

A comparison of orang-utan density in a logged and unlogged forest on Sumatra

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Abstract

Several studies have shown that there is a strong decline in orang-utan densities shortly after logging. Nevertheless, there is little information on whether orang-utan densities return to their pre-logging values when logged forest is left to recover. This study investigates the orang-utan density in a 22-year-old selectively logged forest and compares it with the orang-utan density in a nearby ecologically similar primary forest. The results show that the orang-utan density did not differ significantly between primary forest and the selectively logged forest. Since we found no difference in fruit availability between the selectively logged and primary forest, we suggest that the selectively logged forest regenerated sufficiently well to sustain pre-logging levels of orang-utans. This study confirms previous studies that suggest fruit availability is the best ecological predictor of orang-utan densities and found a positive overall correlation between orang-utan density and fruit availability. The food attraction hypothesis, which explains local fluctuations in orang-utan density as a result of variation in fruit availability, was not supported.

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1. Introduction

The Sumatran orang-utan, *Pongo abelii*, is currently listed on the IUCN Red List of Threatened Species as critically endangered (Hilton-Taylor and Brackett, 2000). It is thought that at present at least 1000 Sumatran orang-utans are lost each year from the island of Sumatra, mainly due to habitat loss and illegal trade in animals (Wich et al., 2003). This trend had reduced the total number of Sumatran orang-utans at the end of 2002 to around 3500 individuals spread over several forest fragments (Wich et al., 2003). Thus, without more intensive protection the Sumatran orang-utan is doomed to be ecologically extinct within less than a decade.

The major threat to the survival of the Sumatran orang-utan is habitat loss as a result of legal and illegal

logging and conversion of forest into plantations (Rijksen and Meijaard, 1999; Robertson and van Schaik, 2001; van Schaik et al., 2001). Even though selective logging operations are less detrimental for orang-utans than the conversion of forest into plantations, they are known to reduce orang-utan density in an area dramatically (Engström, 2000; Rao and van Schaik, 1997; Wich, unpublished data).

Since orang-utans are mainly frugivorous, fruit is known to be the best ecological predictor of orang-utan density across its habitats (van Schaik et al., 1995). Under normal conditions, more than 60% of the diet of orang-utans consists of fruit (Galdikas, 1988; MacKinnon, 1977). Orang-utans also eat leaves and shoots, bark, flowers and insects (Djojosedharmo and Schaik, 1992; Rodman, 1988). These additional resources are particularly important during periods of temporary low food availability (Knott, 1998; Rijksen and Meijaard, 1999). Nevertheless, a lower level of fruit availability as a result of logging operations (Grieser Johns and Grieser Johns, 1995; Johns, 1991; Struhsaker, 1997; Wheatly,

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1982) is thought to be the main reason for the decline in orang-utan density in a logged forest (Rao and van Schaik, 1997).

In addition to fruit availability, Engström (2000) found that an increase in the extent of gaps in the forest was related to a reduction in orang-utan density in logged forest. She suggested that this relationship was a result of higher predation on orang-utans due to them having to build nests at lower heights in logged forest than in primary forest. Additionally, more gaps in the logged forest increase the energy expenditure of orang-utans spent for locomotion since they are forced to travel more (Engström, 2000; Rao and van Schaik, 1997).

There are several studies on orang-utan densities in forests where logging operations have just taken place (Engström, 2000; Payne, 1987; Rijksen, 1978; van Schaik et al., 1995). All these studies indicate a reduction in orang-utan density. However, there is no information on whether orang-utan density increases again once a logged forest is left to regenerate. We therefore conducted a study in which we estimated orang-utan density in a selectively logged forest that was left undisturbed for 22 years. We assumed that the orang-utan density was lower directly after logging (Rijksen, 1978). To assess pre-logging density, we estimated orang-utan density in a primary forest that was near the logged forest and in a similar habitat.

In addition to orang-utan density, fruit-availability and some forest structure parameters were investigated to determine whether they influence density. We expected fruit-availability to have a positive influence on orang-utan density (Blouch, 1994; Buij et al., 2002; van Schaik et al., 1995). The extent of gaps was taken as a forest structure parameter, and it was expected that this would influence the orang-utan density negatively (Blouch, 1994; Engström, 2000). Canopy roughness is another characteristic for the assessment of forest conditions (Brockelman, 1998). It was therefore taken as another forest structure parameter and was expected to influence the density positively.

