is likely resulting in the fragmentation of
90 habitat and the consequent isolation of individual populations, potentially making them
91 increasingly vulnerable to demographic stochastic processes and inbreeding depression.
92 Robust spatial ecology data are lacking for the Sunda clouded leopard, but preliminary
93 analyses suggest that they have relatively large home ranges (Hearn et al., 2013). It is thus
94 conceivable that as forests become increasingly fragmented, and forest patches decline in
95 size, they become less able to support viable populations, resulting in reduced population
96 densities, and, ultimately, local extirpation.

97

98 While recent research has provided new insights into how anthropogenic pressures
99 influence Sunda clouded leopard abundance and habitat selection at a local scale, how
100 these responses translate into changes to their population density remains unknown.
101 Sollmann et al. (2014) estimated that Sunda clouded leopard density from two primary and

102 two mixed forest (primary and secondary) areas in Sumatra ranged from around 0.8 to 1.6
103 individuals per 100 km², but found no statistical support for differences in density between
104 the populations. In the Malaysian state of Sabah, northern Borneo, Brodie & Giordano
105 (2012) estimated that Sunda clouded leopard density from an area of primary forest was
106 1.9 individuals per 100 km², whereas Wilting et al. (2012) presented densities from two
107 selectively logged forests of around 0.8 and 1.0 individuals per 100 km². However, akin
108 with Sollmann et al. (2014), the relatively large, overlapping variances of the Sabah-
109 derived estimates suggest that the population densities were not significantly different.
110 Such low precision estimates are a reflection of the difficulty of obtaining sufficiently
111 large sample sizes. This is typical of studies of elusive forest felids (Foster & Harmsen,
112 2012) and hinders our ability to draw robust conclusions regarding the Sunda clouded
113 leopard's responses to disturbance, potentially masking any underlying problems.

114

115 As obligate carnivores, large felid abundance is directly affected by prey density under a
116 wide range of ecological conditions (Carbone & Gittleman, 2002; Karanth et al., 2004),
117 and so it is reasonable to assume that prey densities are a key limiting factor for Sunda
118 clouded leopards. Quantitative data regarding Sunda clouded leopard diet preferences are
119 lacking, but incidental reports and observations from Borneo (e.g., Rabinowitz et al., 1987;
120 Yeager, 1991; Matsuda et al., 2008) suggest that they exploit a diverse array of mammals,
121 and studies of temporal activity overlaps and patterns of co-occurrence with potential prey
122 (Ross et al., 2013) indicate that ungulates may be a key resource. Thus, the response of
123 Sunda clouded leopards to anthropogenic disturbance may be mediated largely by the
124 responses of their prey to such habitat modification. Bornean mammalian responses to
125 selective logging vary greatly, but their sensitivity to disturbance is positively correlated
126 with their phylogenetic age and dietary specificity, and negatively correlated with their

127 ecological niche width (Meijaard & Sheil, 2008; Meijaard et al., 2008). Brodie et al.
128 (2015a) showed that, compared to estimates in unlogged forest, muntjac (*Muntiacus* spp.)
129 and mousedeer (*Tragulus* spp.) abundance declined, and bearded pig (*Sus barbatus*) and
130 sambar deer (*Rusa unicolor*) increased in old logged forests. The abundance of all four
131 ungulates was lower in recently logged forests. An increased abundance of some species in
132 logged forest may benefit the Sunda clouded leopard and result in elevated abundances
133 compared to primary forest. Conversely, the dense network of logging roads and skids
134 present in production forests permit greater access and thus hunting opportunities for
135 poachers (Laurance et al., 2009), of which ungulates are a favoured quarry (Corlett, 2007).
136 In this balance, increased exploitative competition with humans in selectively logged
137 forests without adequate protection against such threats could result in reduced Sunda
138 clouded leopard densities.

139

140 Here, we develop estimates of Sunda clouded leopard population density using spatially
141 explicit capture-recapture analyses of camera trap data from multiple forest areas in Sabah
142 to investigate how density varies across the landscape and in response to anthropogenic
143 disturbance. We test our *a-priori* hypotheses that Sunda clouded leopard population
144 density will be lower in forests with (i) higher hunting pressure and (ii) higher levels of
145 forest fragmentation. We also hypothesise that (iii) among selectively logged forests, time
146 since logging will be positively associated with Sunda clouded leopard density. We
147 combine our results with those from previously published studies to develop an estimate of
148 Sunda clouded leopard population size in Sabah.

149

150 **Study Areas**

151

152 Between May 2007 and December 2013, we conducted intensive, systematic camera trap
153 surveys of eight protected forest areas in the Malaysian state of Sabah, northern Borneo
154 (Fig 1, Table 1). We selected survey areas that provided a broadly representative sample of
155 the spectrum of forest types, elevations, anthropogenic disturbance and fragmentation
156 present in the state. We surveyed three primary forests, including one predominantly
157 lowland hill (Danum Valley Conservation Area: Danum Valley), and two largely hill
158 dipterocarp and submontane forests (Tawau Hills Park (Tawau) and Crocker Range Park
159 (Crocker)). We surveyed five forest areas that had been exposed to selective logging,
160 including the Lower Kinabatangan Wildlife Sanctuary (Kinabatangan), Tabin Wildlife
161 Reserve (Tabin), and Kabili-Sepilok, Malua and Ulu Segama Forest Reserves.

162

163 **Methods**

164

165 *Camera survey protocol*

166

167 We undertook camera trap surveys designed specifically to estimate Bornean felid
168 population density (Hearn et al., 2016c). Depending on logistical constraints, we deployed
169 cameras according to one of two protocols, applying either a split-grid approach, where the
170 entire grid is sequentially surveyed in two halves, or a simultaneous approach, where all
171 camera stations are deployed in a single phase (Table 2). We deployed cameras primarily
172 along established and newly cut human trails and ridgelines, and occasionally along old,
173 unsealed logging roads, particularly in two of the selectively logged sites (Malua and Ulu
174 Segama; Table 2). Camera stations were spaced approximately 1.5–2.0 km apart, to
175 balance the need for a sufficiently large sampling grid with the need to ensure that each
176 animal's homerange contains several stations (e.g., Foster & Harmsen, 2012). Cameras

177 were positioned around 40–50 cm above the ground and arranged in pairs to enable both
178 flanks of the animal to be photographed simultaneously, to facilitate individual
179 identification.

