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The importance of orangutans in small fragments for maintaining metapopulation dynamics

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Author contribution statement

MA, FO, IL and EM initially conceptualized this study. FO, NA, DS, MJ, MJS, MS, and CT contributed data. MV helped with data analysis and diagram design. MA, EM, FO, JS, CT, MJS, MV, SW, TS and DS helped improve the manuscript.

Keywords

agricultural landscape, translocation, conservation, Borneo, Oil palm, Metapopulation, Pongo pygmaeus, Forest fragment, Great ape conservation

Abstract

Word count: 249

Historically, orangutans (*Pongo* spp.) lived in large contiguous areas of intact rainforest. Today, they are also found in highly modified and fragmented landscapes dominated by oil palm or industrial timber plantations; a situation that calls for new conservation approaches. Here we report signs of orangutan presence in more than 120 small forest fragments of less than 500 ha in size and isolated in extensive oil palm plantations across Borneo. We confirmed the long-term presence of adult resident females with dependent young in 42% of the fragments assessed by ground survey ($n=50$), and the regular sightings of males traveling across the landscape. We argue that orangutans using and living in small isolated forest patches play an essential part in the metapopulation by maintaining gene flow among larger sub-populations distributed across multiple-use landscapes. In some cases, translocations may be necessary when the animals are in imminent danger of being killed and have no other refuge. However, the impacts of removing animals from spatially dispersed metapopulations could inadvertently decrease critical metapopulation functionality necessary for long-term viability. It is clear that orangutans need natural forest to survive. However, our findings show that forest fragments within agricultural landscapes can also complement conservation areas if they are well distributed, properly connected and managed, and if orangutan killing is prevented. Efforts to better understand the dynamics and the functionality of an orangutan metapopulation in forest-farmland landscape mosaics characteristic of the Anthropocene are urgently needed to design more efficient conservation strategies for the species across its range.

Contribution to the field

Our manuscript compiles information from the literature and observations about the survival of orangutans in small forest fragments across agricultural landscapes: resident females can survive for many years and breed in these fragments, while males travel through the agricultural matrix to mate. While our observations and data are preliminary, we believe that the information is strong enough to warrant publication as a Perspective. This information combines more than 20 years of ground data in agricultural landscapes collected by a team that is gathering more than 150 years of experience with orangutan ecology and conservation. Our key objective is for researchers to pay more attention to orangutans in fragmented landscapes, for government to refocus conservation policies and efforts to protected species outside protected areas, and for sanctuaries to re-evaluate their rescue and translocation policies and practices. The theme of our manuscript seems to be well in line with the overarching theme of the issue on "Fragmentation and Connectivity in Forest Landscapes," and we hope that you agree that this would be of interest to the readership of *Frontiers in Forests and Global Change*.

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In review

1 **Importance of small forest fragments in agricultural landscapes for**
2 **maintaining orangutan metapopulations**

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26 **Keywords: *Pongo pygmaeus*, Metapopulation, Forest Fragment, Oil palm, Borneo,**
27 **Conservation, Translocation.**

28

29 **Abstract**

30 Historically, orangutans (*Pongo spp.*) lived in large contiguous areas of intact rainforest. Today, they
31 are also found in highly modified and fragmented landscapes dominated by oil palm or industrial
32 timber plantations; a situation that calls for new conservation approaches. Here we report signs of
33 orangutan presence in more than 120 small forest fragments of less than 500 ha in size and isolated in
34 extensive oil palm plantations across Borneo. We confirmed the long-term presence of adult resident
35 females with dependent young in 42% of the fragments assessed by ground survey (n=50), and the
36 regular sightings of males traveling across the landscape. We argue that orangutans using and living
37 in small isolated forest patches play an essential part in the metapopulation by maintaining gene flow
38 among larger sub-populations distributed across multiple-use landscapes. In some cases,
39 translocations may be necessary when the animals are in imminent danger of being killed and have
40 no other refuge. However, the impacts of removing animals from spatially dispersed metapopulations
41 could inadvertently decrease critical metapopulation functionality necessary for long-term viability. It
42 is clear that orangutans need natural forest to survive. However, our findings show that forest
43 fragments within agricultural landscapes can also complement conservation areas if they are well
44 distributed, properly connected and managed, and if orangutan killing is prevented. Efforts to better
45 understand the dynamics and the functionality of an orangutan metapopulation in forest-farmland
46 landscape mosaics characteristic of the Anthropocene are urgently needed to design more efficient
47 conservation strategies for the species across its range.