2. Methods

2.1. Study site

The study was conducted in the Sekundur area in the east of the Gunung Leuser National Park, Leuser Eco-system, Sumatra, Indonesia.

The Sekundur area (located at an altitude of 30–100 m above sea level) consists of diverse mixed dipterocarp lowland forests with rich alluvial forest along the rivers (de Wilde and Duyfjes, 1996). Our study areas were located in pristine forest and in forest that was mechanically logged at the end of the seventies, and then

left untouched to recover. During the logging operations, which ended in 1978, an average of 11 large trees per hectare were felled. Five years after the logging operations Abdulhadi et al. (1987) found that 54% of the remaining trees still showed some sort of damage caused by the logging operations. All research in the selectively logged forest was conducted along the Besitang river (3°58'N/98°05'E) (Fig. 1). The studies in the pristine forest were conducted further up the Besitang river. Two flying camps were established there; one around the junction of the river Besitang with the river Sei Badak (3°51'N/98°02'E) and one deeper into the

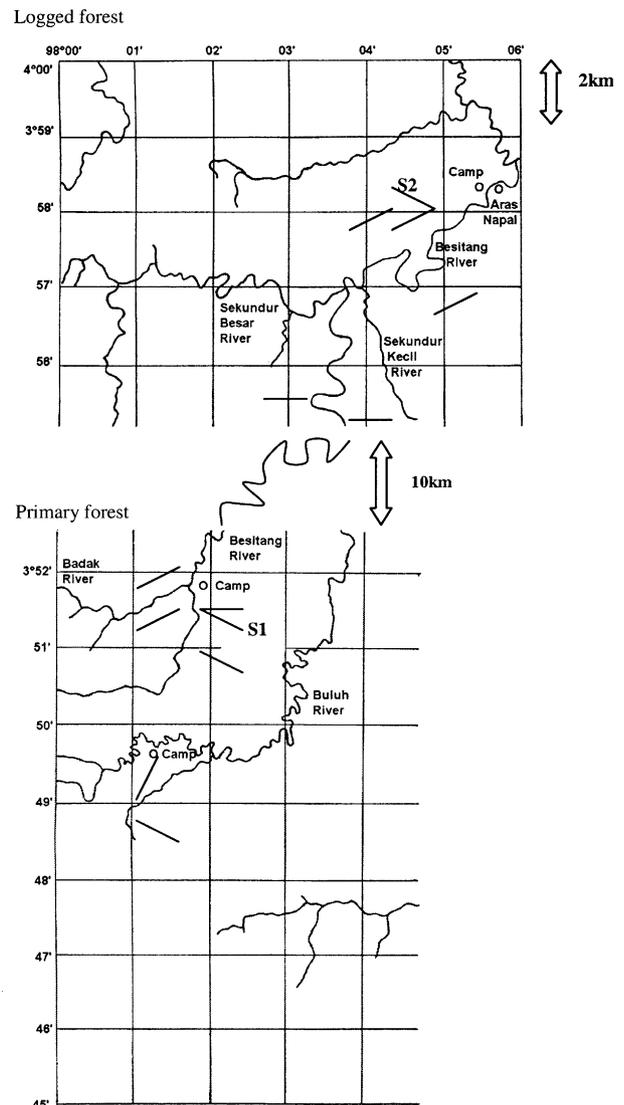


Fig. 1. Maps of the primary and logged forest study sites in the Sekundur area. The primary forest study site was about 10 km further up the Besitang river from the logged forest study site. S1 was the transect for the seasonal movement estimates of orang-utans in the primary forest, S2 was the transect for the seasonal movement estimates of orang-utans in the logged forest. Remaining straight lines are transects in the primary forest and logged forest study site.

forest (3°49'N/98°01'E) (Fig. 1). Each of the two study areas was around 100 km² in extent.

2.2. Plot sampling design

Transects were cut in four different sub-sites in the primary forest and in five different sub-sites in the logged forest. All sub-sites were separated by fairly large rivers that caused a gap in the forest canopy and can therefore be considered independent. The straight line transects in these sub-sites were placed randomly. Usually, transects were cut through the forest, but occasionally parts of existing man-made trails were used. All transects were measured and flagged every 100 m in order to locate the surveyed nests more precisely. In the nine sub-sites, a total of 11 new transects were cut. Nine transects were 1500 m long and used for the mean orang-utan density estimates (Fig. 1). Between March 2001 and May 2001, they were all surveyed at least once in order to obtain the data to compare orang-utan density, fruit availability and forest structure parameters of the two forest types. The remaining two of the 11 transects, one in the logged forest (S2) and one in the primary forest (S1), were both about 3000 m long (Fig. 1). From June 2000 until May 2001, these two transects were surveyed monthly, to investigate seasonal movements of orang-utans in the two forest types.