180

181 *Assessment of poaching pressure*

182

183 We followed the approach of Brodie et al. (2015a) and analysed our camera trap data to
184 provide an estimate of poaching pressure for each study area and to enable comparison
185 with estimates of poaching pressure recorded in their previous studies. Our assessment was
186 based on the photographic encounter rate of presumed poachers, calculated as the mean
187 proportion of days that ≥ 1 poacher was recorded at each camera station. Hunting of birds
188 or mammals of any species is prohibited by law in all our study areas, and people did not
189 live in, or use the forest for any legal purpose other than limited tourism, research and
190 forest management at any of our sites. Excluding obvious records of unarmed park staff,
191 field personnel and tourists, we assumed that any person photographed within the forest
192 was a poacher. In most (86%) cases, people in the forest illegally were photographed
193 carrying shotguns or spears, and/or accompanied by dogs. This approach does not permit
194 assessment of historical poaching pressure, which may arguably be a more important
195 parameter to measure, but does provide a useful, non-subjective assessment of current
196 poaching levels.

197

198 *SECR analyses*

199

200 We developed estimates of Sunda clouded leopard population density using a Spatially
201 Explicit Capture Recapture (SECR) approach (Efford, 2004; Royle & Young, 2008),

202 undertaken within a Bayesian framework (Royale et al., 2009). We used the R (version
203 3.1.2; R Development Team, 2014) package SPACECAP (version 1.1.0; Gopaldaswamy et
204 al., 2012) to conduct all SECR analyses. We used pelage markings and morphology to
205 identify and sex individual animals and developed a unique capture history for each
206 animal. Detections of cubs were recorded but only adult animals were included in the
207 analysis. While it has been shown that gender can affect detection parameters in felids, and
208 inclusion of sex as a covariate can consequently improve parameter estimation precision
209 (e.g. Sollmann et al., 2011), we were unable to model sex-specific detection parameters
210 because of the low number of female recaptures and so data for both sexes were pooled
211 and analysed together. We assigned each 24-hour period as a unique sampling occasion, as
212 short sampling interval lengths may improve model precision (Goldberg et al., 2015). We
213 limited our sampling duration to 90 days, apart from one site (Tabin), where the lengthy
214 transition period, and consequent reduction in camera trapping effort, necessitated a period
215 of 120 days to provide sufficient detection frequencies. Such sampling durations are in-line
216 with similar studies to approximate population closure (e.g., Royle et al., 2011; Wilting et
217 al., 2012).

218

219 We developed a state space, a polygon defined by the addition of a buffer to the outermost
220 coordinates of each trapping grid, within which we established potential home range
221 centres by delineating a grid of regularly spaced points, with a mesh size of 0.25 km².
222 Following Gopaldaswamy et al. (2012) we eliminated potential home-range centres from
223 areas predicted to be unsuitable for Sunda clouded leopards using a GIS (ArcMap 10.2,
224 ESRI, Redlands, California, USA) in conjunction with habitat data derived from field
225 knowledge and hi-resolution aerial images from Google Earth (Images: DigitalGlobe). We
226 assumed that Sunda clouded leopards are restricted to forest cover and not found in oil

227 palm plantations (Hearn et al., 2016b) and so we considered forested areas (both pristine
228 and disturbed) as habitat and all other non-forest land uses, as unsuitable. During a
229 sequence of preliminary runs, we systematically increased buffer size until the probability
230 of detection at the state space boundary was negligible. Accordingly, buffer size varied
231 from 12 to 30 km.

232

233 We ran all SPACECAP density estimation analyses using a half normal detection and
234 Bernoulli's encounter model, with 100,000 Markov-Chain Monte Carlo (MCMC)
235 iterations and a thinning rate of 1. We varied burn-in for each survey until adequate
236 parameter convergence was attained, which we assessed by means of Geweke tests; z
237 scores falling between -1.64 and 1.64 were deemed acceptable. Program SPACECAP
238 applies a data augmentation process in which a theoretical population of zero-encounter
239 history individuals is added to the dataset of known animals (Gopaldaswamy et al., 2012).
240 We varied data augmentation values for each survey, assigning a final value following a
241 series of preliminary runs, increasing data augmentation where necessary to ensure that ψ ,
242 the ratio of the estimated abundance within the state space to the maximum allowable
243 number defined by the augmented value, did not exceed 0.8. Finally, we examined the
244 Bayesian p -value provided by program SPACECAP, which measures the discrepancy
245 between observed data and expected values, to assess the goodness-of-fit of the model;
246 models presenting p -values of around either 0 or 1 were considered inadequate (Gelman et
247 al., 1996; Gopaldaswamy et al., 2012). For each parameter estimated, we present the
248 posterior mean, standard deviation, and 95% Bayesian highest posterior density (HPD)
249 interval. The HPD is the shortest interval enclosing 95% of the posterior distribution.
250 Following Sollmann et al. (2014) we consider parameters from each site to be significantly
251 different if the 95% HPD of one does not include the mean of the other.

252

253 *Estimation of population size in Sabah*

254

255 We developed an estimate of Sunda clouded leopard population size for Sabah based on
256 extrapolation of an estimate of this species' density to an estimate of current available
257 habitat. Following a meta-analysis approach, we calculated a weighted mean population
258 density estimate from estimates developed in this paper (n=6) and from previous published
259 estimates from Sabah (Brodie and Giordano, 2012, n=1; Wilting et al., 2012; n=2), by
260 weighting each unique value by the inverse of their coefficient of variation, based on their
261 respective 95% HPD values. Using the same weighted approach, we calculated a mean
262 upper and lower density estimate, based on each value's upper and lower quantiles. For an
263 approximation of available Sunda clouded leopard habitat, we assumed that these felids are
264 restricted to forest habitats and used an estimate of Sabah forest cover for the year 2015
265 developed by Gaveau et al. (2016), based on analysis of LANDSAT imagery. Gaveau et
266 al.'s (2016) definition of forest included closed-canopy, old-growth and selectively logged
267 dipterocarp, heath, fresh-water and peat swamp forests and mangrove forests, but excluded
268 young forest regrowth, scrublands, tree plantations, agricultural land, and non-vegetated
269 areas, and thus closely matches current predictions for clouded leopard habitat associations
270 (Hearn et al., 2016b). It is important to note that this definition of available habitat
271 includes forest types from which no robust density estimates are currently available (i.e.,
272 heath forests, peat swamp forests and mangrove), and so our population estimate should be
273 treated with appropriate caution.

