Animal Conservation (2004) **7**, 375–385 © 2004 The Zoological Society of London. Printed in the United Kingdom DOI:10.1017/S136794300400157X

Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia

Marc Ancrenaz[1,*], Benoit Goossens[1,2,3], Olivier Gimenez[4], Azri Sawang[1] and Isabelle Lackman-Ancrenaz[1,5]

[1] Kinabatangan Orangutan Conservation Project, PO Box 3109, 90734 Sandakan, Sabah, Malaysia
[2] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Locked Bag 2073, 88000 Kota Kinabalu, Sabah, Malaysia
[3] Biodiversity and Ecological Processes Group, Cardiff School of Biosciences, Cardiff University, PO Box 915, Cardiff CF10 3TL, UK
[4] CEFE/CNRS; 1919, Route de Mende; 34293 Montpellier-Cedex 5, France
[5] Pittsburgh Research Fellowship, Pittsburgh Zoo

(Received 29 October 2003; accepted 2 March 2004)

Abstract

Because of the difficulties encountered in detecting many large tropical forest-dwelling species in their natural habitat, precise figures concerning the distribution, number and trends of many populations remain deficient. In tropical forests, ground surveys are generally carried out by counting objects along straight lines. These counts require a strict compliance with the line-transect methodology before (proper design of the census), during (careful data collection) and after (accurate and correct data processing and analysis) the census itself. In addition, the major source of bias when estimating population size and/or trends comes from the extrapolation of estimates obtained in small sampling areas to the larger, and often incompletely known, distribution of the population. In the Kinabatangan floodplain (Sabah, Malaysia), helicopter surveys were useful in directly assessing the distribution of orang-utans and were a major advantage in the precise estimation of the size of the orang-utan population surviving in this region. Our survey showed that about 1100 orang-utans remain in the multiple-use forests of the Kinabatangan floodplain. These results provide new evidence on orang-utan adaptation to habitat disturbance and indicate the potential of the Kinabatangan multiple-use forests for orang-utan conservation. Helicopter surveys appear to be a promising alternative to ground survey for precise distribution assessment and for monitoring population trends of apes throughout their entire range in Asia and in some parts of Africa.

INTRODUCTION

Conservation and management of endangered species in the wild requires an adequate knowledge of their distribution and population size. Density estimates of large forest-dwelling species may be obtained from direct sightings or from counting signs of their presence (nests, dung, calls) along line-transects (Burnham, Anderson & Laake, 1980; Koster & Hart, 1988) but three independent sources of errors are associated with this method.

First, most censuses are not a total count, and the design of the survey, the quality of data-collection in the field and a sufficient number of randomly located straight transects are key elements for obtaining estimates that are representative of the total population (Anderson *et al.*, 1979).

The second source of error is introduced with the multipliers used to produce an estimated animal density from an estimated sign density. For nest counting, the estimated ape density $\hat{D}$ is usually obtained from the estimated nest density $\hat{D}_n$ as $\hat{D} = \frac{\hat{D}n}{\hat{p}.\hat{r}.\hat{t}}$ where $\hat{p}$ is the proportion of nest-builders in a population, $\hat{t}$ is the nest decay rate (in days) and $\hat{r}$ is the daily-rate of nest production (Tutin & Fernandez, 1984). Estimates of these multipliers show wide confidence limits and large inter-population fluctuations, which decrease their reliability when extrapolated to populations for which values are not available.

The major source of error when estimating ape population sizes is the extrapolation of densities calculated in very small census areas to wider population ranges, which are often insufficiently known. In most surveys, the sampling effort (size of the sampling area divided by the supposed distribution size of the population) is very low and may not be representative of the whole population range. The size of habitat suitable for a population is generally determined from maps that are frequently (1) outdated, (2) do not differentiate precisely between different habitat types and (3) do not reflect recent human activities (van Schaik, Priatna & Priatna, 1995*a*). This imprecision can yield biased estimates and must be taken into serious consideration for the proper determination of population size.

---

[*] All correspondence to: Marc Ancrenaz: KOCP, Austral Park, Lorong 10, House Number 35, 88300 Kota Kinabalu, Sabah, Malaysia. Tel/Fax: 60 88 250 540; E-mail: hutan1@tm.net.my

This paper explores ways to achieve better estimates of ape population size. In our census of orang-utans, strict compliance with line-transect methodology, high sampling effort, accurate determination of the multipliers needed for the estimation of orang-utan densities, utilisation of up-to-date maps and aerial surveys were key elements in the achievement of precise and robust estimates of the population living in the highly degraded forests of the Kinabatangan floodplain (Sabah, Malaysia, Borneo). Our findings showed that about 1100 orang-utans were spread over 50 000 ha of highly fragmented and degraded habitat and indicate the potential of the Kinabatangan multiple-use forests for orang-utan conservation.

MATERIALS AND METHODS

The Lower Kinabatangan

Physical and botanical features

The Lower Kinabatangan floodplain is located in Eastern Sabah (5°10′–5°50′N; 117°40′–118°30′E) and experiences a warm, wet and humid climate. Temperatures vary little throughout the year and mean monthly temperatures range between 21°–34° Celsius. Annual precipitation averages about 3000 mm. The predominant vegetation consists of evergreen freshwater swamp forests that occur over a range of soil conditions, from permanently waterlogged swamps to zones with differing frequencies of flooding. Low-stature forests and grasslands occur in backswamp areas while riparian and mixed lowland dipterocarp forests are found in drier areas located along the banks of the rivers and higher terraces (Azmi, 1998). However, most of the dry lowland forest has been cleared for oil-palm development and the remaining forests have been repeatedly logged over the past century.

Administrative status

In 2002, the State Government of Sabah gazetted 27 000 ha of highly disturbed forests as a Wildlife Sanctuary along the Kinabatangan River. The ten forest blocks (termed ‘lots’) of this Sanctuary are linked to seven patches of protected forests (Virgin Jungle Forest Reserves, VJFR) totalling about 15 000 ha, and they are connected with 10 000 ha of state and private forests at various stages of degradation: see Fig. 1.

Estimation of the orang-utan nest density using ground line-transects

Primary sampling units

Eleven primary sampling units (PSUs) were designed. Each PSU comprised one lot of the Sanctuary and connecting forests, irrespective of their administrative status (Fig. 1).