2.3. Estimation of orang-utan density

To estimate orang-utan density in both primary and logged forests, the line transect method was used (van Schaik et al., 1995). This method provides an estimate of orang-utan densities by first estimating nest densities and then converting them into orang-utan densities.

Orang-utan density is therefore estimated as follows:

$$D = N / (2 * L * w * r * p * t),$$

where D is the density (individuals per km²), N , the number of nests observed, L , the length of transect (km), w is the half the estimated strip width within which all nests should be detected (km), r , the daily nest building rate, p , the proportion of nest builders in the population and t , the number of days that nests remain visible. The parameters w and t were likely to vary between habitats, while p and r were not expected to vary greatly (van Schaik et al., 1995). Therefore, p and r were obtained from previous studies in similar habitat types (van Schaik et al., 1995) and taken as $p = 0.9$ and $r = 1.7$. To estimate w and t , the following two features were noted for each nest: the stage of decay of a nest, using five classes (van Schaik et al., 1995) and the perpendicular distance of the nest to the transect. After the orang-utan density had been estimated, the resulting data were checked for normality. This was done by using a Q-Q-plot, which plots the quantiles of a variable's distribu-

tion against the quantiles of the normal distribution (SPSS, 1999). We then tested whether the mean orang-utan densities differed in the two forest types.

2.3.1. Estimation of strip width (w)

To determine the strip width in both primary and logged forest, the perpendicular distances from the nests to the transects were used. It was expected that the distributions of perpendicular distances would be bell-shaped in both primary and logged forest, but not necessarily the same. This was tested with the Kolmogorov–Smirnov test. The statistical package SPSS 10.0 was used for all tests (SPSS, 1999). When the distributions were similar, the perpendicular distances of primary and logged forest were pooled, to increase accuracy. Extreme values and outliers were discarded (5%) (Burnham et al., 1980). The estimated strip width w was then estimated from a detection function fitted to the observed distribution of perpendicular line-to-nest distances, using the software program “Distance”, described in detail by Buckland et al. (1993). The program calculates the actual area (width) surveyed from the transects by correcting for the decline in detectability with increased distance from the transect (Burnham et al., 1980). For details of the application of this approach for orang-utan density estimates see Buij et al. (2003).

2.3.2. Estimation of nest decay rate (t)

To estimate t the transition matrix technique was used (van Schaik et al., 1995). This method relies on re-recording the stage of decay of nests of known initial stage of decay. This allowed the estimation of the rate of transition between stages of decay. The transitions were considered to represent a Markov chain with an absorbing state. This made it possible to calculate the expected number of steps it takes to reach the absorbing state and hence the mean duration of visibility, which could then be used to calculate the nest decay rate. The nest decay rates were then corrected by multiplying them by 0.85, as it is suggested by Buij et al. (2003).

2.4. Estimation of forest structure parameters and fruit availability

The number of fruit sources per kilometre was used as a parameter for fruit availability (van Schaik et al., 1995). During each nest survey, all fruits that had fallen onto the transect and were produced by different fruit sources were collected. To calculate the number of fruit sources per kilometre along the trail, only one fruit per fruit-producing tree was collected. The extent of gaps was measured by counting the number of gaps per kilometre: any opening in the canopy cover above the transect that was at least 5 m long was defined as a gap (Cannon et al., 1994). The total number of gaps along transects were counted, and the number of gaps

per kilometre was then calculated. Canopy roughness (R) was measured using the point-intercept method suggested by Brockelman (1998). This method provides a parameter of canopy roughness (R): if the canopy is completely flat, R will be 0 and if the canopy has a uniform distribution of heights, as it should be the case in an undisturbed forest, it will approach 1. Mann–Whitney U tests were performed, to determine whether the three parameters, the number of fruit sources per kilometre, the number of gaps per kilometre, and the roughness of canopy differed between the logged forest and the primary forest. Subsequently, an ANCOVA was carried out to estimate their influences on orang-utan density, with the above-mentioned three parameters as covariates. It was then tested whether the residuals meet the assumptions of analysis of covariance (Q–Q-plot, Levene’s test) (Levene, 1960; SPSS, 1999). Only the covariates that showed a significant influence on the orang-utan density in the ANCOVA were taken as predictor variables for further linear regressions.