274

275 **Results**

276

277 *Photographic capture success*

278

279 We recorded 528 independent photographic captures of Sunda clouded leopards, with
280 records stemming from all survey areas apart from Kabili-Sepilok (Table 2). We found
281 evidence of breeding activity at three sites, recording two different cubs in Crocker and
282 one in both Malua and Tawau (Table 2). The number of independent photographic
283 captures within the closed survey period varied greatly across the different sites, ranging
284 from 10 to 101 (mean = 41), and the number of different individual animals recorded
285 within this period ranged from 5 to 10 (Table 3). We could assign individual identity to all
286 but one of the photographic captures, a female from Malua. At most sites, we recorded
287 more individual males than females, and males typically had higher recapture rates than
288 did females (Table 3).

289

290 *Assessment of poaching pressure*

291

292 We found evidence of probable poaching activity in all forest areas, apart from Danum
293 (Table 4). The lowest poacher detection rates were found in Danum, Ulu Segama and
294 Tawau, where camera theft was also low, and the highest in Kinabatangan and Malua,
295 where camera theft was high. Camera theft from Crocker was also relatively high. Tabin
296 had a relatively high poacher detection rate but a relatively low incidence of camera theft.

297

298 *Density estimates*

299

300 We developed estimates of Sunda clouded leopard density at all study sites at which they
301 were detected apart from Malua, in which low numbers of photographic captures

302 prevented SECR model convergence, and so was removed from subsequent analyses. At
303 all other sites Bayesian p -values indicated that the models were of an adequate fit (Table 5)
304 and Geweke tests indicated that all model parameters converged. Sunda clouded leopard
305 density across these six sites varied from 1.39 to 3.10 individuals per 100 km² (Table 5).
306 The two highest density estimates stemmed from the enrichment-planted Ulu Segama
307 (3.10 individuals per 100 km² \pm SD 1.11) and selectively logged Tabin (2.66 \pm SD 1.11),
308 and the lowest from the primary upland Crocker (1.39 \pm SD 0.41) and the highly degraded
309 and fragmented Kinabatangan (1.54 \pm SD 0.70). Sunda clouded leopard density was
310 significantly higher in Ulu Segama than Crocker, Danum and Kinabatangan, and density in
311 Tabin was significantly higher than in Crocker and Kinabatangan, but we otherwise found
312 no statistical support for differences in density between any other sites. The movement
313 parameters from Kinabatangan and Tabin were significantly larger than that from all other
314 sites, and the estimate from Kinabatangan was significantly larger than that from Tabin, by
315 almost a factor of two (Table 5).

316

317

318 *Estimation of population size in Sabah*

319

320 The weighted mean population density developed from nine available density estimates
321 was 1.90 individuals per 100 km², and the weighted lower and upper 95% posterior
322 intervals were 0.82 and 3.37 individuals per 100 km², respectively. Based on data derived
323 from Gaveau et al. (2016), the amount of available habitat in Sabah in 2015 was 39,693
324 km². Extrapolation of the weighted density estimate to this habitat assessment produced an
325 estimated population size of 754 (95% posterior interval 325–1337) individuals for Sabah.

326

327 **Discussion**

328

329 *Influence of anthropogenic disturbance on Sunda clouded leopard density*

330

331 We present estimates of Sunda clouded leopard population density from six of eight forest
332 areas we surveyed in Sabah, Borneo, including the first for this species from enrichment-
333 planted, highly fragmented, and submontane forest types. Our estimates of density from
334 forest areas exposed to varying levels of anthropogenic disturbance ranged from 1.39 to
335 3.10 individuals per 100 km², and are thus comparable with those from previous studies in
336 Sabah (0.84–1.9: Brodie and Giordano, 2012; Wilting et al., 2012), the Indonesian
337 province of Central Kalimantan (0.72–4.41: Cheyne et al., 2013) and Sumatra (0.8–1.6:
338 Sollmann et al., 2014). Nevertheless, statistically significant differences in Sunda clouded
339 leopard population density were evident between several of our study areas.

340

341 While the absence of replication in our study approach limits our ability to draw robust
342 conclusions about the possible influence of anthropogenic disturbance on Sunda clouded
343 leopard densities, our results support our first *a-priori* hypothesis that population density is
344 negatively impacted by poaching pressure. Indeed, the two areas with the lowest estimates,
345 the primary uplands of the Crocker Range Park and the low lying logged forests of the
346 Lower Kinabatangan, were subject to some of the highest levels of poaching pressure,
347 whereas forest areas with a relatively low incidence of poaching, e.g., Danum Valley, Ulu
348 Segama and Tawau, yielded some of the highest densities. In the case of Ulu Segama, the
349 estimate of density was statistically higher than that of the two lowest density sites. It is
350 worth noting that the comparatively low density found in Crocker Range may also be a
351 reflection of higher elevation forest supporting lower productivity. While we are unable to
352 disentangle the possible influence of low detection probabilities as a result of other factors

353 unrelated to abundance (Sollmann et al., 2013), the very low photographic capture success
354 from Malua Forest Reserve, where poaching intensity was the highest of our study areas, is
355 indicative of a low population density relative to our other sites. The high density estimate
356 from Tabin Wildlife Reserve, which was also significantly higher than that of our two
357 lowest density sites, yet was subject to moderate levels of poaching, appears to contradict
358 this trend. However, unlike other areas where poaching activity was more diffuse, most
359 records of poaching activity in Tabin typically involved poachers spot-lighting from four-
360 wheel-drive vehicles along the single access road within the reserve, or occasionally along
361 the western border with an oil palm plantation. It is, therefore, possible that the impact of
362 poaching was not widespread throughout the study area.

363

364 Our data also tentatively support our second *a-priori* hypothesis that Sunda clouded
365 leopard population density will be lower in forests with higher levels of forest
366 fragmentation. Firstly, the Lower Kinabatangan, which is composed of several relatively
367 small forest patches embedded within a largely oil palm plantation landscape, supported
368 the second to lowest density of all our areas. Secondly, we found no evidence of Sunda
369 clouded leopards within the Kabili-Sepilok Forest Reserve, a small (42.76 km²),
370 potentially isolated dipterocarp forest fragment contiguous with a coastal chain of
371 mangrove and nipah palm, but otherwise surrounded by oil palm plantations. Forestry
372 Department staff stationed in the area report that the species had been recorded there in the
373 past, so it is likely that gradual loss of surrounding forest and conversion to oil palm
374 plantations has led to local extirpation. Kabili-Sepilok Forest Reserve is a probable
375 harbinger of the effects of ongoing fragmentation which will be detrimental to Sunda
376 clouded leopard populations across much of its remaining range.