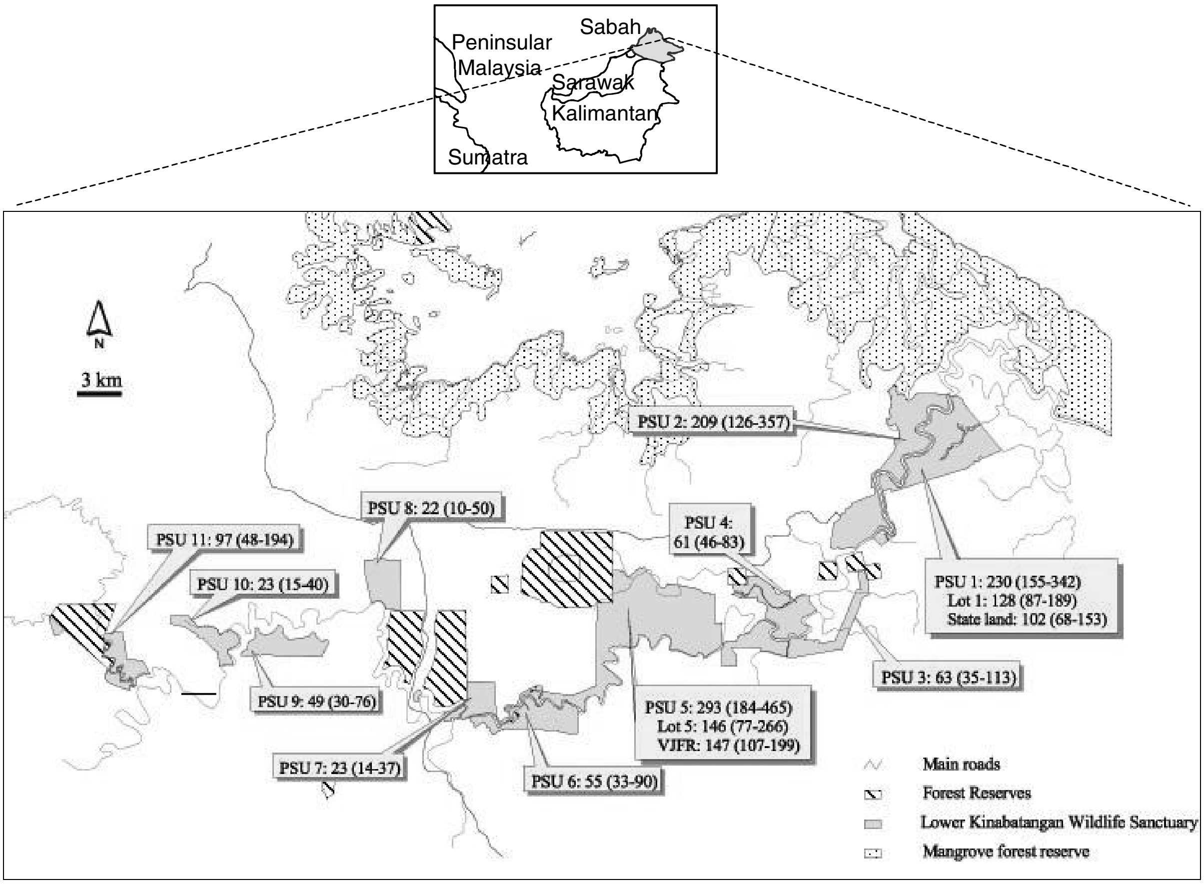

Fig. 1. Map showing the Kinabatangan region and the 11 Primary Sampling Units (PSUs) identified during the orang-utan census.

Table 1. Primary sampling unit (PSU), number and length of line-transects, number of nests and corresponding ‘prt’ value, effective strip width and sampling effort during the census of the Kinabatangan orang-utan population

Primary sampling unit (PSU)				Transects					Nests			
	Status	Size (km^2)	Forest type	No. trans	Av. (m)	Min. (m)	Max. (m)	Tot. L (m)	Tot.	Weighted prt value	ESW (m)	Sampling effort (%)
PSU 1	Lot 1 KWS	33.42	A: 1–2	10	696.2	185	1688	6962	312	128.9	22.2	0.70
	State and private lands	40*	A: 1–2 Mangrove	8	608.4	360	1000	4787	65	128.9		
PSU 2	Lot 2 KWS	37.59	A: 1–2	10	1410.1	900	2560	14100	385	219.9	20.2	1.15
	Private lands	10*										
	Keruak FR	2.01	C: 2	0	–	–	–	–	–	–		
PSU 3	Lot 3 KWS	22.15	A: 1–2	12	1000.0	500	1670	5002	60	150.9	17.8	1.08
	Private lands	7*										
	Pangui FR	4.36	C: 3	4	1298.5	968	1820	5194	64	158.1		
PSU 4	Lot 4 KWS	18.77	A: 1–2	14	982.1	512	1660	13749	260	137.8	21.6	2.26
	Private land	5*	A: 1									
	Bod Tai FR	2.51	C: 3	0	–	–	–	–	–	–		
PSU 5	Lot 5 KWS	74.21	A: 1–2	21	893.9	378	2000	18771	158	148.8	13.6	0.69
	Gomantong FR	45.39	C: 1–3	7	1252	842	1880	8764	171	154.1	16.1	0.62
PSU 6	Lot 6 KWS	26.73	A: 1–2	13	1073.6	500	2480	13957	191	144.8	21.0	2.19
PSU 7	Lot 7 KWS	10.27	B: 1–2	7	805.7	290	1575	5640	75	144.5	37.7	1.14
	Pin Supu FR	26.96	B: 1–2 (burnt)									
PSU 8	Lot 8 KWS	12.01	B: 1–2	4	1310.7	573	2004	5243	25	128.9	28.8	0.84
	Private lands	4*	B: 1									
	Pin Supu FR	20.00	B: 1–2									
PSU 9	Lot 9 KWS	11.21	B: 1–2	5	876.4	318	1550	4382	60	128.9	34.4	0.59
	Private lands	40*										
PSU 10	Lot 10 a KWS	8.68	A: 1–2	4	1319.7	900	1620	5279	70	159.0	26.5	1.68
	Private lands	8*										
PSU 11	Lot 10 b,c KWS	19.40	B: 1–2	9	973.8	422	2721	8764	56	149.7	8.9	0.33
	S. Lokan FR	18.52										
	Private lands	9*										
TOTAL		517.2	–	128	942	185	2721	120600	1952	–	22.4	1.04

* The size of private lands is estimated from available maps and is subject to changes according to further land-use.

Abbreviations used: KWS, Kinabatangan Wildlife Sanctuary; FR, forest reserve; No. trans., number of transects; Av., average; Min., minimum; Max., maximum; Tot. L., total length; (m), metres; Tot., total; prt, Multipliers used to obtain an orang-utan density from a nest density (see Methods). ESW, effective strip width. Forest type: A, disturbed forest; B, heavily disturbed forest; C, undisturbed forest; 1, semi-inundated forest; 2, dry and riverine forest; 3, limestone forest.

Census design and sample stratification

For each PSU, we ran sets of 4–28 transects (Table 1). The starting-point of each transect was randomly located on topographical maps (1:50 000) and was located using a Global Positioning System (Garmin XL 12) in the field. Transects were roughly perpendicular to the large rivers to reduce between-transect variation and to achieve more reliable density estimates (van Schaik *et al.*, 1995*a*; Cassey & McArdle, 1999). Transect length was directly determined using a walking-distance measurer. The computerised botanical maps available for Kinabatangan (satellite image from 1998) and our field observations showed only a slight and unclear gradation between the different habitat types and it was often impossible to distinguish satisfactorily between them. We therefore classified each PSU using three broad types of disturbance with the following criteria: heavily disturbed (most of the data collected along transects showing a tree density of less than 100/ha – with diameter at breast height (dbh) > 10 cm – and/or canopy disruption $> 50\%$, and/or more than five logging roads per km of line transect); slightly disturbed (tree density between 100 and 300/ha, canopy disruption less than 50%, fewer than five logging roads per km of line transect); undisturbed (more than 300 trees/ha, closed canopy, no sign of human activities).

