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Global demand for natural resources eliminated more than 100,000 Bornean orangutans

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78

Summary

80 Unsustainable exploitation of natural resources is increasingly affecting the highly biodiverse

tropics [1,2]. Although rapid developments in remote sensing technology have permitted more

82 precise estimates of land-cover change over large spatial scales [3–5], our knowledge about the

effects of these changes on wildlife is much more sparse [6,7]. Here we use field survey data,

84 predictive density distribution modeling, and remote sensing to investigate the impact of resource

use and land-use changes on the density distribution of Bornean orangutans (*Pongo pygmaeus*). Our

86 models indicate that between 1999 and 2015 half of the orangutan population was affected by

logging, deforestation or industrialized plantations. While land clearance caused the most dramatic

88 rates of decline, it accounted for only a small proportion of the total loss. A much larger number of

orangutans were lost in selectively logged and primary forests, where rates of decline were less

90 precipitous, but where far more orangutans are found. This suggests that further drivers,

4

independent of land-use change, contribute to orangutan loss. This finding is consistent with studies

92 reporting hunting as a major cause in orangutan decline [8–10]. Our predictions of orangutan

abundance loss across Borneo suggest that the population decreased by more than 100,000

94 individuals, corroborating recent estimates of decline [11]. Practical solutions to prevent future

orangutan decline can only be realized by addressing its complex causes in a holistic manner across

96 political and societal sectors, such as in land-use planning, resource exploitation, infrastructure

development, and education, and by increasing long-term sustainability [12].

98

Results

100 ## Bornean orangutan field survey data

To model Bornean orangutan density distribution and derive metapopulation abundances we

102 compiled orangutan field surveys. Estimates of orangutan density and abundance are usually

derived from the observation of their nests [13,14] on line transects [15]. A total of 36,555

104 orangutan nests were observed on 1,491 ground and 252 aerial transects that were surveyed

between 1999 and 2015 throughout the Bornean orangutan range, with a total survey effort of 4,316

106 km (ground: 1388 km, aerial: 2928 km), and a median of 86 transects (interquartile range (IQR): 28

− 156 transects) per year. The cumulative area of land surveyed contained 1,234 km². During the

108 study period, the average yearly encounter rate significantly decreased from 22.5 to 10.1 nests/km

(parameter estimate = -0.06, SE = 0.02, z = -2.25, p = 0.04. The model contained the log-

110 transformed mean nest encounter rate per year as response, weighted by the number of transects per

year and the year as predictor).

112

Estimating change in Bornean orangutan density distribution

114   We built a predictive density distribution model to estimate Bornean orangutan abundance. The full

model included survey year, climate, habitat cover and human threat predictor variables (see

116   methods and key resources table) and explained orangutan density significantly better than the null

model including only the intercept (likelihood ratio test, $\chi^2 = 1,440$, df $= 13$, $p < 0.001$). Mean

118   temperature, lowland and peatswamp forest cover had a significant positive relationship with

orangutan density (Figure S1, Table S2). Study year, rainfall variability and human population

120   density negatively affected orangutan density (Figure S1, Table S2). Intermediate levels of rainfall

in dry months were related to higher densities of orangutans. Topsoil organic carbon content,

122   estimate of orangutan killing and percentage of the population with hunting taboos were not

significantly correlated with orangutan density. While the orangutan density was lower in areas with

124   more montane forest cover, the cover of deforested areas around transects was slightly positively

correlated, but its confidence limits included zero.

126   With the aim of minimizing model uncertainty in spatial model predictions, we used multi-model

inference and evaluated all possible combinations of covariates included in the full model (Table

128   S2). The complete set of all fitted models was then used to estimate the orangutan density

distribution across the range. The estimated distribution was mapped to metapopulations delineated

130   by experts at the Population and Habitat Viability Assessment Workshop (PHVA) for Bornean

orangutans. In this context, the term "metapopulation" was used to identify larger entities which are

132   bound by dispersal barriers, such as rivers, major roads and areas without forests and include one or

more orangutan subpopulations. Only 38 out of 64 identified metapopulations retained more than

134   100 individuals and can thus be considered to contain viable subpopulations [16].

The three largest metapopulations were found in Kalimantan, the Indonesian part of Borneo and

136   have experienced a strong decline over the studied 16-year period (Figure 1).

