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Bornean orangutan *Pongo pygmaeus pygmaeus* population estimate within and around Danau Sentarum National Park, Kapuas Hulu, West Kalimantan

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Abstract

Of the three subspecies of Critically Endangered Bornean orangutans, *Pongo pygmaeus pygmaeus* has the smallest population size. One of its most important habitats is the tropical forest within and around Danau Sentarum National Park (DSNP). Research in the late 1990s estimated that ca. 1025 orangutans inhabited DSNP, while ca. 1717 orangutans inhabited the forest beyond DSNP's boundaries. However, concerns were later raised that incorrectly estimated nest decay rates (*t* values) may have led to the overestimation of the population size. Furthermore, the area experienced forest degradation and land use change between 2000 and 2013. Given these changing landscapes, updated population estimates were needed to inform policy makers and land-use planners on the implications of habitat loss for resident orangutans. We conducted this study to recalculate nest decay rates based on current recommended methods, and to update our knowledge on the orangutan population in the region. Our average nest decay rate was 288.3 days; applying this to the study in the late 1990s generated estimates of 807 individuals within DSNP and 1578 beyond DNSP's boundaries. New surveys of the transects undertaken between

The study found considerable declines of orangutans, and suggests the needs to improve protection of the orangutans and their habitat.

2010 and 2014 revealed that the population size had declined substantially in these two areas, to 202 and 71 individuals respectively. Both declines are considerable, but larger losses occurred in logged-over and cleared forests outside the park. We discuss factors potentially driving these declines, emphasizing the need to improve habitat protection both inside and outside of DSNP, and make recommendations for improving the prospects for future orangutan conservation.

KEYWORDS

Borneo, critically endangered species, deforestation, habitat loss, killing and trade, nest decay rate, oil palm plantations, orangutan

1 | INTRODUCTION

Bornean orangutans have been marginalized and fragmented across their native range, with a steep decline in their population leading to all three Bornean subspecies (*Pongo pygmaeus pygmaeus, P.p. morio* and *P.p. wurmbii*) being classified as critically endangered in the IUCN Red List of Threatened Species (Ancrenaz et al. 2016). Between 1950 and 2025, which represents three orangutan generations, the Bornean orangutan population is projected to have declined by 86%, with the 2016 total population estimate at ~104,700 individuals, and of the three Bornean subspecies, *P.p. pygmaeus* was most recently estimated to have the smallest population, with fewer than 10,000 individuals (Ancrenaz et al., 2016).

One of the most important remaining strongholds for *P.p. pygmaeus* is the tropical forest in and around the Danau Sentarum wetlands in West Kalimantan. In the late 1990s, 1025 orangutans were estimated to survive within the Danau Sentarum National Park (DSNP) area, and an additional 1717 in the proposed greater extension of the park (Russon et al., 2001). A more recent report by Utami-Atmoko et al. (2017) suggested approximately 680 orangutans survived within DSNP and in the forested corridor between DSNP and Betung Kerihun National Park. Major drivers of the decline include habitat loss and fragmentation and other anthropogenic activities such as the illegal pet trade and poaching (Freund et al., 2017; Santika et al., 2017). Although orangutans are officially protected under Indonesian law, their habitat outside protected areas is not, hence timber concessions and other large-scale human development activities, such as new oil palm plantations, mining operations and infrastructure development, can and are being established in these important orangutan habitats (Alamgir et al., 2019; Andilala., 2019; Siregar et al., 2017).

From 2002 to 2005, illegal logging and timber export increased dramatically both within and outside DSNP, with more than 300 trucks of timber per day reportedly transported to Malaysia (Eilenberg, 2012; Heri et al., 2010; Obidzinski et al., 2006). Stricter law enforcement in 2005 reduced logging activities, however deforestation continued through large-scale monoculture plantation establishment. In 2007, 21 oil palm plantation permits were granted in the area surrounding DSNP (Kapuas Hulu Plantation and Forestry Service/DISHUTBUN, 2007), including within defined buffer zones and catchment areas. Significant land clearing took place between 2009 and 2013 and, in two sub districts that cover the western and northern areas of DSNP, an estimated 9740 ha of primary and secondary forests (4.74% of the two sub districts' area) were cleared and replaced by monoculture plantations (see Figure 1, and Yuliani et al., 2022).

Official data also show a decrease of approximately 156,400 ha of state forest area (including 10,600 ha of Protection Forest/*Hutan Lindung*) within the whole Kapuas Hulu District, from 2,512,900 ha (The Ministry of Forestry and Plantation's Decree no. 259/2000) to 2,356,500 ha (The Ministry of Environment and Forestry's Decree no. 733/2014). Local communities reported that orangutan sightings between 2010 and 2012 had declined considerably compared to 1990–2000 (Yuliani et al., 2018).

To update knowledge on the orangutan population in this rapidly altered landscape, we conducted a study to assess changes in population density and distribution over time, in particular, compared to the study in the late 1990s (Russon et al., 2001), and calculate a revised density estimate based on more accurate methods as suggested by Mathewson et al. (2008) and Russon (2008, pers. comm).