48 **1 Introduction**

49 In wildlife conservation, the “Single Large or Several Small” (SLOSS) approach to conservation has
50 been debated for decades (recent review in Fahrig, 2020). Often, the prevailing policies and
51 conservation strategies have favored large, connected “natural” areas, while considering fragments of
52 natural habitat as of little or no value (IUCN, 1980; Sodhi et al., 2010). Indeed, small forest
53 fragments are sensitive to microclimatic, anthropogenic and biological edge effects, support only a
54 small proportion of the biodiversity of the original forest mostly consisting of invasive and generalist
55 species that are of less conservation concern, and their value for conservation is often disregarded
56 (Haddad et al., 2015; Pfeiffer et al., 2017; Williamson et al., 2020). However, the importance of
57 habitat heterogeneity and small habitat patches for biodiversity conservation and species dispersal is
58 increasingly recognized (Azhar et al., 2015; Wintle et al., 2019; Arroyo-Rodriguez et al., 2020;
59 Watling & Fang, 2020), especially for wide-ranging or volant species (Beca et al., 2017; Melo et al.,
60 2017; Scriven et al., 2019).

61 In the past, orangutans (*Pongo sp.*) depended on vast tracts of natural forest. Today they persist and
62 reproduce in forests logged for timber (Husson et al., 2009; Ancrenaz et al., 2010), in industrial
63 timber plantations (Meijaard et al., 2010; Spehar and Rayadin, 2017) and in agricultural landscapes
64 (Campbell-Smith et al., 2011). They are also found in isolated patches of forest, albeit at lower
65 densities than in more extensive natural forests (Ancrenaz et al., 2015; Seaman et al., 2019). In
66 landscapes that have been extensively transformed by humans, orangutan survival is contingent on
67 hunting and killing being minimized (Marshall et al., 2006; Husson et al., 2009; Spehar et al., 2018).

68 Here, we build on more than 20 years of orangutan research in the heavily disturbed and fragmented
69 landscapes of the Kinabatangan floodplain (Sabah, Malaysian Borneo), and compile evidence of
70 orangutans utilizing forest patches in oil palm-dominated landscapes across Borneo. We refine our
71 current understanding of orangutan ecology in fragmented landscapes, identify knowledge gaps about

72 the persistence of the species in these contexts, and provide some recommendations for conservation
73 management of the species in heavily transformed habitats.

74 **2. Orangutans survive and appear to reproduce in the mosaic landscape of Kinabatangan**

75 The Lower Kinabatangan floodplain spans more than 500,000 ha and is largely dominated by oil
76 palm agriculture, with fragmented and degraded forests covering less than 15% of the region (Abram
77 et al., 2014). Hutan, a local non-governmental group, has been studying wild orangutan ecology in
78 this landscape since 1998 (Ancrenaz et al., 2004). For the past 22 years, we have regularly recorded
79 orangutans in small forest patches, irrespective of their size or protection status. In 2008, we
80 conducted helicopter nest surveys and confirmed the presence of orangutan nests in 32 small patches
81 of forest isolated within oil palm estates, with an average size of 31 ha (range: 1 tree to 236 ha) (see
82 detailed methodology in Ancrenaz et al., 2005; Ancrenaz et al., 2015). We limited our ground and
83 aerial investigation to patches <500 ha, which corresponds to the upper limit of a female range in
84 most areas (Singleton et al., 2009). A forest fragment was considered isolated if the closest forest was
85 >500 m away, this gap being above the average daily distance travelled by orangutans in
86 Kinabatangan (Oram, 2018). In 2012, we repeated the same helicopter survey and found that 15
87 forest fragments out of the 32 original patches still existed, the remainder having been cut down. We
88 detected orangutan nests in 12 out of these 15 patches (Ancrenaz et al., 2015).