6

Western Schwaner, the largest metapopulation, lost an estimated 42,700 individuals (95%

138 confidence interval (CI): 12,700 – 73,400) since 1999, with 40,700 (95% CI: 30,000 – 57,200)

remaining in 2015. The second largest population, Eastern Schwaner, lost 20,100 individuals (95%

140 CI: 7,200 – 33,500), and was estimated to contain 16,800 (95% CI: 12,100 – 23,100) in 2015. In

Karangan, the third largest population, 8,200 individuals (95% CI: 1,900 – 15,400) were lost and

142 9,000 (5,900 – 14,200) remained in 2015. The total estimated loss of Bornean orangutans between

1999 and 2015 amounted to 148,500 individuals (95% CI: 48,100 – 252,300).

144 We used predictions of forest cover from Struebig et al. [17] for 2020 and 2050 to project future

orangutan decline (Figure 2). To this end, we assumed that orangutans cannot survive in areas

146 without tree cover. The orangutan abundance in the three largest populations was projected to drop

further and reach 31,100 individuals (95% CI: 22,500 – 44,000) in the Western Schwaner

148 metapopulation area, 14,700 individuals (95% CI: 9,600 – 19,600) in Eastern Schwaner and 6,100

individuals (95% CI: 3,800 – 10,000) in Karangan by 2050. The total future loss for all

150 metapopulations was projected to be 45,300 (95% CI: 33,300 – 63,500). This projected future

decline is only based on the direct consequence of habitat loss. It does not consider the effects of

152 orangutan killing for food and in conflict and is therefore most likely an underestimate. All

estimates are rounded to the nearest hundred.

154

Linking remotely sensed resource use and density distribution

156 To identify possible causes for the estimated orangutan loss, we compared absolute abundance and

density from the beginning and the end of the survey period between land-use types, and assessed

158 differences in change over time. We differentiated areas, in which resource use had altered the

environment and areas in which land-use remained unaltered during the study period. For land-use

160 changes we considered deforestation, conversion to industrial plantations (oil palm and paper pulp)

and selective logging in natural forests. As stable land-use we considered primary and montane

162   primary forest, regrowth forests, industrial plantations established prior to the study period and

'other', comprising non-forest areas.

164   By 2015, 50% of the orangutans estimated to have occurred on Borneo in 1999 were found in areas

in which resource use had altered the environment. A comparison of distinct regions revealed that

166   50%, 60% and 10% of the orangutans were affected by transformation into industrial oil palm or

paper pulp plantations, deforestation, or selective logging in Kalimantan, Sabah and Sarawak,

168   respectively. Rates of orangutan decline were highest in areas deforested or converted to plantations

(63 - 75% loss) in both Kalimantan and Sabah (Figure 3). In Sarawak, there were almost no

170   industrial plantations and deforested areas within the orangutan metapopulation range, together

affecting only 0.4% of area and 2% of the orangutan population. Industrial plantations and

172   deforestation contributed 7% (Kalimantan), 2% (Sabah), and less than 1% (Sarawak) to the overall

estimated loss of orangutans in each of the three regions.

174   Both Kalimantan and Sabah had the highest orangutan abundance in selectively logged forests,

followed by primary forest. In Sarawak, the highest orangutan abundance was found in primary

176   forests. The rate of orangutan decline across the three regions and these two land-use classes was

less precipitous, but still high (49 – 56%). The loss of orangutans in primary and selectively logged

178   forests between 1999 and 2015 accounted for 67% of the total loss in Kalimantan (93,000

individuals, 95% CI: 26,500 - 162,300), 72% in Sabah (6,100 individuals, 95% CI: 2,400 – 10,000)

180   and 83% of the total loss in Sarawak (900 individuals, 95% CI: 250 – 1,600).

182   **Discussion**

8

The unsustainable use of natural resources has caused a dramatic decline of Bornean orangutans.

184 Only 38 out of 64 remaining metapopulations have more than 100 individuals, the assumed

threshold for viability of Bornean orangutan populations [16]. Our findings suggest that more than

186 100,000 individuals have been lost in the 16 years between 1999 and 2015. All three analytical

approaches employed in this study, based on field survey data, spatial covariate modeling, and

188 remote sensing, corroborated the concluded impact of resource use and resulting decline of Bornean

orangutans. The results are also very consistent with the genetic signature of a recent collapse found

190 in an orangutan population in Sabah [18] and evidence of large annual losses of orangutans through

hunting and conflict killing in Kalimantan [8–10]. Our results substantiate the percentage loss

192 estimated by Santika et al. [11] and reinforce the recent uplisting of the Bornean orangutan as

Critically Endangered on the IUCN Red List [19]. The numbers reported here are larger than past

194 estimates [11], but are in line with findings reported for other great ape taxa [20–23].