2 | STUDY SITE

The Danau Sentarum wetlands are situated in the Kapuas Hulu district, West Kalimantan Province, Indonesia (Figure 2). Covering an area of 1320 km^2,

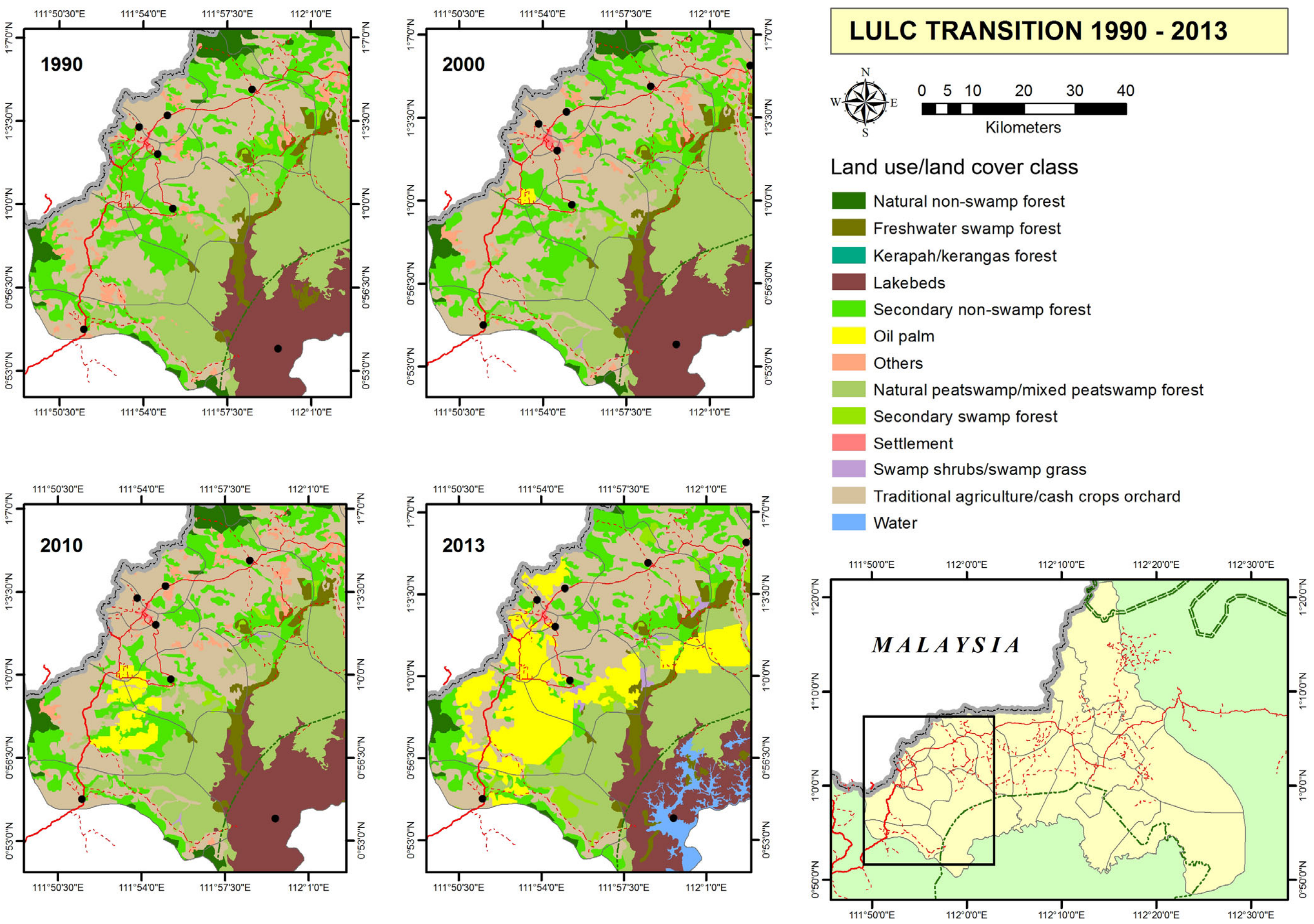

FIGURE 1 Maps of parts of Badau and Batang Lupar sub districts that show land use/land cover changes from 1990 to 2000, 2010 and 2013 (Yuliani et al., 2022).

Danau Sentarum is one of the largest wetlands in Asia, comprising 83 inter-connected lakes and six major types of vegetation; dwarf swamp forest, stunted swamp forest, tall swamp forest, heath forest, lowland forest and hill forest (Giesen & Aglionby, 2000). The lowland and hill forests in the wetlands and surrounding areas provide habitat to multiple species of wildlife–including the orangutan, proboscis monkey (*Nasalis larvatus*), and a number of threatened birds for example, great argus (*Argusianus argus*) and lesser adjutant (*Leptoptilos javanicus*). These forests are dominated by valuable dipterocarp timber species. The wetlands also provide key hydrological functions to the Kapuas River, the longest river in Indonesia. In the driest months (June–August), the wetlands supply 50% of the water for the Kapuas River and in the wettest months (December–February), they absorb 25% of the Kapuas water, thereby reducing flood risks downstream (Klepper et al., 1995).

The wetlands were originally gazetted as the Danau Sentarum Wildlife Reserve (DSWR) in 1983, covering 800 km^2. Prior to gazettement, local people inhabiting the area were mainly Iban forest gatherers who settled in the peripheral hills, and the Malay who historically traveled to the wetlands seasonally to fish but settled there more permanently in the 1980s (Giesen & Aglionby, 2000). In 1999, the DSWR was officially upgraded to a National Park (Danau Sentarum National Park/DSNP), and the boundaries were extended to cover an area of 1320 km^2. Between 2002 and 2009, the boundaries were redefined, and the DSNP area shrunk to 1274 km^2 (the Ministry of Forestry decree No. SK. 4815/Menhut-VII/KUH/2014). The current DSNP boundaries correspond to the proposed moderate extension of DSWR (DSWR-M), while the proposed DSNP buffer zones correspond to the proposed greater extension of DSWR (DSWR-G) in Russon et al. (2000, 2001).