2.5. Estimation of seasonal movements of orang-utans

Since orang-utan density can vary seasonally as a result of fruit availability (Buij et al., 2002) the monthly orang-utan density values of the two 3000-m-long transects were used to perform polynomial univariate regression analyses against the month of study. Seasonal variation in orang-utan density was expected for the primary forest since, in Sumatra primary forests show seasonal variation in fruit availability (Buij et al., 2002; van Schaik, 1986; Wich and Schaik, 2000). To examine the influence of fruit availability on orang-utan density more directly, Pearson correlations were made.

3. Results

3.1. Strip width (w)

The distributions of the perpendicular distances of the nests did not differ significantly between the logged forest and the primary forest, and they were therefore pooled for further analyses (primary forest, $n = 69$, logged forest, $n = 109$, Kolmogorov–Smirnov $z = 1.035$, $p = 0.235$). The application of the program DISTANCES led to a strip width w of 21.2 m (minimum Akaike Information Criterion (AIC) for Uniform model with Cosine adjustments = 1234.945, $p = 0.558$).

3.2. Nest decay rate (t)

The transition matrix technique led to the decay rate $t = 169$ days in the primary forest and to the decay rate $t = 248$ days in the logged forest.

Table 1

Orang-utan densities and nests per kilometre from nine independent transects in primary forest and logged forest of the Sekundur area

Forest	Nests/km	Individuals/km ²
Primary	3.33	0.29
Primary	4.67	0.41
Primary	2.00	0.18
Primary	1.33	0.12
Primary	0.67	0.06
Logged	5.33	0.32
Logged	4.00	0.24
Logged	8.67	0.52
Logged	2.00	0.12

The data were collected during the three months between March 2001 and May 2001.

Table 2

Medians of the predictor variables for orang-utan densities

Forest	Fruit/km	Roughness	Gaps/km
Primary	4.00	0.90	2.67
Logged	4.67	0.84	7.33

Number of fruit sources per kilometre, roughness of canopy and number of gaps per kilometre were sampled during the months March 2001 and May 2001 on five independent transects in the primary forest and on four independent transects in the logged forest.

3.3. Orang-utan densities

The orang-utan densities obtained from the nine independent transects in primary forest and logged forest were distributed normally. There was no significant difference between the orang-utan density in the logged forest and in the primary forest (Table 1, primary forest, $n = 5$, mean = 0.21 ± 0.14 , logged forest, $n = 4$, mean = 0.30 ± 0.17 , $t_7 = -0.863$, $p = 0.893$).

3.4. Forest structure parameters and fruit availability

There were significantly more gaps in the logged forest than in the primary forest (Table 2, primary forest, $n = 4$, logged forest, $n = 5$, $U = 1.00$, $p = 0.026$). There was no difference, however, in fruit availability and canopy roughness between logged forest and primary forest (primary forest, $n = 4$, logged forest, $n = 5$, fruit/km, $U = 9.50$, $p = 0.900$, canopy roughness, $U = 8.00$, $p = 0.624$). The univariate ANCOVA using all covariates together showed a significant influence of only fruit per kilometre (Table 3). A regression analysis of orang-utan density on fruit per kilometre showed a significant influence of the fruit per kilometre on orang-utan density ($y = 0.11 + 0.02x$, $F_{1,7} = 9.43$, $p = 0.018$).

3.5. Seasonal movements of orang-utans

To assess whether orang-utan density in both forest types correlated with fruit availability, Spearman correlations were conducted. These analyses showed no

Table 3

Analyses of the influence of the three covariates fruit per kilometre, roughness of the canopy and number of gaps on the orang-utan density in the Sekundur area

Covariable	$F_{1,4}$ -value	Significance
Fruit/km	16.276	0.016
Roughness	3.577	0.132
Gaps/km	2.582	0.183

Fruit per kilometre had a significant influence on the orang-utan density.

significant correlation between orang-utan density, estimated from counts of new nests only, and fruit availability in either primary or logged forest (primary forest, $n = 11$, $r = 0.498$, $p = 0.119$, logged forest, $n = 11$, $r = -0.265$, $p = 0.431$).