We have established the density distribution of Bornean orangutans with a model-based approach

196 which uses the relationships between predictor variables and observed orangutan abundance to

predict abundance for unsurveyed sites. These predictions are useful for deducing trends at the

198 regional to landscape scale [24], but may be limited at a local scale, where additional demographic

and behavioral drivers can influence orangutan density distribution, e.g., ranging behavior in

200 response to local food resources or conspecifics. Thus, our findings reveal patterns at large spatial

scales, but great care should be taken when inferring from predictions at specific sites.

202 Another aspect of our study that requires critical assessment is the inference of orangutan

abundance from nest counts. Nest decay time, an essential parameter to translate nest density into

204 orangutan density, varies between survey sites. Although factors like rainfall, wood density and

complexity of nest architecture are known to influence nest decay time [13,25,26], additional

206 variability in decay time between sites is not fully understood [27]. We addressed this issue by using

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all available datasets on orangutan nest decay, comprising information on the life span of more than

208 thousand nests (see methods) across Borneo. If our findings of orangutan decline were an artifact of

severely biased nest decay times, this would require nest decay time to have halved over the course

210 of the study period. However, we found no indication of this, and so do not consider this to be a

limitation of our study.

212 Contrary to our expectations, the model coefficient for deforestation indicated a slightly positive

relationship between deforestation in years prior to the survey and orangutan abundance. There are

214 several possible explanations for this observation, suggesting that the model coefficient does not

capture a causal relationship. First, surveys tend to be biased towards areas with known orangutan

216 occurrence. Thus, our dataset possibly lacks sufficient variance for detecting the true impact of

deforestation on orangutan density. Second, some studies have suggested that the number of

218 orangutans in areas adjacent to deforested areas are temporally inflated, due to the displacement of

individuals and subsequent refugee crowding [28,29]. Third, high dietary flexibility allows

220 orangutans to be resilient in the face of some levels of disturbance [30,31]. This may delay the

effects of deforestation on the observed density for several years, before populations eventually start

222 to decline [28]. Irrespective of this, when we compare spatial model predictions and remotely

sensed land-use change, the highest rates of orangutan decline were detected in areas with habitat

224 removal (deforestation and conversion to industrial plantations). This shows that the predictive

density distribution model has indirectly captured the deleterious effects of deforestation on

226 orangutan abundance. Our finding suggests that deforestation and industrial oil palm and paper pulp

plantations are responsible for about 9% (14,000 individuals) of the total loss of orangutan

228 abundance. Whereas in the early years of the study it was mainly degraded land with low orangutan

density that was converted to industrial plantations, after 2005 the conversion of forests to oil palm

230 plantations has been increasing dramatically [32]. Some studies have suggested that orangutans can

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occur in oil palm or paper pulp plantations, when they are managed well and adjacent forest

232   fragments are maintained [33–35]. However, it is unclear whether this is just a transient effect or

whether orangutans can indeed persist over the long-term [33–35].

234   The highest orangutan abundances were found in selectively logged forests in Kalimantan and

Sabah and in primary forests in Sarawak. This finding is consistent with studies reporting that

236   orangutans can occur in selectively logged or regenerating logging concessions, depending on the

type and intensity of logging operations [36–39]. Consequently, successful orangutan conservation

238   is necessarily situated in multi-functional landscapes [36,40], and recognizes the importance of

degraded and logged forests as well as forest fragments in plantation matrices [33,34].

240   Effective partnerships with logging companies, whose concessions harbor the majority of

orangutans, are essential to curb orangutan loss [41]. Similarly, partnerships with oil palm and paper

242   pulp producers are important to promote best practice guidelines for management [33,35,42]. Such

partnerships have already been reported e.g. by Meijaard et al. [43], and could potentially provide

244   co-benefits for biodiversity conservation in general [37]. The Roundtable on Sustainable Palm Oil

(RSPO) and the Forest Stewardship Council (FSC) are examples of certification schemes that

246   incentivize these partnerships, by enabling consumers to favor responsible natural resource

management [42].