89 In addition to aerial surveys, our ground observations in Kinabatangan identified at least eight
90 resident females who have survived for more than ten years in very small (< 50 ha) isolated forest
91 fragments and have raised an infant successfully. We also established that some males traveled up to
92 five kilometers between forest patches throughout the plantations, (Ancrenaz et al., 2015).
93 Orangutans build nests in palms, but they seem, more frequently, to nest in trees left within the
94 monocultural cropland, perhaps because these trees are taller than nearby oil palm plants and offer
95 vantage points and more safety.

96 Rather than being completely isolated, resident females appear to be part of a larger metapopulation,
97 where subpopulations are linked by dispersal (Hastings and Harrison, 1994). In Kinabatangan, the
98 presence of these orangutans established in forest patches, irrespective of their size or protection
99 status, is inherently important to the long-term conservation of the species (Bruford et al. 2010).

100 **3. A similar situation unravels in other oil palm landscapes in Borneo**

101 In 2008, additional helicopter surveys confirmed the presence of orangutan nests in isolated forest
102 patches within the oil palm landscapes of eastern Sabah: Sandakan Bay (confirmed presence of nests
103 in eight patches); Sugut floodplain (nests in 15 patches); Beluran (nests in seven patches), and Lower
104 Segama (nests in 14 patches). Ten years later, using the same aerial methodology, we re-surveyed
105 seven of the 15 patches in Sugut that had nests in 2008, and found nests in all seven patches.
106 Although it is impossible to know whether the nests had been built by the same individuals between
107 successive surveys or by transient animals, the nests' presence shows the use of the fragments by
108 orangutans shortly before our surveys.

109 In 2019 and 2020, we conducted rapid ground assessments in nine oil palm estates located in
110 southern Sabah, and in the West, Central and East provinces of Kalimantan (Indonesian Borneo). We
111 also sent a questionnaire to the visited oil palm estates, and to three orangutan researchers working in
112 these fragmented forest landscapes, about orangutan presence and potential conflicts in their estates,
113 using a previously tested protocol (Meijaard et al., 2011; Ancrenaz et al., 2015).

114 The survey covered 70 patches of forest. Signs of orangutan presence (including pictures collected
115 with camera traps, direct sightings of orangutans or nests) were confirmed in 50 of the 70 patches
116 (i.e. 71% of the total) with an average patch size of 57 ha (range: 1-286 ha; SD=72 ha). Presence of

117 an adult female with young (from one to five years at the time of the surveys) was confirmed in 21
118 fragments (10-236 ha in size; mean 71; SD= 69), and signs of adult females without young, or
119 unflanged males (both types being extremely difficult to tell apart by direct sightings or from
120 pictures) in 10 patches. Flanged males were present in four patches, and 15 patches had signs of
121 orangutan nests without any indication of age and sex. Orangutans were absent from 20 patches at
122 the time of surveys (0.5-369 ha in size; mean 81 ha; SD=101 ha). Similar to our findings from
123 Kinabatangan, estate managers and workers reported that crop damages in mature oil palms (i.e.
124 above 5 years old) were considered non-significant, although several informants said that flower or
125 fruit productivity might be impaired.

