

Orangutan distribution, density, abundance and impacts of disturbance

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6.1 Introduction

Knowledge of a species' distribution, density and population size is essential for conservation, because collecting this information is the only adequate method of assessing a species risk of extinction. As the Sumatran orangutan is considered critically endangered (Singleton *et al.* 2007) and the Bornean orangutan endangered (Ancrenaz *et al.* 2007) it is important to obtain distribution and density data for all orangutan populations. In this chapter we provide a concise overview of orangutan distribution and density. In addition to being essential for orangutan conservation, these data also serve as the basis for studies investigating variation in forest productivity and the effects it might have on orangutan density (Chapter 7).

Earlier studies on orangutan density have generally suggested that Sumatran orangutans are found at higher densities than Bornean orangutans (Rijksen and Meijaard 1999); that orangutan density declines with increasing altitude (Djojosudharmo and van Schaik 1992; Rijksen and Meijaard 1999) and that it is negatively impacted by logging (Rao and van Schaik 1997; Morrogh-Bernard *et al.* 2003; Felton *et al.* 2003; Johnson *et al.* 2005b). Because the orangutan is a frugivore, variation in fruit availability is thought to be the main cause of these variations in density. Fruit availability is higher in Sumatra than Borneo (Chapter 7), declines with altitude on both islands (Djojosudharmo and van Schaik 1992; Cannon *et al.* 2007) and is reduced by logging (Johns 1988; Grieser Johns and Greiser Johns 1995).

These earlier studies have been limited to comparisons between a small number of sites, however, and have often not taken into account variation in survey methods between the sites under comparison. In this chapter we reinvestigate these hypotheses/results, armed with the largest set of density estimates yet available, and attempt to standardize for differences in field survey methods and the parameters used to convert nest-density data to orangutan density estimates.

6.2 Distribution

6.2.1 Historical distribution, dispersal and range contraction

The orangutan emerged as a distinct species around 2–3 million years ago on the Asian mainland, and dispersed southwards throughout South East Asia and the Sundaland region (Steiper 2006). Until 12,500 years ago, orangutans were distributed more or less continuously from the foothills of the Himalaya mountain chain to the large Sunda islands of Sumatra, Borneo and Java—a historical distribution covering at least 1.5 million km² (Rijksen and Meijaard 1999). Environmental changes (Jablonski *et al.* 2000), slash-and-burn agriculture and increasing hunting pressure reduced their range, and since the seventeenth century the orangutan has only occurred in the wild on the islands of Borneo and Sumatra. Reliable records of their distribution did not appear until the 1930s, a comprehensive review of which can be found in Rijksen and Meijaard (1999), and their complete distribution was not satisfactorily known until the beginning of the twenty-first century (Singleton *et al.* 2004).

Orangutans are believed to have entered southern Borneo from Sumatra via the (now submerged) Bangka–Belitung–Karimata land-bridge (Rijksen and Meijaard 1999). They cannot cross wide rivers, so they must have dispersed along Borneo's central mountain chain, traversing the headwaters of the major rivers where they were narrow enough to cross. In the center of Borneo is a mountainous region where the Schwaner mountains meet the Muller mountains and where Borneo's three largest rivers, the Barito, Mahakam and Kapuas, originate. Orangutans that dispersed across the headwaters of the Kapuas gave rise to the populations in western Borneo (West Kalimantan north of the Kapuas, Sarawak, Brunei, and Sabah west of the Padas river) and those that dispersed across the headwaters of the Mahakam resulted in the populations of eastern and northern Borneo (East Kalimantan and Sabah east of the Padas river). These dispersal routes must have closed at some point, perhaps because changes in sea-level and climate made the habitat

in the hills unsuitable for orangutans, or because of hunting or forest clearing by humans. Whatever the reason, evidence suggests that these populations have remained separate from each other, and from those in southern Borneo, for a considerable period of time (Warren *et al.* 2001; Chapter 1) and they are now classed as separate subspecies, *Pongo pygmaeus pygmaeus* in western Borneo, *P. p. morio* in eastern Borneo and *P. p. wurmbii* in southern Borneo.

The headwaters of the Barito river appear to have blocked orangutans from dispersing further along the south of the Schwaner range, as there are few records of the species occurring in and around these headwaters (Rijksen and Meijaard 1999) and the orangutan is virtually absent from the south-east of Borneo, east of the Barito river and south of the Mahakam river, despite the presence of apparently suitable habitat in the region. The only exception is an isolated population between the Barito and Negara rivers, first reported in the 1930s. This small population is most likely the result of changes in the course of the Barito river which separated and then isolated a group of orangutans.