248   The pervasive decline of orangutans in more intact habitat is consistent with various studies

identifying hunting as the main driver of biodiversity loss in the tropics [44,45], including Southeast

250   Asia [2]. More specifically, our observation is supported by the results of extensive interview

surveys in Kalimantan that show that, per year, on average 2,256 orangutans were hunted or killed

252   due to conflict with humans [8–10]. The estimate of orangutan killing in the model is based on a

Borneo wide projection of hunting pressure derived from these interview surveys [10]. In the model

254   this predictor did not show an influence on orangutan density. Possibly, our dataset lacks sufficient

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variance for detecting the impact of killing on orangutan density or the available layer does not

256   represent well the actual hunting pressure. Human population density, on the other hand, had a

significant negative influence on orangutan densities in the model and may have already captured

258   the effect of orangutan killing. Orangutans are also present in the national and international wildlife

trade. Traded orangutans are usually young orphans, and for each orphan adult individuals have

260   been killed [46]. Due to the low reproductive rate of the species, even very low offtake rates of

reproductive females (~1% per year) will drive populations to extinction [16,47]. In the absence of

262   plausible alternative explanations for the observed loss of orangutans in seemingly intact habitats,

such as the occurrence of widespread and highly lethal infectious diseases as observed among

264   African apes [48], killing is the most likely explanation. From this perspective, our prediction of a

further loss of 45,300 orangutans over the next 35 years, based solely on projections of forest cover

266   change is most likely an underestimate. Furthermore, many individuals currently occur in

fragmented, small populations which are assumed not to be viable and will most likely disappear in

268   the near future.

Knowledge about the density distribution of key species is essential to explore the consequences of

270   land-use change, exploitation of natural resources, development of infrastructure, and climate

change. It is also needed to evaluate which conservation interventions are most effective in reducing

272   decline and loss of biodiversity.

In essence, natural resources are being exploited at unsustainably high rates across tropical

274   ecosystems, including Borneo. As a consequence, more than 100,000 Bornean orangutans vanished

between 1999 and 2015. The major causes are habitat degradation and loss in response to local to

276   global demand for natural resources, including timber and agricultural products, but very likely also

direct killing. Our findings are alarming. To prevent further decline and continued local extinctions

278   of orangutans, humanity must act now: biodiversity conservation needs to permeate into all political

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and societal sectors and must become a guiding principle in the public discourse and in political

280 decision-making processes.

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Declaration of Interests

The authors declare no competing interests.

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308

Figure Legends

310 **Figure 1: Abundance of the three largest orangutan metapopulations between 1999 and 2015 and projected abundance for 2020 and 2050.**

312 Orangutan abundance was estimated for the three largest metapopulations with a multi-model approach over the study period (1999 to 2015). Estimates of future orangutan abundance were

314 based on forest cover projections for 2020 and 2050 by Struebig et al. [17] and are indicated by a hashed line. Shaded areas and error bars represent the 95% confidence intervals. On the y-axes the

316 number "10,000" is highlighted in blue to show the scale difference between the three populations. The map shows all identified metapopulations in grey. The three largest metapopulations are

318 indicated by their color. State labels are as follows: Br, Brunei; Sb, Sabah; and Sk, Sarawak in Malaysia; WK, West; EK, East; NK, North; SK South; and CK, Central Kalimantan in Indonesia.

320 See also Figures S1, S2 and Tables S1, S2 and S3.

322 **Figure 2: Spatial distribution of estimated orangutan densities on Borneo for the year 1999 and 2015, and projections to 2020 and 2050.**

324 Bornean orangutan density per 1 km² in the beginning and the end of the study period and for 2020 and 2050. Between 1999 and 2015 high density areas (dark green) disappeared, while medium

326 density areas (light green) declined. Low density areas (beige and purple) expanded. Future estimates are based on projected forest loss [17], therefore map representations between model

20

328   estimates and future projections differ. Areas in which forest was projected to be lost, also lose the

resident orangutans. Hence, maps between 2015 and 2020 seem to lose many fragments inhabited

330   by orangutans, but they already had low density before. Between 2020 and 2050 further areas were

projected to lose forest, but the loss is less visible. See also Figures S1, S2 and Tables S1, S2 and

332   S3.

334   **Figure 3: Linking remotely sensed resource use and density distribution.**

Percent area affected by resource use in orangutan metapopulations during the study period, forest

336   and non-forest classes (pie charts), their spatial distribution (map) and total orangutan abundance

and its change between the first study year (1999) and last study year (2015) (bar-charts). Total

338   areas per province in km² is given in the lower right corner of the pie charts. Areas had either been

transformed into plantations (oil palm and paper pulp), deforested or selectively logged between

340   1999 and 2015, were covered with forest (regrowth, primary or montane primary forest), were

plantations already before the study period or another unspecified non-forest class. The percent

342   orangutan abundance loss in comparison to 1999 is highlighted in rectangles. The error bars

indicate the 95% confidence interval. On the x-axes the number '2000' is highlighted in blue to

344   show the scale differences between the three areas. See also Figure S3.