126 **4. Orangutan translocation may be detrimental to the population**

127 Orangutan populations in a contiguous, but isolated, forest area containing fewer than 50 individuals
128 are generally thought to be non-viable (Utami-Atmoko et al., 2019). Animals found in small forest
129 patches are generally perceived as “doomed”, because of insufficient food, the risk of getting killed
130 by people, or the potential loss of remaining trees due to logging or fire (Sherman et al., 2020).
131 Consequently, many wild orangutans observed in such habitat patches are pre-emptively translocated
132 to large forest blocks presumed to be more suitable for their survival. In Indonesian Borneo between
133 621 and 1,845 wild orangutans were “rescued” from forest fragments in human-modified landscapes
134 between 2007 and 2017, and translocated to other forest areas (Sherman et al., 2020). The few data
135 available on post-translocation monitoring indicate that translocated orangutans struggle to survive
136 (Sherman et al., 2020).

137 Indeed, although orangutans are semi-solitary foragers, they live in diffuse communities of known
138 and related individuals, in which females are resident and philopatric, and males disperse (Arora et
139 al., 2012). Female orangutans are strongly tied to their natal areas, and the home ranges of maternal
140 kin often overlap considerably (van Noordwijk et al., 2012; Ashbury et al., 2020). These inherent
141 features can pose extreme challenges for female orangutans when they are released into new forest
142 areas (Lokuciejewski, 2018). In areas with existing resident females, competition for food will
143 increase (Marzec et al., 2016). Resident adult flanged males aggressively defend an area with females
144 in it, especially when females are sexually receptive (Spillmann et al., 2016), which could increase
145 aggression and social stress when new males are released.

146 It is urgent to better document the fate of translocated individuals (Sherman et al., 2020) and to
147 investigate the possible impact of removing individuals from forest patches on the orangutan
148 metapopulation. Indeed, such a “harvest” could intensify the effects of fragmentation and jeopardize
149 the long-term viability of the overall population. However, we also need to better document the
150 chances of survival of orangutans within fragments and determine whether these small forest
151 fragments serve only as temporary refuge to transient individuals or act like sinks to the overall
152 population. Improved modeling and understanding of orangutan metapopulation dynamics in
153 fragmented landscapes, and its counterfactual – i.e. what would have happened to orangutans had
154 they not been removed from patches – is necessary to gain a better understanding of this new
155 situation.

156 **5. Discussion**

157 Orangutans are highly flexible and adaptable species that can maintain high population densities in
158 production forests (Ancrenaz et al., 2010; Roth et al., 2020), and outside of strictly-protected forests
159 (Santika et al., 2017; Voigt et al., 2018). In these landscapes, orangutans can cope with canopy
160 opening (Davies et al., 2017), disperse on the ground (Ancrenaz et al., 2014), and reproduce (van
161 Noordwijk et al., 2018). Our collation of reports from agricultural landscapes demonstrates

162 substantial use of forest patches by orangutans in fragmented farmland, and gives some hints to better
163 understand the functionality of a population within such a landscape.

164 In Borneo, agriculture development has resulted in significant deforestation across the orangutan
165 range (Gaveau et al., 2016). We can hypothesize that some of the females who survived the initial
166 deforestation took refuge in natural forest patches that were retained within their original range in this
167 newly modified landscape. Indeed, female orangutans are reluctant to leave their natal areas, and this
168 is also likely the case in forest patches (Arora et al., 2012; van Noordwijk et al., 2012). Over the
169 years, these females may have used as many forest patches within their former home-range as
170 possible and likely remained safe by avoiding detection by people (Figure 1). But we can also
171 suppose that some females originating from nearby source populations could recolonize the
172 fragments after deforestation.