377

378 The low number of photographic captures from Malua Forest Reserve, which was
379 surveyed just one year after selective logging operations ceased, provides tentative support
380 for our third *a-priori* hypothesis, that time since logging is positively related to Sunda
381 clouded leopard density in selectively logged forests. Furthermore, our two highest density
382 estimates stemmed from two forests surveyed 16 and 20 years post logging activities, of
383 which one, the enrichment-planted Ulu Segama Forest Reserve, was statistically higher
384 than that from the primary Danum Valley Conservation Area. It is noteworthy that Wilting
385 et al's (2012) survey of the Tangkulap-Pinangah Forest Reserve in Sabah, just eight years
386 after logging operations stopped, yielded a density of 0.84 individuals per 100 km², which
387 is lower than any of our estimates. Brodie et al. (2015a) showed that, compared to
388 unlogged forest areas, the abundance of four ungulate species was lower in recently logged
389 areas, whereas bearded pig and sambar deer were more abundant, and muntjac and
390 mousedeer less abundant in old logged areas. Thus, while we cannot be sure by what
391 mechanism the effect may operate, one hypothesis is that following recent logging there is
392 a direct negative effect on prey abundance and or availability, which declines over time.
393 Another, not mutually exclusive, hypothesis is that the logging operations, and associated
394 proliferation of roads, increases both the number of poachers and their penetration of the
395 forest, reducing prey populations and perhaps also inflicting a by-catch on the Sunda
396 clouded leopards themselves, and that the relative impact of these roads diminishes over
397 time as the roads become unnavigable. Brodie et al. (2015b) found that an increase in road
398 density on Borneo is associated with reduced local occurrence of Sunda clouded leopards,
399 and in Sumatra, Haidir et al. (2013) found that this felid's habitat use was positively
400 affected by distance to forest edge. In another Sumatran study, McCarthy et al. (2015)
401 reported that this species occurred most commonly at moderate distances from roads,
402 rivers and forest edges, all features which assist the movement of people.

403

404 Our results confirm earlier suggestions (e.g., Wilting et al., 2006; Hearn et al., 2016a,b)
405 that selectively logged forest provides an important resource for Sunda clouded leopards,
406 and suggests that appropriate management of these commercial forests could further
407 enhance their conservation value. Our results suggest that the overriding priority is to
408 reduce poaching pressure, both on these felids and their prey, by reducing access to the
409 forest interior along logging roads. Reduction of vehicular access could be achieved
410 through the installation of gates and the destruction of bridges following the cessation of
411 logging activities. This is particularly important in more recently logged forests, which
412 will have a more extensive network of gravel roads that are still passable. Such efforts will
413 not prevent access on foot, and so measures such as anti-poaching patrols, while
414 expensive, are also an essential tool to reduce the threat from poaching in these forests.

415

416 *Estimation of population size in Sabah*

417

418 We provide the first estimate of Sunda clouded leopard population size for the Malaysian
419 state of Sabah based on robust spatially explicit capture recapture density estimates from
420 nine forest areas within the state. Our estimated population size of around 754 (95%
421 posterior interval 327–1337) individuals is a significant methodological improvement on
422 the very approximate estimate of 1500–3200 individuals provided by Wilting et al. (2006),
423 based on extrapolation of a track-based assessment of density from Tabin Wildlife
424 Reserve. Our basic model of population size does not include a minimum patch size or
425 measure of proximity to other patches in its calculation, as such data are currently lacking.
426 Nevertheless, their apparent absence from the relatively small forest fragment of Kabili-
427 Sepilok suggests that our estimate of available habitat may be slightly inflated, and with it

428 our population estimate. In addition, while we made efforts to survey a range of forest
429 types and levels of anthropogenic disturbance, there are a number of forest types that were
430 not included. Of these, mangrove forest, given its potential importance in connecting
431 otherwise isolated populations, is particularly important. Surveys within these habitats and
432 efforts to determine minimum patch sizes for this felid are therefore a priority.

433

434 As forest cover on Borneo declines, there is an increasing need to assess the population
435 size of this felid across the entire island, and thus the conservation status of the Bornean
436 sub species, *Neofelis diardi* ssp. *borneensis*. The Sabah bias of our data, and the lack of
437 robust spatially explicit density estimates from outside this region currently hinders such
438 assessment. While the overall nature of the forests within Sabah broadly parallels those of
439 the island as a whole, outside of this state there are stark differences in forest management
440 and patterns of deforestation (Cushman et al., 2017). Furthermore, the threat from hunting
441 and/or poaching, which we have shown to be a potentially important factor influencing
442 Sunda clouded leopard density, is likely to vary considerably throughout the island. There
443 is increasing evidence that Sabah's forests have hitherto been subjected to lower influences
444 of hunting and poaching than elsewhere and that populations densities may be far lower
445 outside of this region. Indeed, the mean encounter rate of hunters/poachers from five areas
446 in Sarawak were more than an order of magnitude higher than that described in this paper
447 (Brodie et al., 2015a). Furthermore, Cheyne et al. (2016) surveyed eight forest areas in
448 Kalimantan with a comparable effort and approach to that used in our study, and recorded
449 an exceptionally low number of Sunda clouded leopard records (≤ 3) from each of six of
450 these forests, which could be indicative of low population densities. Efforts should thus be
451 made both to establish the incidence of poaching across this felid's range, and to derive

452 robust, spatially explicit estimates of their density outside of Sabah to help better inform
453 the conservation of this elusive wild cat.

454

455

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457

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468

469 **References**

470

471 Brodie, J. & Giordano, A.J. (2012). Density of the Vulnerable Sunda clouded leopard
472 *Neofelis diardi* in a protected area in Sabah, Malaysian Borneo. *Oryx*, 46(3), 427–
473 30. doi: 10.1017/S0030605312000087

474

475 Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-Azlan, J. & Ambu, L.
476 (2015a). Correlation and persistence of hunting and logging impacts on tropical
477 rainforest mammals. *Conservation Biology*, 29(1), 110–121.
478

479 Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J.,
480 Anderson, J. & Ambu, L. (2015b). Evaluating multispecies landscape connectivity
481 in a threatened tropical mammal community. *Conservation Biology* 29(1), 122–
482 132.
483

484 Burnham, D., Hinks, A.E. & Macdonald, D.W. (2012). Life and dinner under the shared
485 umbrella: patterns in felid and primate communities. *Folia Primatologica* 83:148–
486 170.
487

488 Carbone, C. & Gittleman J.L. (2002). A common rule for the scaling of carnivore density.
489 *Science*, 295, 2273–2276.
490