An earlier study on the orangutan population in this region was conducted in the late 1990's (Russon et al., 2001). Russon and colleagues sampled seven areas; three areas within DSWR boundaries (via five transects), three areas within DSWR-M (now DSNP, via nine transects), and one area in the north within DSWR-G (now beyond

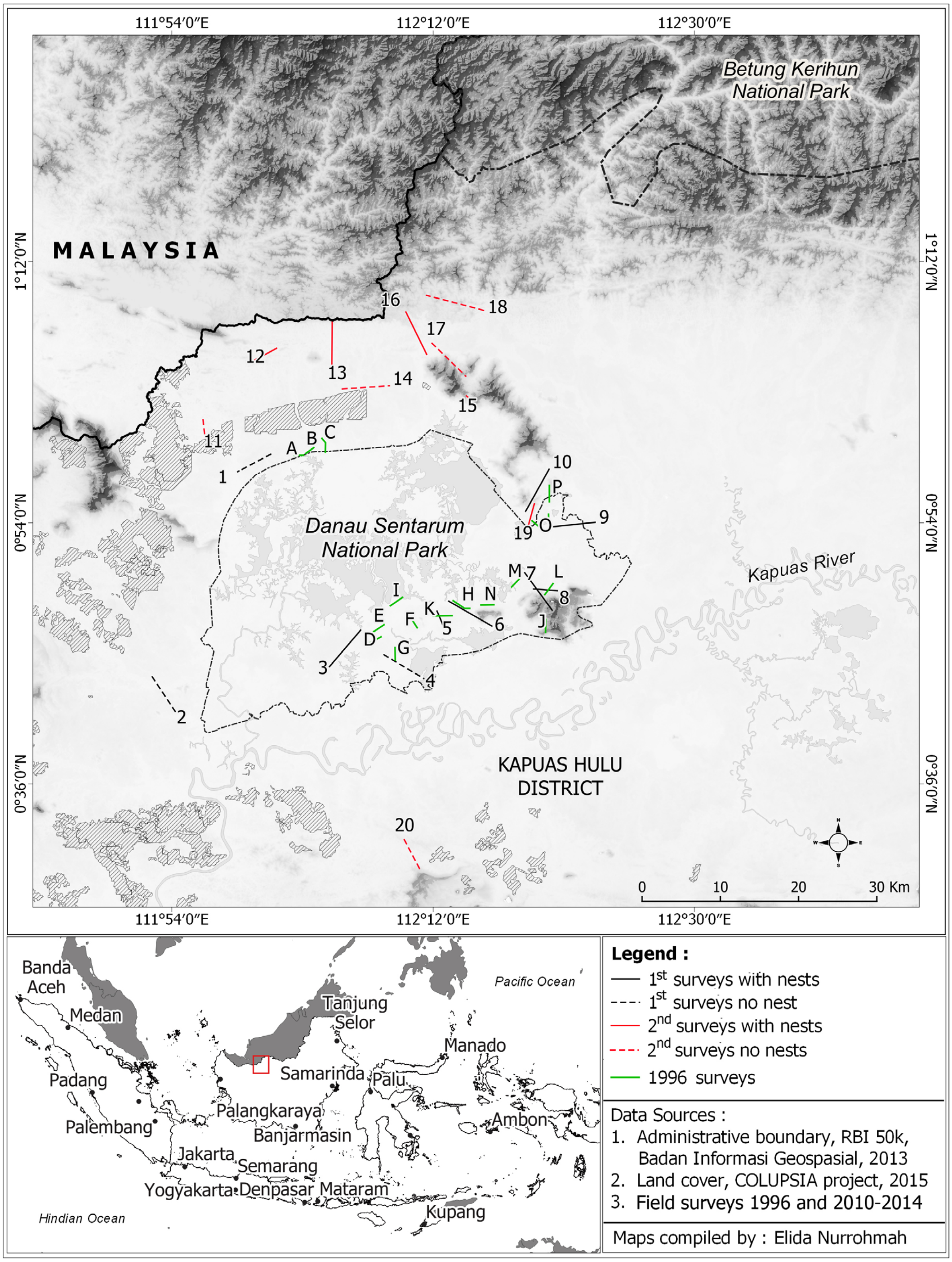

FIGURE 2 Study site and transects locations. 1 = Tangit; 2 = Segerat; 3 = Hutan Nung; 4 = Bekuan-Lupak Mawang; 5 = Leboyan; 6 = Semujan; 7 = Menyukung; 8 = Melingkung; 9 = Meliau; 10 = Pelaik1; 11 = Janting; 12 = Seriang; 13 = Keladan; 14 = Senunuk; 15 = Sepan; 16 = Libung; 17 = Sumpak; 18 = Keluin; 19 = Pelaik2; 20 = Benuis.

DSNP boundaries, via three transects). We aimed to replicate their transect locations but were challenged by the lack of GIS data. Hence, we identified locations based on names and labels available in the literature and personal communication with the team that chose and surveyed these locations (Russon, pers. comm 2010; Erman, pers. comm 2010). The locations we sampled (Figure 2) followed those of Russon et al. (2001); in addition, we selected 11 additional locations randomly outside DSNP to obtain a more representative estimate for the entire DSWR-G area (i.e., increased area and less biased samples).