Field data collection

Along each transect, a team of two cleared a straight-line path and confirmed the bearing with a compass. A second team of three recorded information on forest type and general levels of habitat degradation along the entire length of the transect. Tree density was determined by counting trees with a dbh > 10 cm in a 10×50 m botanical plot located randomly along each transect. For each nest observed, we measured the perpendicular distance from the transect and recorded size, dbh and species of the nesting tree, as well as its approximate age (Ancrenaz, Calaque & Lackman-Ancrenaz, 2004*a*).

Data analysis

Densities were analysed following line-transect analysis guidelines and were computed using the software Distance 3.5 (Buckland *et al*., 1993; Thomas *et al*., 1998). In a first exploratory phase, we built up boxplots of perpendicular distances to identify outliers (values more than 1.5 box-lengths from the 75th percentile) for each PSU. These outliers were then discarded from the data set in setting up a proper truncation level. Heaping was assessed from histograms and data were grouped when necessary (Crain, 1998).

In a second step, the probability of nest detection was estimated using seven models combining probability density functions (uniform, half-normal and hazard-rate) with adjustments (cosines, simple and hermite polynomials). The model with the lowest Akaike's Information Criterion (AIC) was selected for each PSU (Burnham & Anderson, 1998). The adequacy of the selected model to the perpendicular distances was assessed by means of a chi-square goodness-of-fit test on grouped data (Buckland *et al*., 1993).

Finally we estimated the variance of nest density using non-parametric bootstrapping to handle the model selection uncertainty and other sources of variation (Buckland *et al*., 1993). We selected all models that fitted the data equally well for each lot (i.e. the difference in AIC between the model with the lowest AIC and the model under consideration was lower than 2: Burnham & Anderson, 1998). The AIC selection procedure was then applied to these models for each resampled data set.

Transformation of nest density into orang-utan density

In the Kinabatangan, we found that nest decay rate was strongly affected by the species of nesting trees and we distinguished two groups of tree families for our surveys (mean ± standard deviation (SD)):

Group 1($n = 20$): *Eusideroxylon zwageri*, *Dimocarpus sp.*: $\hat{t}_1 = 431 \pm 170$ days

Group 2($n = 95$): other taxa: $\hat{t}_2 = 153 \pm 93$ days

The rate of daily nest construction estimated at the Kinabatangan Orangutan Conservation Project (KOCP) study site was $\hat{r} \approx 1.00$ ($n = 602$ dawn-to-dusk follows) and the proportion of nest builders was $\hat{p} \approx 0.85$ ($n = 92$ individuals: Ancrenaz *et al*., 2004*a*).

Orang-utan densities were obtained from nest density using:

$$\hat{D}_{ou} = \frac{\hat{D}_n}{\hat{p} \times \hat{r} \times (q_1 \times \hat{t}_1 + q_2 \times \hat{t}_2)} \tag{1}$$

with $\hat{D}_{ou}$ being the estimated orang-utan density, $\hat{D}_n$ the estimated nest density, $\hat{p}$ the estimated proportion of nest builders, $\hat{r}$ the estimated daily rate of nest construction, $\hat{t}_1$ and $\hat{t}_2$ the estimated time of nest visibility (in days) for trees with a longer (group 1) and a shorter (group 2) nest decay rate and q_1 and q_2 the proportion of nesting trees from each group (Ancrenaz *et al*., 2004*a*).

We extrapolated the estimated $\hat{r}$ and $\hat{t}$ values determined at the KOCP study site to other PSUs, assuming that all orang-utans living in the lower Kinabatangan had a similar nesting behaviour and that nest decay rates did not fluctuate according to forest blocks.

Estimate precision

To quantify the precision of orang-utan density estimates, we computed an estimated variance of the orang-utan density in each PSU via the δ-method (Seber, 1982):

$$v\hat{a}r(\hat{D}_{ou}) = \hat{D}_{ou}^2 \left\{ cv^2(\hat{D}_n) + cv^2(\hat{r}) + \frac{q_1^2\hat{t}_1^2 cv^2(\hat{t}_1) + q_2^2\hat{t}_2^2 cv^2(\hat{t}_2)}{(q_1\hat{t}_1 + q_2\hat{t}_2)} \right\} \tag{2}$$

with cv being the coefficients of variation and $cv(\hat{D}_n)$ being the bootstrapped standard error divided by $\hat{D}_n$ (as given by Distance 3.5).

For each PSU, a 95% confidence interval was obtained for the population density, assuming that $\hat{D}_{ou}$ was log-normally distributed (Burnham *et al*., 1987) and using a Satterthwaite approximation (Buckland *et al*., 1993). The lower and upper CI limits were:

$$(\hat{D}_{ou}/C,\ \hat{D}_{ou} \times C) \tag{3}$$

with:

$$C = \exp(t_{df}(0.05) \times \sqrt{v\hat{a}r(\log_e \hat{D}_{ou})}),$$

$$v\hat{a}r(\log_e \hat{D}_{ou}) = \log_e \left\{ 1 + \frac{v\hat{a}r(\hat{D}_{ou})}{\hat{D}_{ou}^2} \right\},$$

and $t_{df}(0.05)$ being the two-sided 5%-level t-distribution percentile. The number of degrees of freedom (df) associated with $\hat{D}_{ou}$ was computed as:

$$df = \frac{[cv^2(\hat{D}_n) + cv^2(\hat{r}) + cv^2(\hat{t}_1) + cv^2(\hat{t}_2)]^2}{\frac{cv^4(\hat{D}_n)}{df_{\hat{D}_n}} + \frac{cv^4(\hat{r})}{df_{\hat{r}}} + \frac{cv^4(\hat{t}_1)}{df_{\hat{t}_1}} + \frac{cv^4(\hat{t}_2)}{df_{\hat{t}_2}}} \tag{4}$$

with $df_{\hat{D}_n}$ being the number of observed nests minus the number of estimated parameters in the model, $df_{\hat{r}}$ being the number of degrees of freedom associated with the daily rate of nest-construction and so on for the other quantities.

Estimation of habitat area available for orang-utans in the Kinabatangan

The size of suitable habitat for orang-utan was assessed using helicopter surveys (Bell 206 Jet Ranger) undertaken in 2002. We followed a systematic stratified sampling pattern using parallel line-transects, the location of the first transect being randomly selected on a 1/50 000 map. The pilot kept the helicopter speed and height constant at 70 km/hour and 60–70 m above the forest canopy.