346   # STAR methods

CONTACT FOR REAGENT AND RESOURCE SHARING

348   **Further information and requests for resources should be directed to and will be fulfilled by**

the Lead Contact, Maria Voigt (Maria.Voigt@idiv.de).

350

METHOD DETAILS

21

Study area and orangutan data

For this study we compiled three types of data: 1) line transect nest count data; 2) nest decay time data; and 3) polygons representing areas inhabited by orangutan metapopulations. Bornean orangutan (*Pongo pygmaeus*) nest count line transect data were compiled from surveys undertaken across Borneo between 1999 to 2015. Researchers reported the number of orangutan nests observed along line transects, which were either walked or flown with a helicopter (aerial and ground transects), respectively. The datasets were converted to a standard format to include the number of observed nests, total transect length, year of survey, and start and/or end coordinates of surveyed transect line. All ground transects with perpendicular distances (ppd) to nests were used for the Distance analysis [49] (number of nests = 15,858, 64% of total), to estimate truncation distance and effective strip width (ESW), that is, the perpendicular distance from the transect, below which an equal number of nests was missed as seen beyond [14]. For the predictive density distribution model we also considered aerial and ground transects without ppd and assumed estimated ESW to be representative. The cumulative area of land surveyed was calculated as the transect length multiplied by two times the effective strip width, excluding repeat sampling.

There were only few transects from areas on Borneo in which orangutans are known to be absent. Thus, we added 'virtual' transects with zero nests randomly to expert-delineated areas of orangutan absence [50] to balance this bias in sampling. For each survey year, we set the number of transects in the area of known absences to 50% of the number of surveyed transects in the orangutan range in the given year. We tested the effect of varying the number of absence transects (30%, 50% and 80% density of surveyed transect), but the model proved to be robust and the resulting orangutan abundance estimate did not differ substantially (30% absence density in comparison to 50%: correlation coefficient > 0.99, maximum percent difference = 5.6%; 80 % absence density in

22

comparison to 50%: correlation coefficient > 0.99, maximum percent difference = 3%; n = 16

376 years).

We compiled nest decay information from four sites. For two locations (Sabangau in Central

378 Kalimantan and Lesan in East Kalimantan) nest decay datasets included information from repeated

visits about nest status from construction to disappearance. The dataset from Lesan included 88

380 nests, which were visited between February 2005 and September 2006. In Sabangau 423 nests were

visited between July 2001 and April 2011. For two other sites (Kinabatangan, Sabah and Gunung

382 Palung, West Kalimantan) we used information about nest decay time, estimated by Ancrenaz et al.

and by Johnson et al. [25,51].

384 At the PHVA for Bornean orangutans held between the 24th and 27th of May 2016 in Bogor,

Indonesia, 41 orangutan experts mapped 64 Bornean orangutan metapopulations [16]. The resulting

386 metapopulation polygons covered areas between 6 and 58,157 km², amounting to a total area of

333,250 km². Predictions were extrapolated to this area, and although only a small proportion was

388 actually sampled (0.37%), the surveys were distributed well across the area. Only 23% of the

metapopulation area was located outside the 95 % minimum convex polygon of transect locations.

390

Predictor variables of orangutan abundance

392 We selected predictor variables based on their presumed importance for orangutan ecology, while

guaranteeing data availability for the whole range and minimizing the correlation between them

394 [24]. The final predictor variable set comprised layers depicting climate (mean daily temperature,

yearly variation in rainfall, rainfall in dry months (May - September), habitat (topsoil organic

396 carbon content, peatswamp, lowland and lower montane forest cover), and anthropogenic pressures

on orangutans (deforestation, human population density, orangutan killing estimates, and percent

398 population with religious hunting taboos). The predictor for orangutan killing estimates was based

23

on a Borneo wide model of orangutans killed in years prior to interview surveys [8] by Abram et al.

400   [10]. We included percent Muslim population as a proxy for the proportion of the population that

has hunting taboos, because it had been shown that hunting pressure on primates is lower in areas

402   inhabited by a majority of Muslims [9,52].

Before extraction, we reprojected all predictor layers to the Asia South Albers Equal Area Conic, to

404   allow for accurate representation of metric distances. The layers were resampled to the same extent,

origin and a resolution of 1 km, the coarsest available. Nearest neighbor resampling was used for

406   categorical predictors.