173 Orangutans need forest to survive and reproduce, and although they can feed on leaves, flowers and
174 fruits of oil palms, they need a more diverse diet (Ancrenaz et al., 2015). Diversifying crops and
175 promoting habitat heterogeneity and complexity will likely increase the orangutan's chances of
176 survival in an agricultural context, as shown for other species (Azhar et al., 2014; Syafiq et al., 2016).
177 Improving the overall forest connectivity within the agricultural landscape, and increasing the
178 number, size and quality of forest fragments (enrichment planting for example), are necessary
179 management strategies for increasing survival, but this remains still largely unstudied for orangutans.
180 Another necessity is to ensure that potential negative conflicts between humans and orangutans are
181 prevented or mitigated within these landscapes, and legal prohibitions on orangutan killing are
182 properly enforced (Campbell-Smith et al., 2012).

183 Males are the most frequently observed sex in oil palm plantations, including numerous mentions of
184 them walking on the ground, along rivers or streams and even on plantation roads. Orangutans use
185 forest corridors to move across the landscape, as recorded by Seaman et al. (2019) and during our
186 investigations. For example, one estate included in our analysis allowed natural forest regeneration
187 under unmanaged oil palms in a 40 m wide corridor 1.2 km long, to link two isolated forest patches.
188 Orangutan nests were observed in this corridor within four years following corridor establishment.
189 These corridors are often set aside as high conservation value forests to meet sustainability
190 certification criteria, either as riparian buffers or other linkages between forest patches. Retaining or
191 creating forest corridors within oil palms will improve the permeability of the landscape for many
192 species, in addition to orangutans (Gray et al., 2019; Scriven et al., 2019). The presence of resident
193 adult females and their offspring in some of the isolated forest patches suggests that males are able to
194 cross the human-modified landscape to search for receptive females and reproduce, but this
195 hypothesis needs further investigation.

196 Many questions need to be addressed before we can consider a primarily agricultural landscape as
197 viable long-term habitat for orangutans: What can orangutan eat and how can their dietary needs be
198 met in small forest fragments in landscapes dominated by commercial monoculture, especially at
199 times of low food availability (e.g., during prolonged droughts)?; What is the minimum size of forest
200 patches and the maximum distance between patches to maintain an adequate geneflow? What are the
201 risks associated with edge effects and the persistence of fragments as viable habitats (e.g. with
202 respect to inbreeding, intrusion, etc.)?; What is the fate of young individuals that grow up in small
203 isolated forest fragments: can adolescent females (which are the philopatric sex) disperse?; Is it
204 possible to maintain a viable metapopulation in a fragmented landscape (or in other words: are the
205 fragments acting as a sink or are they supporting a dynamic metapopulation)?; How is the gene flow
206 maintained in a fragmented situation?; What are the risks of disease transmission between people,
207 wild and domestic animals?; What type of management is needed to increase the chances of
208 orangutan survival in a mosaic landscape?; How will the replanting of oil palm, typically every 20-25

209 years, affect orangutan populations utilizing the landscape?; Do the high levels of pesticides and
210 fertilizer used in oil palm cultivation negatively affect orangutans?

211 Exclusively focusing our attention on larger groups of orangutans in contiguous forests (protected or
212 not) will ultimately result in a disjointed distribution range where populations are no longer
213 connected genetically. Here we hypothesize that long-term maintenance of habitat stepping-stones
214 within larger multifunctional landscapes could potentially retain some degree of connectivity
215 between the larger forest areas occupied by orangutans and boost the chances of survival for the
216 metapopulation as a whole. Conservation efforts for orangutans, and other endangered tropical
217 species, must recognize the critical role habitat fragments may play to help stabilize and connect
218 different landscapes at the broader metapopulation level.

219 This approach requires a change in perception about “rescuing and translocating” individuals. A
220 recent analysis of wild-to-wild translocation in Kalimantan showed that at least 90% of the
221 individuals captured were healthy and several of them had healthy infants (Sherman et al., 2020).
222 Recognizing that there is a non-zero mortality risk during wild-to-wild translocations and
223 reintroduction (Wilson and McMahon, 2006; Galdikas, 2018), we argue that, rather than emptying
224 small forest patches of orangutans as a default operational practice, local authorities and conservation
225 organizations ought to develop more proactive solutions, where forest patches are managed in a way
226 that fosters positive coexistence between people and legally protected orangutans, as well as other
227 wildlife.