4. Discussion

Several studies have demonstrated that logging negatively affects orang-utan densities (Engström, 2000; Rao and van Schaik, 1997; Rijksen, 1978; Robertson and van Schaik, 2001; van Schaik and Azwar, 1991; van Schaik et al., 2001; Wich et al., 2003). Most of these studies, however, focused on areas that were logged relatively recently and, as a result, could not address the long-term recovery of orang-utan density in logged forests. This study aimed at assessing orang-utan densities 22 years after selective logging. The results suggest that there is no significant difference in orang-utan density between primary forest and regenerated logged forest 22 years after logging. In both primary and logged forest, densities were very low (<1 ind/km²) compared to other study sites (van Schaik et al., 1995; van Schaik et al., 2001; Wich et al., 2003). The low orang-utan density in the primary forest could be due to the low densities of large strangling figs, which are an important fallback food source for Sumatran orang-utans in areas where large figs occur (Rijksen, 1978; van Schaik et al., 1995; Wich et al., 2003).

The orang-utan density in the logged forest did not differ from that in the primary forest, suggesting that the logged forest regenerated to such an extent that there is little or no measurable effect of logging left on the orang-utans. This suggestion is supported by the lack of difference in overall fruit availability between the primary forest and the logged forest. The number of trees per hectare (>10 dbh) and tree basal area also showed no difference between the primary forest and the logged forest (Wich, unpublished). This also indicates that the logged forest has regenerated well. Structurally, the primary forest had fewer gaps than the logged forest, but canopy roughness did not differ significantly.

We should be cautious with extrapolating these results to other habitats or even the same habitat in an-

other area. First, lowland dipterocarp forests in Sumatra harbour low orang-utan densities. This is probably because dipterocarps are the dominant tree family and are not important orang-utan food sources (except during mast years). It could be, therefore, that the logging of dipterocarps affects orang-utan density less than the logging of major orang-utan fruit sources (such as *Neesia* sp and *Tetrameristra* sp in swamp forests Van Schaik pers. comm.). In addition, the logged area that we studied was still continuous with primary forest which might have been an important prerequisite for recovery the orang-utan density in the logged area.

Previous studies indicate that orang-utan density differences between habitats and movements within and between habitats can largely be explained as a function of fruit availability (Buij et al., 2002; van Schaik et al., 1995; Wich et al., 2003). Our study does not corroborate those results since we found no correlation between fruit availability and orang-utan density. The monthly variation in orang-utan density found in this study could possibly be explained by variation in the number of receptive females as proposed by te Boekhorst et al. (1990).

In conclusion, our results suggest that orang-utan density in an old logged forest has recovered its pre-logging density (as estimated from the density in a nearby primary forest). Nevertheless, we have no information about the demography of the orang-utan population in the logged forest or about its health. More research is therefore needed to address these issues, in order to determine the long-term survival probability of orang-utan populations in logged forests.

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References

- Abdulhadi, R., Mirmanto, E., Kartawinata, K., 1987. A lowland dipterocarp forest in Sekundur, North Sumatra, Indonesia: five