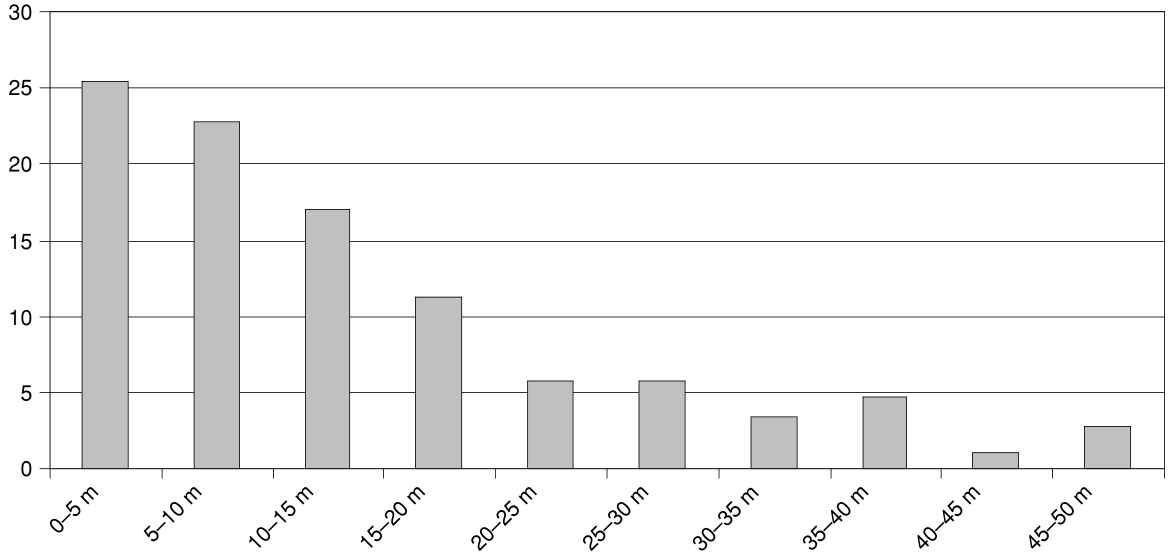

Fig. 2. Distribution of classes (in %) of nest to transect distances ($n = 1952$ nests) during the orang-utan nest census in Kinabatangan.

The co-pilot checked the flight plan using a GPS and recorded information on habitat type, canopy disturbance and human activities. Two rear seat observers searched for orang-utan nests from either side of the aircraft while a third person recorded all of these sightings.

In each PSU, the length of aerial transects flown over unsuitable orang-utan habitat (large areas with no trees and/or no nests, such as open swamps, oxbow lakes, grasslands and large gaps in the forest) was calculated and divided by the total length of aerial transects to obtain the proportion of unsuitable habitat.

RESULTS

Results from ground line-transects

A total of 1952 orang-utan nests was recorded along 128 line transects (total length 120.6 km): see Table 1. The mean effective strip-width was 22.4 m (Fig. 2) and our ground sampling effort ranged between 0.33% (PSU 11) and 2.26% (PSU 4) with an average of 1.04% for all PSUs.

Estimation of the size of suitable orang-utan habitat from aerial surveys

Helicopter surveys were conducted over 37 lines (totalling 293 km) with an average strip width of about 300 m, giving a total survey effort of 8.6–19.7% (mean: 16.9%) depending on the PSU. Our aerial estimations showed that about 41 300 ha (or 79.4% of the 52 000 ha of forests identified on maps) was suitable for orang-utans (Table 2): 24 000 ha in the Sanctuary (89% of 27 000 ha), 8750 ha in VJFRs (58% of 15 000 ha) and 8500 ha in state and private lands (85% of 10 000 ha). Aerial and ground observations provided a broad classification of the different sampling areas: undisturbed (Gomantong and Pangui VJFRs), disturbed (lots 1, 2, 3, 4, 5, 6 and 10b) and heavily disturbed (lots 7, 8, 9 and 10a).

Estimates of density and orang-utan population size

Orang-utan densities varied from 0.7 (0.3–1.6) individuals/km^2 (PSU 8) to 6.0 (3.9–9.2) individuals/km^2 (lot 1 of the Sanctuary, included in PSU 1): Table 2. Densities differed significantly between the different PSUs (Kolmogorov–Smirnov test for normality: $t = 7.12$, $df = 14, p < 0.001$). These differences were not correlated with PSU's size (spearman correlation test $r_s = -0.09$, $p = 0.75$) but a multiple comparison (Siegel & Castellan, 1988) between the PSUs located downriver (PSUs 1–3: mean = 4.1), upriver (PSUs 8, 9, 10A and 10B: mean = 1.6) and in between (PSUs 4–7: mean = 2.5) showed a significant difference between downriver and upriver. No significant difference was recorded between the left and the right side of the river (PSUs 1, 3, 6 and 9 against other PSUs: Wilcoxon test, $p = 0.81$).

Kruskal–Wallis multiple comparisons showed that orang-utan densities were significantly higher in undisturbed forests (mean = 3.23) and disturbed forests (mean = 3.51) than in heavily disturbed forests (mean = 1.36): $p = 0.016$ (Table 3). A significant difference was also found when primary and disturbed forests were pooled and tested against heavily disturbed forests (Wilcoxon test; $p = 0.004$).

The estimated size of the orang-utan population living in the whole of Lower Kinabatagan floodplain was 1125 individuals (691–1807): Table 2. A total of 898 orang-utans was found in protected forests (670 in the Sanctuary and 228 in the Forest Reserves) while 227 individuals were found in non-protected forests (Fig. 1).

DISCUSSION

Limitation of line-transect methodology

Unlike strip-transects, line-transect methodology allows for some objects to go undetected without inducing major biases in the final density estimates (Burnham *et al.*, 1980) and this methodology is widely used for censusing

Table 2. Nest and orang-utan densities, estimation of suitable orang-utan habitat size and mean orang-utan population size for all PSUs identified during the 2001 Kinabatangan census