3 | METHODS

3.1 | Field data collection methods

To estimate orangutan density in the DSNP area, we replicated the methods used in the earlier study (Russon et al., 2001), that is, nest surveys along line-transects (Blouch, 1997; Page et al., 1997; van Schaik et al., 1995), with some modifications (detailed in subsequent paragraphs) to obtain more accurate results as suggested by Russon et al. (2001) and Mathewson et al. (2008).

Orangutan density (*d*) was estimated by adjusting nest density (d_{nest}) for three nest-related parameters using the equation: d = d_{nest}/(p x r x t), to take into account the proportion of animals that actually build nests (*p*), the rate at which nests are produced (*r*), and the rate at which nests remain visible after construction (*t*) (van Schaik et al., 1995). The *p* and *r* parameters must be based on observed values from known populations (MacKinnon, 1974; Singleton, 2000; van Schaik et al., 1995), however there is no published literature on these parameters from our study site. As there has been no report of significant variation of proportion of nest builders among the three subspecies of Bornean orangutan, we used a *p* value of 0.9 which was generated by a long-term study in Gunung Palung, West Kalimantan (Johnson et al., 2005). The *r* value for Bornean orangutans varies between 0.9 and 1.2 nests per day (Morrogh-Bernard et al., 2003; Ancrenaz et al., 2004; Johnson et al., 2005), therefore we used 1.08, the average of Borneo-specific *r* values (Ancrenaz et al., 2004; Johnson et al., 2005). Russon used an *r* value of 1.6–1.7, which was taken from studies in Sumatra that were the only estimates available at that time. In order to be comparable, we also re-estimated the orangutan population in 1996 using the Borneo-specific *r* value.

The *t* value is more difficult to estimate than *p* and *r* values. As variation in this value will cause variation in the density estimates, methods to estimate the *t* value have been a subject of numerous studies. Direct observations of nest decay are considered to provide relatively accurate estimates of the *t* value, however their main limitation is the laborious and long period of data collection entailed (Rijksen, 1978). Therefore, many researchers resort to estimating the nest decay time by modeling the states of nest progression (i.e., the nest age classes) from fresh nest to complete decays as an absorbing Markov Chain (Kemeny & Snell, 1976), since it requires much less time in the field (Mathewson et al., 2008). This technique uses a mathematical model to describe the probability of a sequence of events based on the previous event, which in this case is the probability of the orangutan nest's transitioning from one class to another.

To apply the matrix technique to a data set, a sufficient number of nests must be monitored until they completely disappear (Buij et al., 2003; Johnson et al., 2005), hence we modified field data collection methods in order to achieve this and to gather a more representative data set. During the previous study, each area was sampled along 3 km of line transects, however in some areas, transects sampled only the periphery of the forests due to access difficulties, hence Russon et al. (2001) recommended that future studies go further inland. Therefore, in our study we increased our transect length to 6 km wherever possible, although geographical limitations hampered this for some transects.

The nest surveys commenced in January 2010, in 10 locations (eight within and two outside DSNP), with nests monitored a total of seven times between April 2010 and September 2011. A second series of nest surveys was conducted from December 2012 to February 2014, in 10 locations outside DSNP (indicated by red lines in Figure 2). To maximize the number of fresh nests, additional fresh nests encountered during monitoring were included to increase sample size for estimating the *t* value and were monitored until they had completely decayed. Intervals between monitoring individual transects ranged from 51 to 110 days. The surveys were undertaken by an ecologist, four members of the Danau Sentarum National Park Authority and two members of a local NGO (Riak Bumi), all of whom were trained and experienced in orangutan nest surveys.

Along each transect, we recorded nests that were visible from the transect. We surveyed each transect twice, the second time walking in the opposite direction and recording all additional nests found (Buij et al., 2003). For each nest, we recorded the age class, geographical coordinates and perpendicular distance from the transect. We used Johnson et al. (2005) criteria to assign nest age class, as follows: one (fresh, leaves still green), two (still fairly fresh, mixture of green and brown leaves), three (leaves all/mostly brown, but nest remains intact), four (nest had begun to fall apart; chunks of the nest and leaves missing) and five (leaves gone, only the nest's branch and twig structure remained).

In each survey, we also recorded other factors that might affect the nest decay rate directly or indirectly, that is, soil pH, air temperature, humidity, nest height from the ground, tree height, local name of the tree, and habitat type (van Schaik et al., 1995). Precipitation and wind might affect the nest construction and decay rates (Bessone et al., 2021), however we did not measure these factors due to limitations on available equipment. We also observed and recorded evidence or indications of all habitat disturbances along each transect–primarily forest clearing, forest degradation, logging, fire and local farming–then coded an overall disturbance level for that location based on the degree of damage observed: high if evidence of habitat disturbances were clearly visible and forest cover along the transect (including 20 m to the left and to the right of the transect) was estimated to be less than 25%; medium if indications of some of habitat disturbances were visible and forest cover was between 25% and 50%; and low if there was no or minimum disturbances and forest cover was more than 50%, We validated the coded data against vegetation cover data at 1:50,000 available from https://www2.cifor.org/map/vegetation/ (Laumonier et al., 2020).

To estimate the extent of usable habitat at the time of our surveys, we used vegetation cover data from the same source and calculated the extent of various types of natural and logged-over forests, including hill forest (300–800 m a.s.l.); lowland forest; freshwater, peat and mix swamp forests; and riparian forest within the boundaries of DSNP and the proposed buffer zone (DSWR-G).