We extracted climate and habitat variables within a radius of 1 km around each transect, resulting in

408   an area of at least 3.14 km², depending on the transect length. This approximates the size of the

home range of female orangutans on Borneo and ensures that climatic and ecological predictors that

410   have an effect on the population are appropriately represented. Variables indicating anthropogenic

pressures were obtained within a distance of 10 km, approximating the distance over which human

412   influence is most likely (E. Meijaard, unpublished observation).

Information about habitat cover was available for three time points (2000, 2010 and 2015 [53,54]).

414   We used the habitat cover information from 2000 for all transects surveyed between 1999 – 2005,

the layer from 2010 for all transects surveyed between 2006 and 2012, and the layer from 2015 for

416   transects sampled in 2013 to 2015. At the time of the analysis, deforestation maps were available for

each year between 2000 and 2014 [3]. For each transect, we considered the percent area deforested

418   in the years prior to the survey in a 10 km-buffer around the transect.

When the start or the end-point of a transect was unknown, we extracted the predictor variables

420   with a radius of half the transect length [sensu 55]. We determined the proportion of each class

within the neighborhood for categorical and the mean value for continuous predictor variables.

24

422 We repeated the extraction for a 1 x 1 km grid covering the metapopulation areas, to enable the

estimation of orangutan abundance over the whole range. It was visually verified that all predictors

424 had an approximately symmetrical distribution, and human population density was subsequently

log-transformed. We also ensured that the range of variable values extracted for the transect

426 observations was broad enough to meaningfully allow prediction to the range of values extracted for

the metapopulation areas by comparing the distribution of both. We found that the majority of

428 predictors covered more than 75% of the predictor space to which estimates were extrapolated. The

exceptions were the predictors deforestation (63% cover of sampled predictor range), mean

430 temperature (50 % cover) and human population density (> 1% cover). For the predictor mean

temperature the low values were not included. These occur in high elevation areas, which were

432 sampled less as they are difficult to access and harbor fewer orangutans [28]. The surveys also did

not include areas with high human population density. As the density of orangutans decreases to

434 zero in high elevation areas and areas with high human population density, the extrapolation error

cannot become large. Thus, we did not consider the low coverage for these predictors to be a

436 limitation. The cover of predictor values was at most 3% lower, when excluding the absence

transects, except for rainfall variability. For this predictor, the absence transects increased the cover

438 of predictor values by 19%. Finally, all predictors were standardized to a mean of zero and a

standard deviation of one to facilitate the comparison of model parameters [56].

440

Future orangutan abundance

442 We used information about remaining forest cover on Borneo projected for 2020 and 2050 from

Struebig et al. [17,41] together with the orangutan density distribution estimated for 2015 and

444 predicted orangutan distribution 5 and 35 years after the last study year. Assuming that orangutans

will not be able to survive in the long-term in areas that are not forested, we excluded all individuals

446   occurring in cells that were predicted to lose forest cover by 2020 and 2050, respectively.

448

QUANTIFICATION AND STATISTICAL ANALYSIS

450   As an analytical approach, we used a combination of negative binomial regression models [57] and

design-based inference [15,58] to estimate the parameters necessary for building a spatial density

452   distribution model for Bornean orangutans as proposed by Hedley et al. [59].

454   ## Calculating model offset

In the predictive density distribution model, we used an offset term [60] to convert the number of

456   orangutan nests per transect, into the number of individuals per square kilometer. It included the

product of the area that was effectively sampled and the relationship between number of nests and

458   number of orangutans. The area that was sampled is described by the length of each transect (l)

multiplied by twice the ESW.

460   The number of orangutans per observed nest was estimated using the proportion of nest builders in

a population (p), the daily production rate of nests (r), and the nest decay rate (t), which represents

462   the number of days for which a nest remains visible in the forest [13,14]. For these parameters we

used p = 0.88 and r = 1.12 nests/day/individual from Spehar et al. [61], representing a combination

464   of the most current nest life-history parameters for Bornean orangutan populations (see below how t

was determined).