491 Cheyne, S.M., Stark, D.J., Limin, S.H. & Macdonald, D.W. (2013). First estimates of
492 population ecology and threats to Sunda clouded leopards *Neofelis diardi* in a peat-
493 swamp forest, Indonesia. *Endangered Species Research*, 22, 1–9.
494

495 Cheyne, S.M., Sastramidjaja, W.J., Muhahir, Rayadin, Y. & Macdonald, D.W. (2016).
496 Mammalian communities as indicators of disturbance across Indonesian Borneo.
497 *Global Ecology and Conservation*, 7, 157–173.
498

499 Corlett, R.T. (2007). The impact of hunting on the mammalian fauna of tropical Asian
500 forests. *Biotropica*, 39(3), 292–303.
501

502 Costantini, D., Edwards, D.P. & Simons, M.J. (2016). Life after logging in tropical forests
503 of Borneo: A meta-analysis. *Biological Conservation*, 196, 182–188.
504

505 Cushman, S.A., Macdonald, E.A., Landguth, E.L., Malhi, Y., & Macdonald, D.W. (2017).
506 Multiple-scale prediction of forest loss risk across Borneo. *Landscape Ecology*, 1–
507 18.
508

509 Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 10, 598–610.
510

511 Foster, R.J. & Harmsen, B.J. (2012). A critique of density estimation from camera-trap
512 data. *The Journal of Wildlife Management*, 76(2), 224–236.
513

514 Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. &
515 Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in*
516 *Ecology and Evolution*, 23, 538–545.
517

518 Gaveau, D.L., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M.,
519 Nasi, R., Quinones, M., Wielaard, N. & Meijaard, E. (2014). Four decades of forest
520 persistence, clearance and logging on Borneo. *PLoS ONE*, 9(7), e101654.
521

522 Gaveau, D.L., Sheil, D., Husnayaen, Salim, M.A., Arjasakusuma, S., Ancrenaz, M.,
523 Pacheco, P. & Meijaard, E. (2016). Rapid conversions and avoided deforestation:

524 examining four decades of industrial plantation expansion in Borneo. Scientific
525 Reports, 6. Doi: 10.1038/srep32017.

526

527 Gelman, A., Meng, X.L. & Stern, H. (1996). Posterior predictive assessment of model
528 fitness via realized discrepancies. *Statistica sinica*, 6(4), 733–760.

529

530 Goldberg, J.F., Tempa, T., Norbu, N., Hebblewhite, M., Mills, L.S., Wangchuk, T.R. &
531 Lukacs, P. (2015). Examining temporal sample scale and model choice with spatial
532 capture-recapture models in the common leopard *Panthera pardus*. *PLoS ONE*,
533 10(11). doi: 10.1371/journal.pone.0140757

534

535 Gopaldaswamy, A.M., Royle, J.A., Hines, J.E., Singh, P., Jathanna, D., Kumar, N.S. &
536 Karanth, K.U. (2012). Program SPACECAP: software for estimating animal
537 density using spatially explicit capture-recapture models. *Methods in Ecology and*
538 *Evolution*, 3(6), 1067-72. doi: 10.1111/j.2041-210X.2012.00241.x

539

540 Haidir, I.A., Dinata, Y., Linkie, M. & Macdonald, D.W. (2013). Asiatic golden cat and
541 Sunda clouded leopard occupancy in the Kerinci Seblat landscape, West-Central
542 Sumatra. *CatNews*, 59, 7–10.

543

544 Hearn, A.J. (2016). Assessing the influence of anthropogenic disturbance on sympatric
545 felids on Borneo with special reference to the Sunda clouded leopard. Doctor of
546 Philosophy Thesis, University of Oxford.

547

548 Hearn, A., Sanderson, J., Ross, J., Wilting, A. & Sunarto, S. (2008). *Neofelis diardi* ssp.
549 *borneensis*. The IUCN Red List of Threatened Species 2008: e.T136945A4351615.
550 <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T136945A4351615.en>.
551 Downloaded on 13 September 2016.
552
553 Hearn, A.J., Ross, J., Pamin, D., Bernard, H., Hunter, L., & Macdonald, D.W. 2013.
554 Insights into the spatial and temporal ecology of the Sunda clouded leopard
555 *Neofelis diardi*. Raffles Bulletin of Zoology, 61(2): 871–875.
556
557 Hearn, A., Ross, J., Brodie, J., Cheyne, S., Haidir, I.A., Loken, B., Mathai, J., Wilting, A.
558 & McCarthy, J. (2016a). *Neofelis diardi*. The IUCN Red List of Threatened
559 Species 2016.
560
561 Hearn, A.J., Ross, J., Macdonald, D.W., Bolongon, G., Cheyne, S.M., Mohamed, A.,
562 Samejima, H., Brodie, J.F., Giordano, A., Alfred, R., Boonratana, R., Bernard, H.,
563 Loken, B., Augeri, D.M., Heydon, M., Hon, J. Mathai, J., Marshall, A.J., Pilgrim,
564 J.D., Hall, J., Breitenmoser-Würsten, C., Kramer-Schadt, S. & Wilting, A. (2016b).
565 Predicted distribution of the Sunda Clouded leopard *Neofelis diardi* (Mammalia:
566 Carnivora: Felidae) on Borneo. Raffles Bulletin of Zoology, Supplement No. 33,
567 165–172.
568
569 Hearn, A.J., Ross, J., Bernard, H., Bakar, S.A., Hunter, L.T.B. & Macdonald, D.W.
570 (2016c) The first estimates of marbled cat *Pardofelis marmorata* population
571 density from Bornean primary and selectively logged forest. PLoS ONE, 11(3),
572 e0151046. doi:10.1371/journal.pone.0151046

573

574 Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004). Tigers and
575 their prey: Predicting carnivore densities from prey abundance. Proceedings of the
576 National Academy of Sciences, 101(14), 4854–4858.

577

578 Laurance, W.F., Goosem, M. & Laurance, S.G.W. (2009). Impacts of roads and linear
579 clearings on tropical forests. Trends in Ecology and Evolution, 24, 659–669.

580

581 Mathai, J., Duckworth, J.W., Meijaard, E., Fredriksson, G., Hon, J., Sebastian, A.,
582 Ancrenaz, M., Hearn, A.J., Ross, R., Cheyne, S., Borneo Carnivore Consortium &
583 Wilting, A., (2016). Carnivore conservation planning on Borneo: identifying key
584 carnivore landscapes, research priorities and conservation interventions. Raffles
585 Bulletin of Zoology, Supplement No. 33, 186–217.

586

587 Matsuda, I., Tuuga, A., & Higashi, S. (2008). Clouded leopard (*Neofelis diardi*) predation
588 on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Primates 49, 227–
589 231.