- years after mechanized logging. In: Kostermans, A.H. (Ed.), *Proceedings of the Third Round Table Conference on Diptero-carps*, UNESCO, Jakarta, Indonesia, pp. 255–273.
- Blouch, R.A., 1994. Orangutans. In: *Densities and Distributions of Primates in the Lanjak Entimau Wildlife Sanctuary and Recommendations for Sanctuary Management*. International Tropical Timber Organization Unit, Sarawak, Malaysia, pp. 20–26.
- Brockelman, W.Y., 1998. Study of tropical forest canopy height and cover using a point intercept method. In: *Forest Biodiversity Research, Monitoring and Modelling: Conceptual Background and Old Case Studies*. Paris and Parthenon Publishing, New York, pp. 521–531.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 1993. *Distance Sampling. Estimating Abundance of Biological Populations*. Chapman and Hall, London.
- Buij, R., Wich, S.A., Lubis, A.H., Sterck, E.H.M., 2002. Seasonal movements in the Sumatran orang-utan (*Pongo pygmaeus abelii*) and consequences for conservation. *Biological Conservation* 107, 83–87.
- Buij, R., Singleton, I., Krakauer, E., van Schaik, C.P., 2003. Rapid assessment of orang-utan density. *Biological Conservation*.
- Burnham, K.P., Anderson, D.R., Laake, J.L., 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72, 202.
- Cannon, C.H., Peart, D.R., Leighton, D.R., Kartawinata, K., 1994. The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. *Forest Ecology and Management* 67, 49–68.
- de Wilde, W.O., Duyfjes, B.E., 1996. Vegetation, floristic and plant biogeography in Gunung Leuser National Park. In: Schaik, C.P.v., Supriatna, J. (Eds.), *Leuser, a Sumatran Sanctuary*. Yayasan Bina Saina Hayati Indonesia, Depok, Indonesia, pp. 49–103.
- Djojosedharmo, S., Schaik, C.P.v., 1992. Why are orang-utans so rare in the highlands? *Tropical Biodiversity* 1, 11–22.
- Engström, L., 2000. Effects of selective hand – logging on orang-utan habitat quality and population density in Gunung Palung National Park, Borneo, Indonesia; with focus on forest structure and nest resources.
- Galdikas, B.M.F., 1988. Orang-utan diet, range and activity in Tanjung Puting, Central Borneo. *International Journal of Primatology* 9, 1–31.
- Grieser Johns, A., Grieser Johns, B., 1995. Tropical forest primates and logging: long-term co-existence? *Oryx* 29, 205–211.
- Hilton-Taylor, C., Brackett, D., 2000. IUCN red list of threatened species IUCN, Gland.
- Johns, A.D., 1991. Forest disturbance and Amazonian primates. In: Box, H.O. (Ed.), *Primate Responses to Environmental Change*. Chapman and Hall, London.
- Knott, C.D., 1998. Changes in orang-utan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology* 19, 1061–1078.
- Levene, H., 1960. In *Contributions to Probability and Statistics*. Stanford University Press, Stanford, CA. p. 278.
- MacKinnon, J., 1977. The future of orang-utans. *New Scientist* 74, 697–699.
- Payne, J., 1987. Surveying orang-utan populations by counting nests from a helicopter: a pilot study in Sabah. *Primate Conservation* 8, 92–103.
- Rao, M., van Schaik, C.P., 1997. The behavioral ecology of Sumatran orang-utans in logged and unlogged forest. *Tropical Biodiversity* 4, 173–185.
- Rijksen, H.D., 1978. A Field Study on Sumatran Orang-utans (*Pongo pygmaeus abelii* Lesson 1872). H. Veenman and Zonen B.V., Wageningen.
- Rijksen, H.D., Meijaard, E., 1999. *Our Vanishing Relative: The Status of Wild Orang-utans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Dordrecht.
- Robertson, J.Y., van Schaik, C.P., 2001. Causal factors underlying the dramatic decline of the Sumatran orang-utan. *Oryx* 35, 26–38.
- Rodman, P.S., 1988. Diversity and consistency in ecology and behaviour. In: Schwartz, J.H. (Ed.), *Orang-utan Biology*. Oxford University Press, New York, pp. 31–51.
- SPSS, 1999. *SPSS Base System Users Guide* [10], Chicago (Ref type: Computer program).
- Struhsaker, T.T., 1997. *Ecology of an African Rainforest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. University Press of Florida, Gainesville.
- te Boekhorst, I.A., Schurman, C.L., Sugardjito, J., 1990. Residential status and seasonal movements of wild orang-utans in the Gunung Leuser reserve (Sumatra, Indonesia). *Animal Behaviour* 39, 1098–1109.
- van Schaik, C.P., 1986. Phenological changes in a Sumatran rainforest. *Journal of Tropical Ecology* 2, 327–347.
- van Schaik, C.P., Azwar, 1991. Orang-utan densities in different forest types in the Gunung Leuser National Park (Sumatra), as determined by nest counts. In: Report to PHPA, LIPI and L.S.B. Leakey Foundation, Durham, NC, USA.
- van Schaik, C.P., Azwar, Priatna, D., 1995. Population estimates and habitat preferences of orang-utans based of line transects of nests. In: Nadler, R.D. (Ed.), *The Neglected Ape*. Plenum Press, New York, pp. 129–147.
- van Schaik, C.P., Monk, K.A., Robertson, J.Y., 2001. Dramatic decline in orang-utan numbers in the Leuser Ecosystem, northern Sumatra. *Oryx* 35, 14–25.
- Wheatly, B.P., 1982. Energetics of foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a selective advantage of large body size in the orang-utan. *Primates* 23, 348–363.
- Wich, S.A., Schaik, C.P.v., 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16, 563–577.
- Wich, S.A., Singleton, I., Utami-Atmoko, S.S., Geurts, M.L., Rijksen, H.D., van Schaik, C.P., 2003. The status of the Sumatran Orang-utan *Pongo abelii*: an update. *Oryx* 37, 49–54.