PSU	Nest density† (S.E.)	Orang-utan density (95% C.I.)	Size of suitable habitat (km^2)	Population size (95% CI)
PSU 1				
Lot 1 KWS	775.3 (144.4)	6.0 (3.9–9.2)	21.33	128 (87–189)
State land	439.8 (84.8)	3.4 (2.2–5.3)	30	102 (68–153)
Total PSU 1			**51.33**	**230 (155–342)**
PSU 2				
Lot 2 KWS	664.8 (185.6)	5.0 (2.8–8.9)	29.53	148 (86–260)
Private lands			7	35 (20–62)
KOCP Study site	1149.9 (188.5)	5.5 (3.8–7.9)	4	22 (16–31)
Kerouak FR*	–	2*	2	4
Total PSU 2			**42.53**	**209 (126–357)**
PSU 3				
Lot 3 KWS	290.1 (91.1)	1.9 (1.0–3.6)	21.83	42 (22–79)
Private lands			5	10 (5–18)
Pangui FR	415.1 (65.1)	2.6 (1.8–3.7)	4.36	11 (8–16)
Total PSU 3			**31.19**	**63 (35–113)**
PSU 4				
Lot 4 KWS	433.0 (65.1)	3.1 (2.2–4.5)	13.23	41 (30–57)
Private lands			5	15 (11–21)
Bod Tai FR*	–	2*	2.50	5
Total PSU 4			**20.73**	**61 (46–83)**
PSU 5				
Lot 5 KWS	310.5 (96.1)	2.1 (1.1–3.5)	70.13	146 (77–266)
Gomantong FR	592.5 (84.1)	3.8 (2.8–5.4)	38.20	147 (107–199)
Total PSU 5			**108.33**	**293 (184–465)**
PSU 6				
Lot 6 KWS	308.6 (75.9)	2.1 (1.3–3.6)	25.78	55 (33–90)
PSU 7				
Lot 7 KWS	185.8 (47.4)	1.3 (0.8–2.2)	8.50	11 (7–18)
Pin Supu FR			8.89	12 (7–19)
Total PSU 7			**17.39**	**23 (14–37)**
PSU 8				
Lot 8 KWS	87.5 (38.4)	0.7 (0.3–1.6)	12.01	8 (4–19)
Private lands			4.00	3 (1–6)
Pin Supu FR			15.60	11 (5–25)
Total PSU 8			**31.61**	**22 (10–50)**
PSU 9				
Lot 9 KWS	209.0 (45.8)	1.6 (1.0–2.6)	10.52	17 (10–26)
Private lands			20.00	32 (20–50)
Total PSU 9			**30.52**	**49 (30–76)**
PSU 10				
Lot 10a KWS	283.5 (73.9)	1.8 (1.1–3.1)	6.88	12 (8–21)
Private lands			6.00	11 (7–19)
Total PSU 10			**12.88**	**23 (15–40)**
PSU 11				
Lot 10bc KWS	360.7 (124.8)	2.4 (1.2–4.8)	16.75	40 (20–80)
Private lands			7.78	19 (9–37)
Segaliud FR			16.00	38 (19–77)
Total PSU 11			**40.53**	**97 (48–194)**
KWS (total size: 274,4 km^2)			240.5	670 (404–1105)
Private/State Land (total size:123 km^2)			84.8	227 (141–366)
Forest Reserves (total size:119,7 km^2)			87.5	228 (146–336)
Total all PSUs (total size: 517,1 km^2)			**412.8**	**1125 (691–1807)**

* Some Virgin Jungle Forest Reserves (VJFRs) were not surveyed from the ground and estimates available from the literature were used for the calculations (Payne & Davies, 1987).

† With all models found to fit the data ($p > 0.1$).

Abbreviations used: PSU, primary sampling unit; S.E., standard error; CI, confidence interval; KWS, Kinabatangan Wildlife Sanctuary; KOCP, Kinabatangan Orangutan Conservation Project; FR, forest reserve.

Table 3. Orang-utan densities documented at different lowland locations (below 500 m above sea level) in Sumatra and Borneo

Site	Forest type	Density	Author
Sumatra			
Suaq Balimbing	FWSF–PSF*	6.9	Van Schaik *et al*., 1995*a*,*b*
Sikundur	SILF disturbed	1.4	
	DLF disturbed	1.2	
Pucuk Lembang	SILF disturbed	0.7	
Manggala	DLF*	1.2	
Ketambe	DLF*	5.2	
Ketambe	DLF*	6.6	Rao & van Schaik, 1997
	DLF disturbed	2.6	
Kalimantan (Borneo)			
Danau Sentarum	FWSF–PSF disturbed	3.3	Russon *et al*., 2001
Berau	DLF*	2.0 (CI: 1.6–2.5)	Marshall, 2002
Sebangau	PSF*	2.4 (CI: 1.8–3.0)	Morrogh-Bernard *et al*., 2003
	PSF disturbed	4.2 (CI: 2.6–5.8)	
	PSF heavily disturbed	1.1 (CI: 0.7–1.5)	
Gunung Palung	PSF*	4.1 (3–5.5)	Johnson *et al*., 2004
	PSF disturbed	3.2 (2.7–3.7)	
	DLF*	3.2 (2.7–3.8)	
	DLF disturbed	3.0 (2.3–3.9)	
Sabah (Borneo)			
Ulu Segama	DLF*	1.5	McKinnon, 1972
	DLF*	0.3	Johns, 1989
	DLF disturbed	0.5–2.1	
Kinabatangan	SILF*	2.0	Payne & Davies, 1987
	SILF disturbed	2.0	Sharma, 1992
	SILF*	3.2 (CI: 2.3–4.5)	This study
	SILF disturbed	3.5 (CI: 2.2–5.7)	
	SILF heavily disturbed	1.4 (CI: 0.8–2.4)	

* indicates undisturbed habitat; FWSF, Fresh Water Swamp Forest; PSF, Peat Swamp Forest; SILF, Semi-Inundated Lowland Forest; DLF, Dry Lowland Forest; CI, confidence intervals.

large forest-dwelling species. However, a few major assumptions must be met to obtain valid density estimates, namely: random location of straight transects, detection of all objects located on or above the transects, no measurement error and independence of sighting events (Anderson *et al*., 1979). Great ape nests are unevenly distributed in space and through time in the forest (Furuichi, Hashimoto & Tashiro, 2001; Buij *et al*., 2002) and inappropriate stratification can produce seriously distorted density estimates (Cassey & McArdle, 1999). During our surveys, particular emphasis was given to cutting straight, randomly located transects, running approximately perpendicular to the main rivers in order to reduce between-transect variation. A combination of straight and recce transects is an alternative approach to increase survey efforts in large areas (Walsh & White, 1999).

Missing objects located above or close to the line-transects are a common problem in dense equatorial forests and this potentially underestimates true densities (Singleton, 2000). Properly trained surveyors will minimise but not eradicate this source of bias. A second count of the same transects is one way to estimate the fraction of nests that goes undetected during a single survey (Ghiglieri, 1984; Buij *et al*., 2003; Johnson *et al*., 2004). Outliers and heaping are other common biases in multi-layer tropical forests (Singleton, 2000). Empirically, outliers are defined as being the 5 or 10% most extreme values of a full data set (Buckland *et al*., 1993). In our survey, outliers were identified objectively using boxplots, giving the level of truncation to be applied to each PSU (from 0% to 16%). Heaping was overcome by using manual grouping of values when necessary (Crain, 1998). Finally, bootstrapping allowed all parsimonious and competitive models to contribute to the final determination of nest density confidence intervals, providing a robust statistical method of determining confidence limits for our final estimates (Burnham & Anderson, 1998).