590

591 McCarthy J.L., Wibisono, H.T., McCarthy, K.P., Fuller, T.K. & Andayani, N. (2015).
592 Assessing the distribution and habitat use of four felid species in Bukit Barisan
593 Selatan National Park, Sumatra, Indonesia. Global Ecology and Conservation, 3,
594 210–21. doi: 10.1016/j.gecco.2014.11.009

595

596 Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T.,
597 Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S. & O'Brien,

598 T. (2005). Life after logging: Reconciling Wildlife Conservation and Production
599 Forestry in Indonesian Borneo. Center for International Forestry Research, Bogor,
600 Indonesia.

601

602 Meijaard, E. & Sheil, D. (2008). The persistence and conservation of Borneo's mammals
603 in lowland rain forests managed for timber: observations, overviews and
604 opportunities. *Ecological Resources*, 23, 21–34.

605

606 Meijaard, E., Sheil, D., Marshall, A.J., & Nasi, R. (2008). Phylogenetic age is positively
607 correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica*,
608 40(1), 76–85.

609

610 R Development Team. (2014). R: A Language and Environment for Statistical Computing.
611 R Foundation for Statistical Computing, Vienna, Austria. [http://www.R-](http://www.R-project.org)
612 [project.org](http://www.R-project.org)

613

614 Rabinowitz, A., Andau, P. & Chai, P.P. (1987). The clouded leopard in Malaysian Borneo.
615 *Oryx*, 21(2), 107–111.

616

617 Ross, J., Hearn, A.J., Johnson, P. J., & Macdonald, D.W. (2013). Activity patterns and
618 temporal avoidance by prey in response to Sunda clouded leopard predation risk.
619 *Journal of Zoology*, 290(2), 96–106.

620

621 Royle, J.A. & Young, K.V. (2008). A hierarchical model for spatial capture–recapture
622 data. *Ecology*, 89, 2281–2289.

623

624 Royle, J.A., Karanth, K.U., Gopaldaswamy, A.M. & Kumar, N.S. (2009). Bayesian
625 inference in camera trapping studies for a class of spatial capture–recapture
626 models. *Ecology*, 90(11), 3233–44. doi: 10.1890/08-1481.1

627

628 Royle, J.A., Magoun, A.J., Gardner, B., Valkenburg, P. & Lowell, R.E. (2011). Density
629 estimation in a wolverine population using spatial capture–recapture models. *The*
630 *Journal of Wildlife Management*, 75(3), 604–11. doi: 10.1002/jwmg.79

631

632 Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T., Tôrres, N.M. &
633 Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting
634 for sex-specific detection and movements using spatial capture–recapture models
635 for jaguars in central Brazil. *Biological Conservation*, 144(3), 1017–1024.

636

637 Sollmann, R., Mohamed, A., Samejima, H. & Wilting, A. (2013). Risky business or simple
638 solution–relative abundance indices from camera-trapping. *Biological*
639 *Conservation*, 159, 405–412.

640

641 Sollmann, R., Linkie, M., Haidir, I.A. & Macdonald, D.W. (2014). Bringing clarity to the
642 clouded leopard *Neofelis diardi*: first density estimates from Sumatra. *Oryx*,
643 48(04), 536–539.

644

645 Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. & Koh, L.P. (2013). Navjot’s
646 nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia.
647 *Trends in Ecology and Evolution* 28, 531–40.

648

649 Wilting, A., Fischer, F., Bakar, S.A. & Linsenmair, K.E. (2006). Clouded leopards, the
650 secretive top-carnivore of South-East Asian rainforests: Their distribution, status
651 and conservation needs in Sabah, Malaysia. *BMC Ecology* 6, 16.

652

653 Wilting, A., Mohamed, A., Ambu, L.N., Lagan, P., Mannan, S., Hofer, H. & Sollmann, R.
654 (2012). Density of the vulnerable Sunda clouded leopard *Neofelis diardi* in two
655 commercial forest reserves in Sabah, Malaysian Borneo. *Oryx*, 46(03), 423–426.

656

657 Yeager, C.P. (1991). Possible antipredator behaviour associated with river crossings by
658 proboscis monkeys (*Nasalis larvatus*). *American Journal of Primatology*, 24, 61–
659 66.

660

661 Yue, S., Brodie, J.F., Zipkin, E.F. & Bernard, H. (2015). Oil palm plantations fail to
662 support mammal diversity. *Ecological Applications*, 25(8), 2285–2292.

663

664 **Biographical sketches**

665

666 ANDREW J. HEARN's interests lie in the distribution, status, spatial ecology, and
667 conservation of the guild of sympatric felids on Borneo. JOANNA ROSS's research
668 focuses on the ecology and conservation of members of the Bornean felid guild and other
669 threatened Bornean Mammals. HENRY BERNARD has research interests in Bornean
670 small mammal communities and proboscis monkeys. SOFFIAN A. BAKAR's core
671 interests lie in the conservation and sustainable management of wildlife in Sabah. BENOIT
672 GOOSSENS is Director of the Danau Girang Field Centre in Sabah where he is running

673 long-term programmes on an array of tropical forest species to understand their biological
 674 responses to rainforest fragmentation and oil palm monoculture. LUKE HUNTER
 675 oversees the direction and strategy of Panthera’s global wild cat conservation programs.
 676 DAVID W. MACDONALD has a background in behavioural ecology, with an emphasis
 677 on carnivores.

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687 Table 1. Details of the eight forest study areas in Sabah, Malaysian Borneo. Study areas
 688 are arranged in approximate order of increasing disturbance (level of fragmentation and
 689 exposure to selective logging practices).