3.2 | Data analysis

To estimate the *t* value from irregular intervals between monitoring with Markov Chain Analysis, we modeled the data using five nest age classes, with class 1 being "fresh nest", class 5 being the absorbing "complete decays" and classes 2, 3 and 4 representing intermediate classes. Using the well-established property of an absorbing Markov Chain, we calculated the probability of nests transitioning between classes in order to obtain an estimate of the expected nest decay time (in days). We performed sensitivity analysis by comparing this approach for calculating the transition matrix and the expected nest decay time to the more computationally-intensive approach from Craig and Sendi (2002), which was based on Expectation–Maximization (EM) algorithm, and found that our approach overestimates the nest decay time by less than 5%. Detailed calculation and formulae are provided in the Supplementary Material.

When calibrated against actual decay rates, Markov analyses tend to overestimate the *t* value (Buij et al., 2003; Johnson et al., 2005; van Schaik et al., 1995). A correction factor (Cf) is usually applied to provide a more accurate *t* value estimate (Mathewson et al., 2008), hence we corrected the *t* value we obtained from the Markov analysis using a Cf of 0.89, which is considered appropriate for Borneo (Johnson et al., 2005).

To estimate the nest density and strip width, only nest count and perpendicular distance data from the first surveys were used. We used the R package *Distance* version 0.9.8 to estimate the strip width and nest density. As there was wide variation across sites in the number of nests, we performed two types of analysis, that is, site-specific analysis to estimate the local populations, and an aggregate analysis to estimate the overall populations inside and outside the DSNP. The R package uses the same sample distance sampling methodology (Buckland et al., 2001) as the DISTANCE software used with other orangutan surveys (e.g., Johnson et al., 2005; Mathewson et al., 2008). Using half-normal detection and Fourier series adjustment (Burnham et al., 1980), we estimated the strip width to be 0.01531 km. The half-normal detection function was chosen as the best fit to the data when comparing the observed and theoretical detection probabilities. Models with and without Fourier series adjustments were fitted and compared in terms of their Akaike Information Criterion (AIC). The model with Fourier series adjustment was selected because it has lower AIC, which implies a better fit to the data.

We performed two sets of calculations on our nest count data. One set used the *t* value from Russon's work in this area to compare the population estimate with previous studies, and the second set used the *t* value from our surveys.

4 | RESULTS

4.1 | Nest decay rate estimate

In our first surveys and resurveys, we recorded 425 nests in total by the end of the nest decay monitoring period. Of those, we discarded 44 nests due to damage to the nest through natural tree fall events. Of the remaining 381 nests, only 11 fresh nests (class 1) and 56 fairly fresh nests (class 2) were observed until they had completely decayed (class 5). For these data, the time from class 1 to completely decayed varied between 211 and 413 days, and from class 2 to completely decayed between 113 and 413 days. Using Markov Chain analysis, we obtained an average nest decay rate estimate of 323.9 days. Using the recommended Cf (correction factor) for Borneo of 0.89, the corrected nest decay rate (t_{cor}) is 288.3 days. Applying this t_{cor} to the earlier 1996 study generated estimates of 807 individuals within DSNP and 1578 beyond DNSP's boundaries.

4.2 | Nest count, orangutan distribution pattern and local population estimates

During our first surveys, we located 169 nests (109 nests from six sampled areas inside DSNP and 60 nests from five areas outside DSNP), but no nests in the other seven areas sampled (one inside and six outside the park

TABLE 1 Nest count data, nest densities and transect locations from our two series of surveys (2010–14), compared with 1996 surveys

Transect location	Dominant ecosystem types along the transect	2010–2014 surveys						1996 surveys					
		Dist. level[a]	N_1	N_{total}	L	d_{nest}	d	Transect name[a]	Dist. level[a]	N	L	d_{nest}	d
INSIDE DSNP													
Melingkung	MSW, TSW, LOW, HILL	Low	35	75 (11)	3.03	367.60	1.31	L	Medium	6	1.00	187.85	0.67
Menyukung	MSW, LOW, HILL	Low	38	83 (12)	5.91	204.62	0.73	J, M	Medium	49	2.00	767.06	2.74
Meliau	TSW, LOW	Low	15	45 (4)	5.51	134.47	0.48	Q	Medium	19	1.00	782.72	2.79
Semujan	MSW, TSW, LOW, HILL	Low	11	58 (2)	6.36	86.63	0.31	H	Medium	7	1.50	594.87	2.12
Leboyan	MSW	Medium	9	31 (1)	2.13	55.04	0.20	K	Medium	25	1.00	146.11	0.52
Hutan Nung	TSW, MSW	Medium	1	14 (2)	6.10	5.22	0.02	D, E	High	3	1.50	62.62	0.22
Bekuan - Lupak Mawang	TSW, RPR	High	0	0	5.91	0	0.00	G	High	0	1.00	0	0
OUTSIDE DSNP													
Pelaik1	TSW, LOW	Low	38	85 (11)	6.14	248.34	0.89	P	High	46	1.00	1440.20	5.14
Sepan	AGROF, LOW, HILL	Low	2	2	0.50	160.51	0.57	n.s	n.s	n.s	n.s	n.s	n.s
Pelaik2	LOW, HILL	Low	9	18	3.30	109.44	0.39	O	High	10	1.00	313.09	1.12
Seriang	LOW, OF, YF, AGROF	High	4	6	3.10	51.78	0.18	n.s	n.s	n.s	n.s	n.s	n.s
Libung	OF, YF, AGROF, TRAD	Medium	5	5	5.99	33.49	0.12	n.s	n.s	n.s	n.s	n.s	n.s
Keladan	TSW. RPR, AGROF, TRAD	High	2	3 (1)	5.96	13.47	0.05	n.s	n.s	n.s	n.s	n.s	n.s
Tangit	TSW, MSW bordering on cleared forest for oil palm	High	0	0	4.67	0	0.00	A,B,C	Low	87	3.00	907.95	3.24
Segerat	TSW, MSW	Low	0	0	5.84	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s
Benuis	OF, LOW	High	0	0	4.24	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s
Janting	OF, LOW	High	0	0	1.88	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s
Keluin	LOW, OF, YF, AGROF	Medium	0	0	5.44	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s
Senunuk	SW	High	0	0	6.01	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s
Sumpak	SW, AGROF, YF, RPR	High	0	0	5.98	0	0.00	n.s	n.s	n.s	n.s	n.s	n.s