Precise determination of multiplier values

The proportion of nest builders, $\hat{p}$, is similar between orang-utan populations and ranges from 0.85 (Ancrenaz *et al*., 2004*a*) to 0.9 (Sumatra: van Schaik *et al*., 1995*a*; Singleton, 2000). Values for the parameters $\hat{r}$ and $\hat{t}$ are available only for a few ape populations and show wide variation between sites. For orang-utans, the published values for $\hat{r}$ are around 1.0 (Ancrenaz *et al*., 2004*a*) and 1.2 (Johnson *et al*., 2004) in Borneo, and 1.7 in Sumatra (Singleton, 2000), suggesting that Bornean orang-utans build fewer nests. Use of the two extreme values, 1.0 and 1.7, gives a 59% difference in the final density estimates.

Thus, it appears essential to use $\hat{r}$ values that are specific for each island.

In Sumatra, statistical models such as Markov chains have been proposed for generating orang-utan nest decay rate based on temperature and altitude (van Schaik *et al.*, 1995*a*), or pH (Buij *et al.*, 2003) but their validity for Borneo needs further investigation (Johnson *et al.*, 2004). Recent studies have shown that a logistic regression may achieve a robust estimate of decay rate as a function of time with a single follow-up visit of the nests, making possible the determination of site-specific nest decay rates (Laing *et al.*, 2003). In the Kinabatangan, mean nest life-span was significantly influenced by nesting tree species (Ancrenaz *et al.*, 2004*a*). An average weighted $\hat{t}$ based on taxa-specific nest decay rates could be used for orang-utan nest surveys. Average weighted $\hat{t}$ values are commonly used in Africa with five different types of chimpanzee and gorilla nests being distinguished during nest surveys (Tutin & Fernandez, 1984; Blom *et al.*, 2001).

Extrapolation of densities to population size

In most surveys with large forest-dwelling species, the overall sampling effort is well below 0.5% of potential habitat (see Table 4 for ape censuses) and it tends to decrease with an increase in the range of the population under study. Extremely small sampling effort can introduce strong biases unless sampling is representative of the general population to be sampled, which is frequently unknown. At 1.04%, our average sampling effort is the highest documented so far for ape-nest censuses, but this required more than 450 man days of fieldwork to cover a relatively small area (52 000 ha). Larger and more inaccessible areas will require even greater investment of human and time resources, and frequently this is impossible.

The size of habitat occupied by a population is generally extrapolated from existing maps that do not reflect variations of density that occur within a given habitat type and do not show the impact of poaching and other human disturbance (Rijksen *et al.*, 1995). To compensate for these imprecisions, a 'safety' factor was determined empirically for orang-utans: 0.60 for Borneo (Rijksen *et al.*, 1995) and 0.75 for Sumatra (van Schaik *et al.*, 1995*b*). The use of this correction factor would result in an underestimate of the current Kinabatangan orang-utan population size by about 20%. This illustrates the need for developing more refined census methodologies in order to estimate more precisely ape population sizes.

Aerial surveys provide an alternative to empirical correction factors and are of special interest in areas that are difficult to survey from the ground (Caughley, 1974). In the Kinabatangan, the use of a helicopter increased our sampling effort from 1.04% (ground census) to 16.9% and showed that 21% of the forests identified as potential orang-utan habitat from updated digitalised maps were, in fact, not suitable habitat. In addition to precise orang-utan distribution assessment, helicopter surveys also provided an efficient way to estimate nest density over

Table 4. Sampling effort (ratio between sampled area and estimated size of the population range) of several ape surveys using nest-count along line-transects

Location	Author	Species	Size of the population range (km^2)	Transect			ESW (m)	Sampled area (km^2)	Sampling effort (%)
				Random	Number	Tot. L. (km)			
Gabon	Tutin & Fernandez, 1984	Gorilla	6066	Yes	n.a.	615.8	n.a.	12.81	0.211
		Chimpanzee						21.13	0.348
Ivory Coast	Marchesi *et al.*, 1995	Chimpanzee	22 936	n.a.	n.a.	154.4	20	6.18	0.027
Kalinzu, Uganda	Hashimoto, 1995	Chimpanzee	137	n.a.	8	19.8	13.1	0.52	0.379
Salonga NP Congo	van Krunkelsven, 2001	Bonobo	18 280	Yes	3	7.5	25	0.37	0.002
Danau Sentarum, Borneo	Russon *et al.*, 2001	Orang-utan	1900	No	17	15.75	16	0.50	0.026
Berau, Borneo	Marshall, 2002	Orang-utan	1400	Yes	n.a.	93.5	22.4*	3.85	0.299
Sebangau, Borneo	Morrogh-Bernard *et al.*, 2003	Orang-utan	7300	Yes	n.a.	17.23	22.4*	0.71	0.011
Kinabatangan, Borneo									
Ground census	This study	Orang-utan	520	Yes	128	120.6	22.4	4.97	1.044
Aerial census				Yes	37	293	150	87.9	16.9

* When effective strip width (ESW) was not available, we applied the value of 22.4 m determined during the Kinabatangan census.

Abbreviations used: NP, National Park; n.a., not available; Tot. L., total length.

the entire range of the species in Sabah (Ancrenaz *et al.*, 2004*b*). Helicopter censuses may be useful for documenting the current distribution and abundance of other ape populations. However, two major problems might arise with an aerial census of African apes: (1) gorilla nests are usually low in the canopy and are likely to be difficult to detect from a helicopter (Blom *et al.*, 2001; Yamagiwa, 2001); (2) it may be impossible to distinguish between gorilla and chimpanzee nests where the two species are sympatric (Tutin & Fernandez, 1984; Blom *et al.*, 2001).

The value of the degraded forests of the Kinabatangan for orang-utan survival

Orang-utans have been known to occur in the Lower Kinabatangan floodplain since the 1960s (Haile, 1963; MacKinnon, 1971; Horr, 1975) and we estimate today that the 52 000 ha of remaining disturbed forests are home to about 1100 individuals. The current orang-utan abundance in these patches of disturbed habitat results from recent habitat losses and consecutive concentration of the population in the remaining forests (Rijksen & Meijaard, 1999). Only long-term ecological studies will document the extent to which orang-utans can adapt to drastic habitat changes and whether the disturbed forests of the Kinabatangan are suitable for their long-term survival.

Our study yielded mean orang-utan densities (0.7–3.2 individuals/km^2) that were in the range reported previously for Kinabatangan (Payne, 1988; Sharma, 1992) and for Borneo (see Table 3). Densities were higher in the lower parts of the Kinabatangan floodplain where the habitat is generally less disturbed than in the upper parts, indicating that heavy habitat disturbance has a negative impact on orang-utan densities.

Most of the data published so far indicate that orang-utans adapt poorly to habitat disturbance (e.g. Rao & van Schaik, 1997; Rijksen & Meijaard, 1999). However, several authors have documented higher ape densities in old disturbed habitats than in undisturbed forests (orang-utans: Payne, 1988; Johns, 1989; Russon, Erman & Dennis, 2001; gorillas: Blom *et al.*, 2001; chimpanzees: Hashimoto, 1995). Other studies found no clear correlation between signs of human disturbances and ape density (Johns & Skorupa, 1987; Plumptre & Reynolds, 1994; Onderdonk & Chapman, 2000; McNeilage *et al.*, 2001; Plumptre & Johns, 2001) or reported that apes may move away from active disturbance and return once it is over (MacKinnon, 1971; Morrogh-Bernard *et al.*, 2003).