466

Effective strip width

468   For the ground transects, the effective strip width (ESW) was estimated using Distance 6.0 [49]. We

used a truncation distance of 27 m. The models were fitted to the observed data with and without

470   grouping for different habitat categories, using various key functions and adjustment terms. The

model fit was tested with χ^2 statistics for which we set distance intervals under the "diagnostics"

472   tab. The fit of the model using habitat specific detection functions was not better than the fit of the

model that used a single detection function across habitats, as established by Akaike Information

474   Criterion (AIC). As a consequence, we applied a global detection function and resulting effective

strip width (ESW) to all ground transects. The model with the best fit, based on the lowest AIC and

476   χ^2 statistics, was one with a half-normal key function and a simple polynomial adjustment of order

4.

478   Nests with a ppd larger than the truncation distance were excluded from the dataset. We assumed

that nests without ppd were distributed at similar distances along transects as the nests for which

480   ppds were reported. Therefore, we truncated them by randomly excluding the same proportion of

nests that were excluded from transects with known distances, leaving 34,415 nests in the dataset.

482   The estimated ESW was 15.95 m, and nest detection probabilities for ground transects was 0.59.

This is in line with reported detection probability for other ape surveys [55].

484   Helicopter surveys did not contain information about the ppds from the transects to the nests. Thus,

the ESW for those surveys was set to 75m, which corresponds to half of the maximum visibility

486   from the helicopter to the sides of the survey line [62]. Yearly abundance estimates were tested for

sensitivity to the assumed aerial ESW, but did not vary significantly (abundance estimate with aerial

488   ESW = 100 m in comparison to 75 m: correlation coefficient > 0.99, maximum difference 2.127%,

aerial ESW = 50 m in comparison to 75 m: correlation coefficient = 1, maximum difference

490   3.904%, n = 16 years).

27

Estimation of nest decay rate and extrapolation

492

We updated the nest decay rate for two sites in the Bornean orangutan range (Sabangau in Central

494 Kalimantan and Lesan in East Kalimantan), using the modification of the approach from Laing et

al. [57], used in Wich et al. [55]. Additionally, we used site-specific decay rates available from the

496 literature for Kinabatangan, Sabah [25] and Gunung Palung, West Kalimantan [51]. For the

calculation of the nest decay time we used logistic models (left-truncated with normalized intercept,

498 log-transformed and reciprocal) [57] and nest age as the only predictor. The product of the daily

decay probability and time since nest construction was summed over 2000 days to calculate mean

500 decay time. The model estimates from the three approaches were model-averaged using their AIC

weights. The time until nest decay for Sabangau was found to be 496.3 days (n = 423, 95% CI:

502 453.1 to 542.9 days) and 582.5 days (n = 88, 95% CI: 461.2 to 753.1) for Lesan, which is similar to

the nest decay rate estimated in Spehar et al. [61] for this area. We bootstrapped the data 1,000

504 times and determined the 95% confidence interval by model-averaging the 2.5% and 97.5% lower

and upper confidence limits.

506 The sites, for which we had nest decay values, experience different environmental conditions. The

respective values were thus used for different parts of the Bornean orangutan range, based on the

508 location of transects within provinces and forest types: (a) Sabangau nest decay, 496.3 days (this

publication), for peatswamp forests in Central Kalimantan; (b) Lesan nest decay, 583 days (this

510 publication), for East and South Kalimantan; (c) Average of Gunung Palung lowland forest, lowland

hill and mid-elevation nest decay, 276 days [51], for lowland forests in Sarawak, West and Central

512 Kalimantan; (d) Gunung Palung montane forest nest decay, 321.3 days [51], for montane forests (>

800 m above sea level (asl)) in Sarawak, West and Central Kalimantan; (e) Gunung Palung

514 peatswamp forest nest decay, 399 days [51], for peatswamp forests in West Kalimantan and

Sarawak; (f) Kinabatangan nest decay, 202 days [25], for Sabah.

28

Model structure and multi-model inference

518 We used a Generalized Linear Model with a negative binomial error structure and log link function

[60] to assess the effect of climate, habitat and anthropogenic pressures on orangutans and predict

520 the density distribution across the range. The full model, including all predictor variables and the

offset term, had the following structure: orangutan nest count on transect ~ year + mean temperature

522 + rainfall variability + rainfall in dry months + rainfall in dry months² + topsoil organic carbon

content + peatswamp cover + lowland forest cover + lower montane forest cover + deforestation +

524 human population density + orangutan killing estimates + percent population with religious hunting

taboos + offset + dispersion parameter. It had been shown that higher orangutan densities occur in

526 areas of intermediate levels of rainfall in dry months [11], therefore we included the squared rainfall

in dry months. A negative coefficient indicates highest orangutan densities at intermediate values of

528 rainfall.