690

Study area	Location (Lat/ Lon)	Size (km ²) ^a	Level of isolation /fragmentation of forest patch	Dominant landcover type(s) / logging exposure	Time since logging (Years)
Danum Valley	4° 58' N, 117° 46' E	438	<u>Low.</u> Part of ca. 1 million ha Central Sabah Forest complex	Primary, lowland & hill dipterocarp.	N/A
Tawau	4° 27' N, 117° 57' E	280	<u>Medium.</u> Large, relatively isolated forest block, contiguous with commercial Forest Reserve to North.	Primary, lowland & hill dipterocarp, sub-montane & montane.	N/A
Crocker	5° 26' N, 116° 02' E	1399	<u>Medium.</u> Large, relatively isolated forest block.	Primary, hill dipterocarp, sub- montane & montane.	N/A

Ulu Segama	4° 59' N, 117° 52' E	2029	<u>Low.</u> Part of ca. 1 million ha Central Sabah Forest complex	Selectively logged (1978-1991), lowland Dipterocarp. Medium density of open and semi-closed logging roads. Enrichment planted in 1993.	16
Tabin	5° 14' N, 118° 51' E	1,205	<u>Medium.</u> Large, relatively isolated forest block. Possible connectivity with coastal mangrove to North.	Selectively logged (1969-1989), lowland dipterocarp. Low density of open and semi-closed logging roads.	20
Kabili-Sepilok	5° 51' N, 117° 57' E	42.9	<u>High.</u> Small, isolated fragment. Possible connectivity along coastal mangrove system	Partially selectively logged (low impact, ceased 1957), lowland Dipterocarp, heath forest & mangrove.	>50
Kinabatangan	5° 29' N, 118° 08' E	260	<u>High.</u> Relatively isolated, highly degraded patches of forest along large river.	Selectively logged, mosaic of forest types, including riparian forest, seasonally flooded forest, swamp forest, limestone forest.	>20
Malua	5° 08' N, 117° 40' E	340	<u>Low.</u> Part of ca. 1 million ha Central Sabah Forest complex	Twice-logged (1960s & 2006-2007), lowland dipterocarp. High density of open logging roads and skid trails.	1

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692

693 Table 2. Details of camera trap sampling regimes and Sunda clouded leopard photographic
694 capture data derived from surveys of eight forest study areas in Sabah, Malaysian Borneo.
695 ^a Camera trap grid area is defined by a 100% Minimum Convex Polygon around all
696 camera stations. ^bWe followed two survey protocols, Split-grid: where the entire grid was
697 sequentially surveyed in two halves, and Simultaneously (Sim): where all camera stations
698 were deployed in a single phase. ^cNumber of photographic captures of different individuals
699 or images obtained more than 1 hour apart. ^dValues within parentheses represent capture
700 data for male, females and cubs, respectively.

701

Study area	Camera trap grid				Survey effort and Sunda clouded leopard capture data				
	Area (km ²) ^a	Protocol ^b	No. cam. stations	No. cam. stations on road / trail	Mean elevation and range (m.a.s.l)	Survey dates	No. trap days	No. independent captures ^{c, d}	No. different animals recorded ^d
Danum Valley	157.0	Split	79	0 / 79	384 (153–804)	24/3/12–6/10/12	5837	88 (82,6,0)	9 (6,3,0)
Tawau	149.0	Sim.	77	0 / 77	706 (209–1195)	21/10/12–30/12/13	17397	239 (219,20,1)	12 (7,5,1)
Crocker	149.7	Sim.	35	3 / 32	1029 (383–1452)	6/10/12–27/2/12	4059	51 (46,5,2)	8 (4,4,2)
Ulu Segama	60.1	Sim.	22	19 / 3	252 (150–408)	24/5/07–18/10/07	2847	83 (70,13,0)	11 (6,5,0)
Tabin	159.0	Split	74	12 / 74	175 (11–431)	18/09/09–22/4/10	6462	41 (36,5,0)	9 (5,4,0)
Kabili Sepilok	49.4	Sim.	35	0 / 35	66 (8–134)	9/2/11–25/5/11	2054	0	0
Kinabatangan	359.5	Split	66	0 / 66	35 (5–135)	24/7/10–17/12/10	4340	15 (8,7,0)	5 (2,3,0)
Malua	102.8	Sim.	38	38 / 0	177 (68–286)	9/7/08–12/2/09	3869	11 (9,2,1)	6 (4,2,1)

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705 Table 3. Sampling specifications and Sunda clouded leopard capture data from the closed
 706 survey periods from seven study areas in Sabah, Malaysian Borneo. ^a Number of
 707 independent photographic captures that were used in the SECR analysis. ^b Values in
 708 parentheses represent values for males, females and cubs, respectively. ^c Values in
 709 parentheses represent the number of different camera stations that each individual was
 710 recorded at during the closed survey period.

711

Study area	Closed survey period	No. sampling occasions	No. trap days	No. captures _{a,b}	No. different animals recorded ^b	No. captures per individual ^c	
						Males	Females
Danum Valley	23/06/2012 – 20/09/2012	90	3376	46 (43,3,0)	8 (6,2,0)	23(13), 8(5), 7(4), 2(2), 2(1), 1(1)	2(2), 1(1)
Tawau	11/3/2013 – 8/6/2013	90	6471	101 (92,9,0)	10 (5,5,0)	49(24), 30(17), 7(4), 4(3), 2(2)	3(3), 3(2), 1(1), 1(1), 1(1)
Crocker	17/11/2011 – 14/02/2012	90	3005	37 (34,3,2)	6 (3,3,2)	21(11), 9(3), 4(1)	1(1), 1(1), 1(1)
Ulu Segama	21/06/2007 – 18/09/2007	90	1980	59 (48,11,0)	10 (6,4,0)	22(6), 10(6), 6(4), 5(3), 3(1), 2(1)	5(4), 2(2), 2(1), 1(1)
Tabin	11/11/2009 – 10/3/2010	120	3677	21 (18,3,0)	8 (5,3,0)	10(6), 4(4), 2(2), 1(1), 1(1)	1(1), 1(1), 1(1)
Kinabatangan	20/8/2010 – 17/11/2010	90	3060	13 (7,6,0)	5 (2,3,0)	6(3), 1(1)	4(4), 1(1), 1(1)
Malua	30/9/2008 – 28/12/2008	90	2577	10 (8,2,1)	6 (4,2,1)	3(2), 2(2), 2(1), 1(1)	1(1), 1(1)

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714 Table 4. ^aIndication of relative poaching pressure in each study area based on photographic
715 detection rate of presumed poachers and percentage of camera traps stolen; see methods
716 for full description.

717

Study area	Mean hunter encounter rate \pm SD ^a	% camera stolen
Danum Valley	0.000 \pm 0.000	0
Ulu Segama	0.071 \pm 0.228	0
Tawau	0.090 \pm 0.455	1.3
Kabili-Sepilok	0.144 \pm 0.704	5.7
Crocker	0.288 \pm 0.642	11.1
Tabin	0.381 \pm 2.366	2.7
Kinabatangan	0.434 \pm 1.138	6.1
Malua	0.576 \pm 0.899	26.3

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732 Table 5. Posterior summaries of the Bayesian-SECR model parameters of camera trap data
733 of the Sunda clouded leopard from six study areas in Sabah, Malaysian Borneo. 95%
734 HPD: the Bayesian highest posterior density interval, that is the shortest interval enclosing
735 95% of the posterior distribution; σ : movement parameter, related to home range radius;
736 λ_0 : baseline trap encounter rate, the number of independent photographic detections per
737 day; ψ : the ratio of the estimated abundance within the state space to the maximum
738 allowable number defined by the augmented value; N : number of individuals in the state
739 space; D : density \pm SD (individuals per 100 km²).