In fact, much may depend on the forest types that existed initially (Plumptre & Reynolds, 1994) and a mosaic of lowland habitats, such as that of the Lower Kinabatangan floodplain, which has been defined as the best primary type of habitat for orang-utans (Leighton *et al.*, 1995), could potentially still harbour significant numbers of orang-utans following heavy disturbance of the ecosystem. Ultimately, the level of hunting is most probably the prime factor determining the survival of many animal species in exploited forests rather than the disturbance of the habitat *per se* (Robinson & Bennet, 2000; Fimbel, Grajal & Robinson, 2001). Illegal killing for bushmeat or for the pet trade is frequently associated with logging and is the main driving force to local extinction of apes in logged forests (Haile, 1963; Hashimoto, 1995; Leighton *et al.*, 1995). The very low hunting pressure affecting apes and other non-human primates in the Kinabatangan (KOCP, unpublished data) is probably the main reason accounting for orang-utan survival in the multiple-use forests of the floodplain.

CONCLUSION

Precise and robust estimates of orang-utan densities were obtained in the disturbed forests of the lower Kinabatangan floodplain by strictly complying with the ground line-transect methodology. These estimates, combined with results of aerial surveys that gave the exact distribution of orang-utans, provided precise knowledge of the size of this population. Helicopter surveys appear to be a promising tool to help determine the status of remnant wild ape populations, as well as monitoring population trends over time in Asia and potentially in Africa.

With approximately 1100 individuals, the multiple-use forests of the Kinabatangan suggest that the value of certain types of disturbed forests for orang-utan conservation in Sabah should not be underestimated. However, only long-term studies will reveal whether the results documented in Kinabatangan can be extrapolated to other orang-utan populations surviving in degraded forests, and to what extent great ape species are able to adapt to habitat disturbance over the long-term.

Acknowledgements

For permission to work in Sabah we are grateful to the Economic Planning Unit, to Patrick Andau, Director of the Sabah Wildlife Department, staff of the Department, and the partners providing financial support to KOCP: Apenheul Zoo, Bos-USA, Bush Gardens, Brookfield Zoo, Chester Zoo, Cleveland Metroparks, Columbus Zoo, Darwin Initiative-UK, Dierenpark, Disney's Animal Kingdom Conservation Fund, Lincoln Park Zoo, National Geographic Society, Pittsburgh Zoo, US Fish & Wildlife Service, WWF (Malaysia, Netherlands, UK, USA), Zooparc de Beauval, Zoo La Palmyre and several other private sources. We would also like to thank L. Chikhi, J. Setchell, S. Buckland and anonymous reviewers for their useful comments on the manuscript. Last but not least, the KOCP would not exist without the commitment of the 30 research assistants employed by the project who are dedicated to conserve the natural resources of the Kinabatangan floodplain and we are extremely grateful to all of them.

REFERENCES

Ancrenaz, M., Calaque, R. & Lackman-Ancrenaz, I. (2004*a*). Orang-utan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. *Int. J. Primatol*. **25**. (In press)

Ancrenaz, M., Gimenez, O., Ambu, L., Ancrenaz, K., Andau, P., Goossens, B., Payne, J., Sawang, A., Tuuga, A. & Lackman-Ancrenaz, I. (2004*b*). Aerial surveys give new estimates for orang-utans in Sabah, Malaysia. *PLOS-Biol.* In press.

Anderson, D. R., Laake, J. L., Crain, B. R. & Burnham, K. P. (1979). Guidelines for line transect sampling of biological populations. *J. Wildl. Mgmt*. **43**: 70–78.

Azmi, R. (1998). *Natural vegetation of the Kinabatangan floodplain. Part 1: background and preliminary checklist. Report*. Kota Kinabalu, Sabah: WWF-Malaysia.

Blom, A., Almasi, A., Heitkonig, I. M. A., Kpanou, J.-B. & Prins, H. H. T. (2001). A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: a comparison between the census and survey methods of estimating the gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes*) nest group density. *Afr. J. Ecol*. **39**: 98–105.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. (1993). *Distance sampling: estimating abundance of biological populations*. London, UK: Chapman & Hall.

Buij, R., Wich, S. A., Lubis, A. H. & Sterck, E. H. M. (2002). Seasonal movements in Sumatran orang-utan (*Pongo pygmaeus abelii*) and consequences for conservation. *Biol. Conserv*. **107**: 83–87.

Buij, R., Singleton, I., Krakauer, E. & van Schaik, C. P. (2003). Rapid assessment of orangutan density. *Biol. Conserv*. **114**: 103–113.

Burnham, K. P. & Anderson, D. R. (1998). *Model Selection and Inference: a Practical Information Theoretic Approach*. New York: Springer.

Burnham, K. P., Anderson, D. R. & Laake, J. L. (1980). Estimation of density from line transect sampling of biological populations. *Wildl. Monogr*. **72**: 1–202.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. P. (1987). *Design and analysis methods for fish survival experiments based on release–recapture*. Bethesda, Maryland, USA: American Fisheries Society Monograph **5**.

Cassey, P. & McArdle, B. H. (1999). An assessment of distance sampling techniques for estimating animal abundance. *Environmetrics* **10**: 261–278.

Caughley, G. (1974). Bias in aerial survey. *J. Wildl. Mgmt*. **38**: 921–933.

Crain, B. R. (1998). Some comments on line transect grouped data analysis. *Ecol. Model*. **109**: 243–249.

Felton, A. M., Engstrom, L. M., Felton, A. & Knott, C. D. (2003). Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol. Conserv*. **114**: 91–101.

Fimbel, R. A., Grajal, A. & Robinson, J. G. (2001). *The cutting edge: conserving wildlife in logged tropical forests*. New York: Columbia University Press Book.

Furuichi, T., Hashimoto, C. & Tashiro, Y. (2001). Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees. *Int. J. Primatol*. **22**: 913–928.

Ghiglieri, M. P. (1984). *The Chimpanzees of Kibale Forest*. New York: Columbia University Press.

Haile, N. S. (1963). Orang–human co-existence in north Borneo. *Sarawak Mus. J*. **11**: 259–261.

Hashimoto, C. (1995). Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. *Primates* **36**: 477–488.

Horr, D. A. (1975). The Bornean orang-utan: population structure and dynamics in relationship to ecology and reproductive strategy. *Primate Behav*. **4**: 307–323.

Johns, A. D. (1989). *Timber, the environment and wildlife in Malaysian rainforests*. Report to ODA/NERC project F3CR26/G1/o5. Aberdeen: Institute of South-east Asian Biology.

Johns, A. D. & Skorupa, P. (1987). Responses of rain-forest primates to habitat disturbance: a review. *Int. J. Primatol*. **8**: 157–187.