We tested for collinearity, which was not an issue (largest Variance Inflation Factor = 4.429, see

530 also Table S1) and leverage values as well as DFBeta values did not indicate obviously influential

cases [63,64]. The model was not strongly overdispersed (dispersion parameter: 1.675).

532 As a test of the significance of the predictors, we compared the fit of the full model [65], as

described above, to the null model, only including the intercept and the offset term. The comparison

534 was based on a likelihood ratio test. We fitted the models in R (version 3.x, [66]) using the function

glm.nb of the R package MASS and determined Variance Inflation Factors using the function vif of

536 the R package car [67].

To minimize model uncertainty in spatial model prediction, we applied multi-model inference and

538 assessed all possible combinations of covariates included in the full model (n = 6,144) [see also 55].

Out of all possible models, only 18 models were in the confidence set, combining 95% of the AIC

540 weight (Table S2). The best model was the full-model lacking the orangutan killing estimates and

percent population with religious hunting taboos (Table S2 and S3). Predictions of all models were

542 averaged, after weighting by the models' AIC weight [68] and used to predict the orangutan density

for all 1x1 km cells across the range. We model averaged in link space and only after that

544 exponentiated the averaged predictions to get the abundance estimate per grid cell.

In the output of the density distribution models, all pixels outside the previously defined

546 metapopulations were excluded to avoid overestimating Bornean orangutan density, assuming that

all larger populations are known to date. Density estimates were summed for each metapopulation

548 and land-use category of interest to retrieve total abundance per metapopulation or category [16].

550 ## Parametric bootstrapping to estimate confidence limits

The 95% confidence limits of the model predictions were estimated using parametric bootstrapping

552 (n=1,000). The model-averaged fitted estimates and their standard errors (SE), as well as estimate

and SE for the dispersion parameter, theta, were used to generate 1,000 new instances of model

554 estimates by sampling from normal distributions with means and standard deviations being the

model estimates and their standard errors, respectively. These bootstrapped estimates were then

556 used, together with the model offset and the predictors, to sample an instance of the response from a

negative binomial distribution with a mean and dispersion parameter determined by the

558 bootstrapped estimates.

We fit the models with the bootstrapped response, resulting in bootstrapped model estimates and

560 AIC-values for each model. Using the bootstrapped model-estimates, a prediction was made for

each grid cell and study year and from these, the confidence limits of the mean and total abundance

562 of cells or groups of cells were determined using the percentile method [69].

30

Spatial overlap of orangutan density distribution and resource use

566 With the aim of assessing the differences in the orangutan abundance and change in response to

resource use during the survey period, we compared the orangutan density distribution from the first

568 and last year of the survey period with maps for land-cover classes and area converted into

industrial agriculture (oil palm and paper pulp plantations) [32,70]. The lack of repeat sampling

570 through time in areas of land-cover change made it necessary to approach this study in two steps.

First, we fitted the model using habitat cover and threat predictors and second, overlaid the

572 estimated densities with independent maps of land-cover change to infer about patterns of

orangutan loss. However, as these maps represent related information, we cannot entirely exclude

574 potential circularity in the approach taken. The only approach that completely allows to avoid this

problem is to systematically sample across gradients of land-use change through time.

576 From the land-use layers we extracted three classes representing changes of orangutan habitat due

to resource use (establishment of industrial oil palm and paper pulp plantations, deforestation, and

578 selective logging) that occurred during the study period (1999 – 2015), three classes representing

forested areas in 2015 (regrowth forest, primary forest, and primary montane forests ($>$ 750 m asl)),

580 and two classes depicting non-forested areas in 2015 (industrial plantations established before 2000

and 'other'). Regrowth forests were areas that were non-forest in 1973, but had forest cover in

582 2015. The category 'other' included scrublands, urban, agricultural and non-forest areas that were

not contained in the other categories. It was possible that during the study period an area was first

584 selectively logged or deforested, and then industrial plantations were established. In our analysis,

we counted these areas only as industrial plantations, as this was the final stage of the land-use

586 transition. We then pooled the average abundance and density in each land-use class or resource use

category and calculated the 95% confidence interval.

DATA AND SOFTWARE AVAILABILITY

590 All raw datasets used in this study can be requested from the IUCN SSC. A.P.E.S database

(http://apesportal.eva.mpg.de/). The processed data and data underlying the figures were deposited

592 under https://portal.idiv.de/owncloud/index.php/s/gU6BXYGoEWWdkyg. The code was deposited

under https://git.idiv.de/mv39zilo/manuscript_code.git.