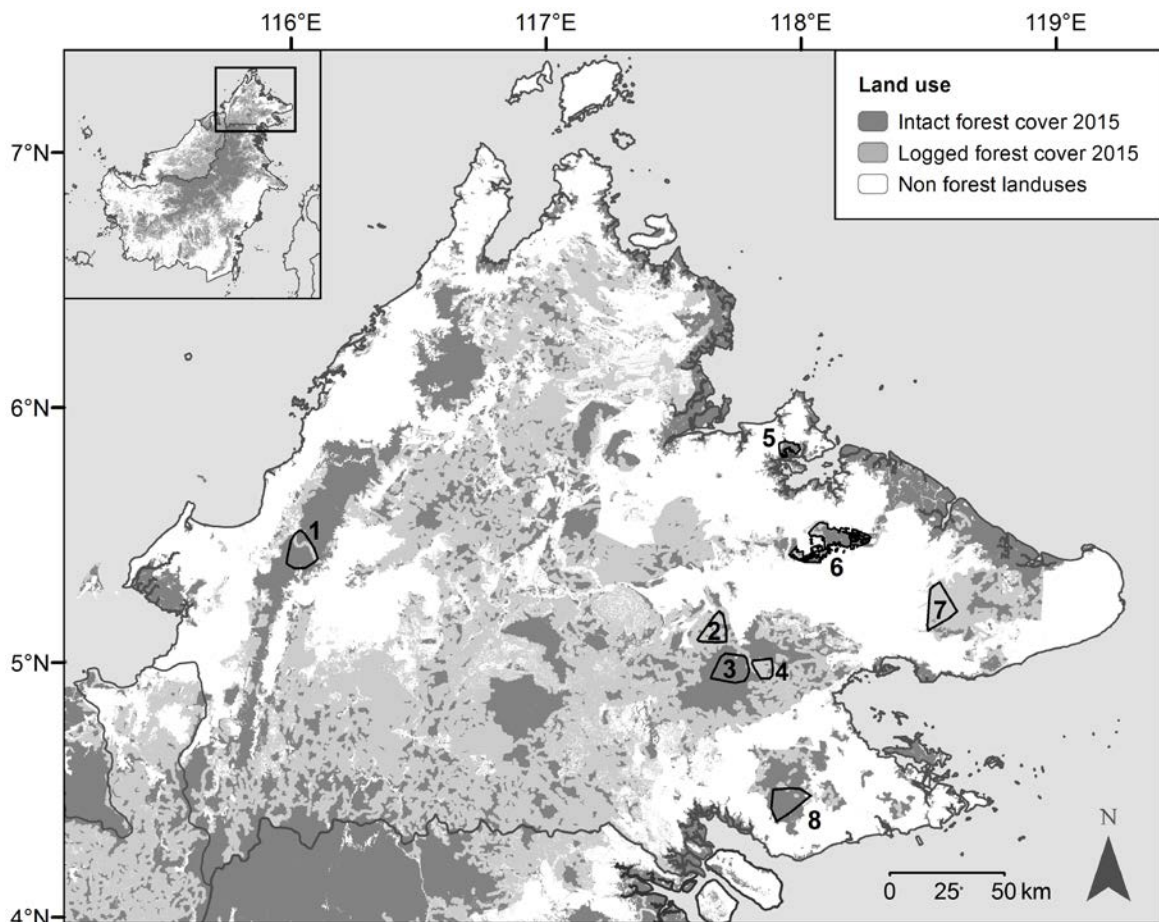
740

Parameter	Danum Valley		Tawau Hills		Crocker		Ulu Segama		Tabin		Kinabatangan	
	Mean \pm SD	95% HPD	Mean \pm SD	95% HPD	Mean \pm SD	95% HPD	Mean \pm SD	95% HPD	Mean \pm SD	95% HPD	Mean \pm SD	95% HPD
σ	3074 \pm 432	2341– 3937	3915 \pm 354	3284– 4625	3688 \pm 479	2815– 4638	2692 \pm 408	1970– 3470	4649 \pm 1616	2325– 7575	9104 \pm 2672	5151– 13986
λ_0	0.017 \pm 0.004	0.009– 0.025	0.013 \pm 0.002	0.009– 0.017	0.023 \pm 0.006	0.012– 0.035	0.043 \pm 0.015	0.020– 0.072	0.004 \pm 0.002	0.001– 0.007	0.003 \pm 0.002	0.001– 0.007
ψ	0.353 \pm 0.118	0.142– 0.591	0.400 \pm 0.111	0.194– 0.619	0.283 \pm 0.100	0.100– 0.480	0.319 \pm 0.118	0.114– 0.555	0.284 \pm 0.122	0.084– 0.529	0.316 \pm 0.146	0.072– 0.609
N	25.5 \pm 8.0	12.0– 41.0	19.8 \pm 4.6	11.0– 28.0	12.6 \pm 3.7	7.0– 20.0	44.3 \pm 15.9	18.0– 76.0	30.3 \pm 12.6	9.0– 54.0	26.5 \pm 12.0	7.0– 50.0
D	1.73 \pm 0.54	0.81– 2.78	2.23 \pm 0.52	1.35– 3.27	1.39 \pm 0.41	0.77– 2.21	3.10 \pm 1.11	1.26– 5.32	2.66 \pm 1.11	0.79– 4.74	1.54 \pm 0.70	0.41– 2.90
p -value	0.523		0.573		0.501		0.496		0.697		0.606	

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746 Fig 1. The locations of the eight camera trap survey areas in Sabah, Malaysian Borneo,
747 showing land use in 2015. Numbered polygons represent the different study areas: 1.
748 Crocker Range Park; 2. Malua Forest Reserve; 3. Danum Valley Conservation Area; 4.
749 Ulu Segama Forest Reserve; 5. Kabili-Sepilok Forest Reserve; 6. Lower Kinabatangan
750 Wildlife Sanctuary; 7. Tabin Wildlife Reserve; 8. Tawau Hills Park. Inset shows the island
751 of Borneo. Land use data derived from Gaveau et al. (2016). Note, intact forest includes
752 both primary forest as well as previously logged forest, the impacts of which were no
753 longer visible via analysis of satellite images in 2015; see Gaveau et al. (2016) for further
754 details.

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