228 An additional problem with translocations is that removing orangutans from a forest patch decreases
229 its conservation value. Indeed, the presence of a fully protected species confers to a fragment a status
230 of “High Conservation Value” with a specific set of management measures, including no-
231 deforestation, hence reducing the likelihood of conversion (Carlson et al., 2018). The loss of the
232 forest patch would then also mean the loss of all other wildlife that was not rescued, and of
233 ecosystem services provided by the forest (Lucey et al., 2014; Wells et al., 2016).

234 Last we need to consider that at least 10,000 orangutans are surviving in multiple use landscapes in
235 Borneo alone (Meijaard et al., 2017); rescuing all of them and finding suitable habitat to translocate
236 them is unfeasible. Our preliminary investigation of orangutan survival in agricultural landscapes
237 indicates that *in situ* management is a reasonable and in fact perhaps better conservation approach
238 than translocating individuals which brings high risk to the animal at substantial financial cost.

239 Of course, there remain circumstances when the health of animals surviving in small fragments is
240 compromised, e.g. food scarcity, forest destruction, physical harm or killing, and in such cases,
241 translocations will still be needed when the alternative is a dead orangutan. Translocation is a part of
242 the overall conservation toolbox, but this kind of intervention should be the exception rather than the
243 norm.

244 For orangutans and other species to survive in mixed-use landscapes, farmers and companies must
245 improve management and adopt biodiversity-friendly practices (Azhar et al., 2017). For example,
246 forest fragments must be protected, monitored, managed, and enhanced if necessary. At a local scale,
247 habitat heterogeneity could be improved by interspacing crops, planting trees, and promoting ground
248 vegetation cover (Jambari et al., 2012). Non-hazardous chemicals (pesticides or herbicides,
249 fertilizers) should be used rationally or phased out by promoting integration with livestock grazing
250 and other environmentally-friendly practices (Jambari et al., 2012; Azhar et al., 2017). Workers need
251 to learn to not harass orangutans; conflicts need to be addressed peacefully; and risks of accidents
252 (roads, feral dogs, culling) must be minimized (Azhar et al., 2013).

253 In today's reality on Borneo and Sumatra, our observations indicate the need to consider orangutan
254 metapopulation dynamics and gene flow in mixed-use landscapes. In other words, we hypothesize
255 that most orangutan populations across fragmented landscapes could be viable if we maintain both
256 existing larger protected areas and essential habitat fragments (even as small as a few ha), and
257 minimize unnatural deaths or removal from the landscape. Therefore, the conservation unit to be
258 managed should then not only be the animals in relatively well-protected larger forest areas, but the
259 metapopulation that is ranging across the entire mixed protected–privately administered landscape as
260 a whole. Eventually, the future of orangutans in the Anthropocene will primarily depend on the
261 collaborative attitude of all land users and government working together to target a peaceful
262 coexistence between people and orangutans outside and inside protected areas.

263 **Acknowledgments**

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270 submit the article for publication.

271 **Author contributions**

272 MA, FO, IL and EM initially conceptualized this study. FO, NA, DS, MJ, MJS, MS, and CT
273 contributed data. MV helped with data analysis and diagram design. MA, EM, FO, JS, CT, MJS,
274 MV, TS, SW and DS helped improve the manuscript.

275 **Conflict of interest**

276 The authors declare that the research was conducted in the absence of any commercial or financial
277 relationships that could be construed as a potential conflict of interest. Authors are directly supported
278 by conservation organizations and research institutions to implement conservation research and
279 management, while some have current or past consultancy arrangements with companies and
280 organizations engaged with palm oil production and oil palm management.

281 **Data Availability Statement**

282 The datasets analyses for this study can be found in the HUTAN library.

283

284

285

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In review

Figure 1.JPEG