[a]In 1996 surveys, transects were labeled with letters. Transects D, E, F, G and I were within DSWR boundaries, H, J, K, L, M, N, O, P and Q were within DSWR-M which correspond to DSNP boundaries, A, B and C were within DSWR-G (now outside DSNP).

Abbreviations: AGROF, agroforest; LOW, lowland forest; MSW, mixed swamp forest; n.s., not surveyed; N_1, nest count in the first surveys; N_{total}, total number of nests found in first surveys plus new nests found during resurveys. In parentheses: number of discarded nests; OF, old fallow; RPR, riparian forest; SW, swamp forest; TRAD, traditional cultivation field; TSW, tall swamp forest; YF, young fallow.

boundary) (Table 1). The highest nest densities of sampled areas were found in the tall swamp forest, lowland forest and hill forest in the eastern parts of DSNP known as Melingkung, Menyukung, Semujan, Meliau, Leboyan, Pelaik and Sepan. Outside DSNP boundaries, the highest nest densities were found in tall swamp forest and lowland forest of an Iban village known as Pelaik and lowland forest and hill forest of Sepan. These findings support earlier studies' (Ancrenaz, 2006; Prayogo et al., 2016), in that the forested corridor between Danau Sentarum and Betung Kerihun was important habitat for the orangutans.

Orangutan nests were also found in small patches of logged-over lowland forests and hill forests surrounded by oil palm plantations and cultivation fields outside DNSP boundaries, particularly in Seriang, Keladan and Libung areas. These findings also support earlier studies on orangutan adaptation and resilience through their use of small forest fragments and plantations (Spehar & Rayadin, 2017) and emphasizes the need to better protect the orangutans living in small patches of forests as these play an essential role in maintaining gene flow between larger sub-populations distributed across multiple-use landscapes (Ancrenaz et al., 2021).

The most serious declines, or complete disappearances of orangutans, were found in peat swamp forest outside the northern DSNP boundary (Tangit village), which is an area classified as Other Land Uses. In the 1996 surveys, tall swamp forest and lowland forest in the north of DSNP were also important habitats of resident orangutans. Russon et al. (2001) reported that along transects A, B and C (Tangit area), which were classified as habitat with low-moderate disturbance, they found 41, 26 and 20 nests respectively during their survey. These figures were higher than the number of nests found inside DSNP. During our surveys in the Tangit area, however, we found no nests; the forest there was in the process of being cleared to establish a large-scale oil palm plantation. Although our nest census transect was 0.5 km away from the area being cleared, the absence of orangutan nests indicates strong influence of other threats to resident orangutans (detailed in the next section).

4.3 | Orangutan densities and population estimates inside and outside DSNP

Estimated orangutan densities inside and outside DSNP were calculated using two different *t*-values (145 from the previous study, 288.3 from present study); results are shown in Table 2. With t_{cor} 288.3 days, our estimate of

TABLE 2 Orangutan density and population estimates

Aggregate analysis	2010–2014 surveys: Usable habitat (km^2)	d_{nest} (/km^2)	SE of d_{nest}	95% confidence interval of d_{nest}	Orangutan density estimate (indiv./km^2) (CI 95%): t = 145	t_{cor} = 288.3	Orangutan population estimate (indiv.) (CI 95%): t = 145	t_{cor} = 288.3	1996 surveys: Usable habitat (km^2)	Orangutan density estimate (indiv./km^2): t = 145	t_{cor} = 288.3	Orangutan population estimate (indiv.): t = 145	t_{cor} = 288.3
Inside DSNP (=DSWR-M in 1996 surveys)	571.66	99.25	42.36	37.09–265.56	0.70 (0.26–1.88)	0.35 (0.13–0.95)	402.56 (150.44–1077.13)	202.49 (75.67–541.79)	754	1.36	1.07	1025	806.73
Outside DSNP (=DSWR-G in 1996 surveys)	489.67	40.77	25.16	11.88–139.98	0.29 (0.08–0.99)	0.15 (0.04–0.50)	141.65 (41.27–486.34)	71.25 (20.76–244.63)	552	3.11	2.86	1716	1578.30

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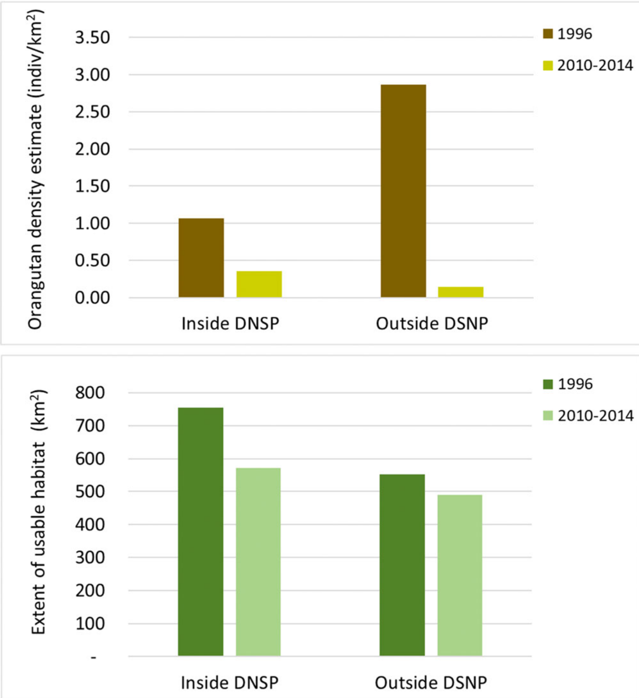