Johnson, A. E., Knott, C. D., Pamungkas, B., Pasaribu, M. & Marshall, A. J. (2004). A survey of the orangutan (*Pongo pygmaeus pygmaeus*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. *Biol. Conserv.* In press.

Koster, S. H. & Hart, J. A. (1988). Methods of estimating ungulate populations in tropical forests. *Afr. J. Ecol*. **26**: 117–126.

van Krunkelsven, E. (2001). Density estimation of bonobos (*Pan paniscus*) in Salonga National Park, Congo. *Biol. Conserv*. **99**: 387–391.

Laing, S. E., Buckland, S. T., Burn, R. W., Lambie, D. & Amphlett, A. (2003). Dung and nest survey: estimating decay rates. *J. Appl. Ecol*. **40**: 1102–1111.

Leighton, M., Seal, U. S., Soemarna, K., Adjisasmito, Wijaya, M., Mitra Setia, T., Shapiro, G., Traylor-Holzer, K. & Tilson, R. (1995). Orang-utan life history and vortex analysis. In *The neglected ape*: 97–107. Nadler, R. D., Galdikas, B. F. M., Sheeran, L. K. & Rosen, N. (Eds). New York: Plenum Press.

MacKinnon, J. R. (1971). The orang-utan in Sabah today. *Oryx* **11**: 141–191.

MacKinnon, J. R. (1972). *The behaviour and ecology of the orang-utan, **Pongo pygmaeus**, with relation to other apes*. PhD thesis: Oriel College, Oxford.

MacKinnon, J. R. (1987). Conservation status of primates in Malaysia with sepecial reference to Indonesia. *Prim. Conserv*. **6**: 175–183.

Marchesi, P., Marchesi, N., Fruth, B. & Boesch, C. (1995). Census and distribution of chimpanzees in Cote d'Ivoire. *Primates* **36**: 591–607.

Marshall, A. J. (2002). *Summary of orang-utan surveys conducted in Berau District, East Kalimantan*. Report. Samurinda, Indonesia. The Nature Conservancy.

McNeilage, A., Plumptre, A. J., Brock-Doyle, A. & Vedder, A. (2001). Bwindi Impenetrable National Park, Uganda: gorilla census 1997. *Oryx* **35**: 39–47.

Morrogh-Bernard, H., Husson, S., Page, S. E. & Rieley, J. O. (2003). Population status of the Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. *Biol. Conserv*. **110**: 141–152.

Onderdonk, D. A. & Chapman, C. A. (2000). Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *Int. J. Primatol*. **21**: 587–611.

Payne, J. (1988). *Orang-utan conservation in Sabah*. WWF-Malaysia International, Report 3759 Kuala Lumpur, Malaysia: WWF-Malaysia International.

Payne, J. & Davies, G. (1987). *A faunal survey of Sabah*. IUCN/WWF Malaysia project 1692. Kuala Lumpur, Malaysia: IUCN/WWF Malaysia.

Plumptre, A. J. & Johns, A. G. (2001). Changes in primate communities following logging disturbance. In *The cutting edge: conserving wildlife in logged tropical forests*: 71–92. Fimbel, R. A., Grajal, A. & Robinson, J. G. (Eds). New York: Columbia University Press.

Plumptre, A. J. & Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol*. **31**: 631–641.

Rao, M. & van Schaik, C. P. (1997). The behavioral ecology of Sumatran orangutans in logged and unlogged forest. *Trop. Biodivers*. **4**: 173–185.

Rijksen, H. D. & Meijaard, E. (1999). *Our vanishing relative*: *the status of wild orang-utans at the close of the twentieth century.* Dordrecht, The Netherlands: Tropenbos Foundation, Kluwer Academic Publishers.

Rijksen, H. D., Ramono, W., Sugardjito, J., Lelana, A., Leighton, M., Karesh, W., Shapiro, G., Seal, U. S., Traylor-Holzer, K. & Tilson, R. (1995). Estimates of orang-utan distribution and status in Borneo. In *The neglected ape*: 117–121. Nadler, R. D., Galdikas, B. F. M., Sheeran, L. K. & Rosen, N. (Eds). New York: Plenum Press.

Robinson, J. G. & Bennett, E. L. (2000). *Hunting for sustainability in tropical forests*. New York: Columbia University Press.

Russon, A. E., Erman, A. & Dennis, R. (2001). The population and distribution of orangutans (*Pongo pygmaeus pygmaeus*) in and around the Danau Sentarum Wildlife Reserve, West Kalimantan, Indonesia. *Biol. Conserv*. **97**: 21–28.

van Schaik, C. P., Priatna, A. & Priatna, D. (1995*a*). Population estimates and habitat preferences of orangutans (*Pongo pygmaeus*) based on line transects of nests. In *The neglected ape*: 129–147. Nadler, R. D., Galdikas, B. F. M., Sheeran, L. K. & Rosen, N. (Eds). New York: Plenum Press.

van Schaik, C. P., Poniran, S., Utami, S., Griffiths, M., Djojosudharmo, Setia, M., Sugardjito, J., Rijksen, H. D., Seal, U. S., Faust, T., Traylor-Holzen, K. & Tilson, R. (1995*b*). Estimates of orang-utan distribution and status in Sumatra. In *The neglected ape*: 109–122. Nadler, R. D., Galdikas, B. F. M., Sheeran, L. K. & Rosen, N. (Eds). New York: Plenum Press.

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. 2nd edn. London: Charles Griffin and Company Ltd.

Sharma, D. (1992). *A wildlife survey of the proposed Kinabatangan park, Sabah*. WWF-Malaysia report. Petaling Jaya, Malaysia: WWF-Malaysia.

Siegel, S. & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences*. 2nd edn. New York: McGraw-Hill.

Singleton, I. (2000). *Ranging behaviour and seasonal movements of Sumatran orangutans* (***Pongo pygmaeus abelii***) *in swamp forests*. PhD Thesis: University of Kent at Canterbury, UK.

Thomas, L., Laake, J. L., Derry, J. F., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Strindberg, S., Hedley, S. L., Burt, M. L., Marques, F. F. C., Pollard, J. H. & Fewster, R. M. (1998). *Distance 3.5*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available: http://www.ruwpa.st-and.ac.uk/distance/

Tutin, C. E. G. & Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla. g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am. J. Primatol*. **6**: 313–336.

Tutin, C. E. G., Parnell, R. J., White, L. J. T. & Fernandez, M. (1995). Nest building by lowland gorillas in the Lope Reserve, Gabon: environmental influences and implications for censusing. *Int. J. Primatol*. **16**: 53–76.

Yamagiwa, J. (2001). Factors influencing the formation of ground nests by eastern lowland gorillas in Kahuzi-Biega National Park: some evolutionary implications of nesting behaviour. *J. Human Evol*. **40**: 99–109.

Walsh, P. D. & White, L. J. T. (1999). What will it take to monitor forest elephant populations? *Conserv. Biol*. **13**: 1194–1202.