FIGURE 3 Comparison between 1996 and 2010–2014 surveys: orangutan density estimates (top), extent of usable habitat (bottom).

orangutan density was 0.35 (CI 95%, 0.13–0.95) orangutans/km^2 within the park and 0.15 (0.04–0.50) orangutans/km^2 in the areas surveyed outside the park. Our estimates of the extent of usable habitat inside and outside DSNP were 571.66 km^2 and 489.67 km^2 respectively. Using these figures, our overall population estimate is 202.49 orangutans (CI 95%, 75.67–541.79) within the park, and 71.25 orangutans (CI 95%, 20.76–244.63) outside the park.

Comparison with the 1996 estimates showed that the orangutan densities both inside and outside DSNP have declined, from 1.07 to 0.35 individuals per km^2 (66.89%) and 2.86 to 0.15 individuals per km^2 (94.91%) respectively (Figure 3, top). The declines are much steeper than the overall rate of decline in Borneo, which was estimated at 25.3% (Santika et al., 2017). Meanwhile, the extent of usable habitat in the areas surveyed inside DSNP declined from 754 km^2 to 571.66 km^2 (i.e., to 24.18%) and outside DSNP from 552 km^2 to 489.67 km^2 (i.e., to 11.29%) (Figure 3, bottom).

These two sets of figures suggest that other drivers, in addition to habitat loss, caused the severe declines of the orangutan populations. The local community members who accompanied us during the surveys reported that the orangutan trade had increased along with widespread timber sales to Sarawak, Malaysia. This anecdotal information was corroborated by the findings of other researchers (e.g., Erman, 2005; Heri et al., 2010) that between 2002 and 2005, approximately 100 to 200 infant orangutans from in and around DSNP were held temporarily in illegal logging camps and eventually sold to zoological gardens in Sarawak. In addition, an estimated 100 to 150 orangutans were killed for food by timber company employees, particularly in Tangit IV, Tangit II and Seriang (north); Piyam, Semanyus and Batu Pansap (west); and Semangit, Sei Luar and Lubuk Bandung (east). The employees were reportedly outsiders who came from other regions, and these killings of orangutans had caused concern among local communities, mainly the Iban, whose traditional beliefs help to protect the orangutans (Bakara, 2013). The co-occurrence of poaching and trade of infant orangutans with other threats, mainly commercial logging and deforestation for large-scale agriculture, was also reported elsewhere (Freund et al., 2017; Nijman, 2009; Stiles et al., 2013).

Other factors that might have contributed to the declines are rescues, translocations, disease, inbreeding depression or insufficient food (Nater et al., 2017; Nasution et al., 2018; Ashbury, 2020). Based on interviews with staff of the Conservation Agency and National Park Authorities, they did not recall any records of rescue or translocation particularly from the transect locations from the late 1990s until 2014. They also explained that the extent of the decline in usable habitat inside DSNP was mainly caused by illegal logging in the early 2000s, when the DSNP managing authority (*Balai Taman Nasional*) was not yet established. Although the area was officially declared a national park in February 1999, the managing authority was not established until 2007 (see also Aglionby, 2010; Colfer & Yuliani, 2010). Between 1999 and 2007, the park was minimally guarded by three forest rangers of the West Kalimantan Conservation Agency. They admitted that three personnel was insufficient to effectively protect this large park from illegal activities. With regards to other possible factors, more specific studies are required.

5 | DISCUSSION

This study resulted in three major findings: an updated estimate of the orangutan population in the region compared to an earlier estimate, which shows considerable decline in the interim; the distribution of the orangutans in the region including the presence of small populations in fragmented forests surrounded by agricultural land; and the indication of more serious threats that might have co-occurred with forest conversion activities. Better landscape management, law enforcement and awareness-raising programmes, which were also recommended by other studies (Freund et al., 2020; Knott et al., 2021; Pandong et al., 2019), are urgently needed to protect the remaining orangutans and their habitat both inside and outside protected areas.

In large-scale plantations currently operating in the area, the prescribed "conservation areas" were only in the forms of riverbanks (with a total width around 200 m) and local communities' sacred sites (the extent of which was around 0.5–2 ha each). These 'conservation areas' were much smaller than Bornean orangutan home ranges (0.4–3.0 km^2 for females and 1.0–6.0 km^2 for males) (McConkey, 2005). A full High Conservation Value (HCV) area assessment, therefore, should be made obligatory by law prior to establishing such large-scale plantations, and HCV areas should be given legal protection (Colchester et al., 2009). To protect the orangutans, the HCV areas should be sufficient to meet the requirements for maintaining the orangutan population, such as the minimum forest extent and canopy closure and sufficient food resources (e.g., fruiting trees), as well as serious and thorough efforts by the company and relevant authorities involved to reduce hunting (Davies et al., 2017).

Our results also show that the orangutan population was much larger inside DSNP than it was outside the park, suggesting that national park status and programmes (e.g., patrols), particularly after the DSNP Authority was established in 2007, have provided much better protection for both the orangutans and their habitat. This resonates with earlier studies (e.g., Knott et al., 2021; Pandong et al., 2019) that habitat protection, enforcement and awareness raising programmes played major roles in slowing down the decline of orangutan populations.

The higher estimates of orangutan densities in the eastern parts of the park also support earlier findings (e.g., Ancrenaz, 2006; Prayogo et al., 2016) that the forested corridor between Danau Sentarum and Betung Kerihun, known as the Labian-Leboyan corridor, continues to serve as important habitat for orangutans in this area, and therefore should be fully protected. When the corridor was classified as *Kawasan Ekosistem Esensial/KEE* (Essential Ecosystem Area) in the 2014–2034 *Rencana Pembangunan Jangka Menengah Daerah/RPJMD* (Regional Medium-term Development Plan), it brought new hope for better protection. However, in the 2014–2034 *Rencana Tata Ruang dan Wilayah/RTRW* (Regional Spatial Planning Map), parts of this area are now classified as *Hutan Produksi* (State Production Forest) and *Area Penggunaan Lain/APL* (Other Land Uses). The forested landscapes under State Production Forest status could be unsafe for the orangutans due to possible co-occurrences of poaching and illegal trade with the logging activities. The Other Land Uses are lands intended for development, therefore highly prone to conversion. This suggests the need for a more integrated approach and government planning process which protects the corridor while simultaneously providing long-term benefits for local peoples' livelihoods, for example through legal recognition of customary laws and territory including forests, and building social capital of the local people (see also Roslinda, 2018; Sunkar & Santosa, 2018).

In various discussions, ecotourism was often suggested as a potential solution to bridge conservation and development objectives. However, it should be very carefully assessed from a conservation perspective, as such tourism has potential dangers to the orangutans and other wild primates (Russon & Wallis, 2014). The most often reported risks are pathogen transmission from humans to non-human primates (Dunay et al., 2018; Sapolsky, 2014) and habitat damage (Duffus & Dearden, 1990; Russon & Susilo, 2014), both caused in part by unclear objectives in national and regional policies on ecotourism, unpreparedness of the key institutions, and the fact that ecotourism is largely driven by private sector and political agendas (Nasution et al., 2018; Rhama, 2018).

Experience from the field has shown that the main threat to orangutans and their habitat was not poverty (IIED & CIFOR, 2012; Shanahan, 2012), and the people who wanted to give up their forest for large scale plantations, or those who were involved in killing or illegal trading, were not always those classified as poor (Yuliani et al., 2020). This suggests the need to find approaches to nature conservation that are not based solely on economics alone. Local people often have positive conservation goals and preferences (Vermeulen & Sheil, 2007) and/or traditional beliefs that support protection of orangutans and their habitat (Yuliani et al., 2018). They can then be part of solutions, for example through partnerships, the integration of traditional values/norms/beliefs that protect the orangutans with formal regulation, and participatory forest patrol and orangutan monitoring. In the last few years, the DSNP Authority has improved its efforts to develop collaborative management of the Park with local communities, for example, through capacity building and partnerships for park patrols including land and forest fire prevention. To evaluate the outcomes for conservation, including for orangutans, further long-term monitoring is recommended.

Outside DSNP, broader and more integrated approaches to land use planning and implementation also have the potential to mitigate issues of linking conservation and human development in Kapuas Hulu, for example through multi-stakeholder processes/platforms (MSPs). This recommendation resonates with Spehar et al., (2018) who highlighted the need for multifaceted, landscape-scale approaches to orangutan conservation that leverage sound policy and collaboration among multiple stakeholders to prevent hunting, mitigate human-orangutan conflict, and preserve and reconnect remaining natural forests. Such MSPs are currently being piloted, among others, by CIFOR and partners through the COLANDS initiative (www2.cifor.org/colands/), for example to jointly develop a Collaborative Management Plan for the Danau Sentarum Catchment Areas for a five-year period (2022–2026). Through multi-stakeholder processes, it is expected that orangutan habitat in the area will be better managed and preserved, killing and illegal trading will be significantly reduced and that local people's livelihoods will be better supported.

AUTHOR CONTRIBUTIONS

- Elizabeth Linda Yuliani: developed research design and methodologies on nest surveys, involved in nest surveys monitoring, put data into matrix, interpret the results and wrote the manuscript.
- Denny O. Bakara: contributed in development of methodologies and selecting sites, and conducted nest surveys monitoring.
- Mohammad Ilyas: contributed in development of methodologies and selecting sites, and conducted nest surveys monitoring.
- Anne E. Russon: guided Yuliani in developing the methodologies and selecting sites, reviewed the results of data analysis, identified possible biases and discussed how to minimize the possible biases, and contributed in the writing of the manuscript.
- Agus Salim: analyzed nest class monitoring data to obtain nest decay rate, and developed mathematical models to calculate strip-width and nest density.
- Jim Sammy: contributed in development of methodologies and selecting sites, and conducted nest surveys monitoring.
- J.L. Sunderland-Groves: contributed in writing funding proposal for the study, developing the methodologies, interpreting the results and writing the manuscript.
- T.C.H. Sunderland: contributed in writing funding proposal for the study, developing the methodologies, and writing the manuscript, including linking the study and its findings with global and national context of great ape conservation, poverty alleviation, landscapes approaches and national land use policies.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest

DATA AVAILABILITY STATEMENT

Data will be available and accessible on CIFOR data repository.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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