Orangutans once inhabited all suitable habitat in Sumatra and Borneo, apart from the south-east corner of Borneo, but by the end of the twentieth century they had disappeared from many parts of their former range. There are no reliable recent records of orangutans in the north-west of Borneo (Sarawak north of the Rajang River and the coastal zones of Brunei and western Sabah); the Kayan–Mentarang water catchment in East Kalimantan or most of the eastern lowlands of Sumatra. These regions are the traditional homes for several tribes of hunter-gatherer peoples who probably hunted the orangutan to extinction in these forests (Rijksen and Meijaard 1999).

Nearly the entire remaining orangutan forest habitat has been exploited in some way, as detailed in Rijksen and Meijaard (1999). Large areas of forest have been cleared, initially by indigenous groups of shifting-cultivators, and more recently to expand settlements, build transport links and for growing food crops. International trade in timber and agricultural products, including palm

oil, tobacco and rubber, began during the colonial period and has become a major source of revenue for Indonesia and Malaysia. In Sumatra, most of the forests surrounding Lake Toba have been converted to plantation, and there has been considerable encroachment and forest clearance all around the Leuser Ecosystem, notably in the Alas Valley, Bengkung, Deli and Langkat regions. In the orangutan's Bornean range, the lowland forests of the Kapuas basin in West Kalimantan were more or less cleared during the twentieth century for agriculture and commercial logging. Large oil palm plantations have been established in most of the lowland area between the Sampit river in Central Kalimantan and Gunung Palung National Park in West Kalimantan. Oil palm has also been grown on former forest land in much of the coastal regions of Sabah and Sarawak. Large-scale forest fires have occurred in much of eastern and southern Borneo, resulting from drought, peatland drainage and arson, so that there is now virtually no lowland forest remaining in East Kalimantan south of the Sangkulirang peninsula, or in south-east Central Kalimantan between the Sabangau and Barito rivers. The opening up of forest to logging concessions has led to increased opportunities for hunting. During the mid- to late-twentieth century this has been as much for the pet trade as for meat or for cultural reasons. It is likely that orangutans have been hunted to extinction in areas of forest that naturally supported low orangutan densities, such as in the Schwaner mountains around the headwaters and tributaries of the Katingan and Barito rivers, and in most of the Barisan mountain chain in Sumatra.

6.2.2 Current distribution

Orangutan distribution in 2003 was described at the Jakarta Orangutan Population and Habitat Viability Analysis Workshop (Singleton *et al.* 2004). Using a combination of ground and aerial field surveys, LANDSAT and MODIS imagery and Indonesian Ministry of Forestry data, Wich *et al.* (2008) identified 306 separate forest blocks in Borneo and 12 in Sumatra that potentially contained orangutans in

2002. Of these, 32 in Borneo and 6 in Sumatra support at least 250 individuals, the proposed minimum viable population size (Singleton *et al.* 2004; Chapter 22). Only 17 habitat blocks in Borneo and 3 in Sumatra support populations in excess of 1000 individuals. This distribution is shown in Figures 6.1 and 6.2.

Orangutans are found in dry lowland and hill forests dominated by tree species from the Dipterocarpaceae family; peat-swamp forest in poorly drained river basins; and freshwater swamp forest and alluvial forest in river valleys. These are the prime habitats for orangutan, which provide sufficient food to support permanent populations (Chapters 7–9). Orangutans also occur in a range

of other habitats including heath forest (*kerangas*) on sandy soils (Payne 1987; Galdikas *et al.* unpublished data) and limestone-karst forest (Marshall *et al.* 2006, 2007), and they have also been recorded in *Nypa* palm stands and mangrove forest in Sabah (Ancrenaz and Lackman-Ancrenaz 2004), albeit at very low density. Orangutans are generally rare or absent at high altitudes (more than 500 m above sea level (asl) in Borneo and 1500m asl in Sumatra; Rijksen and Meijaard [1999]). They are thus rarely found in submontane and montane forests, although the submontane (800–1000 m asl) forest in Gunung Palung National Park occasionally supports high densities of orangutan (Johnson *et al.* 2005b) and the highest density of orangutan

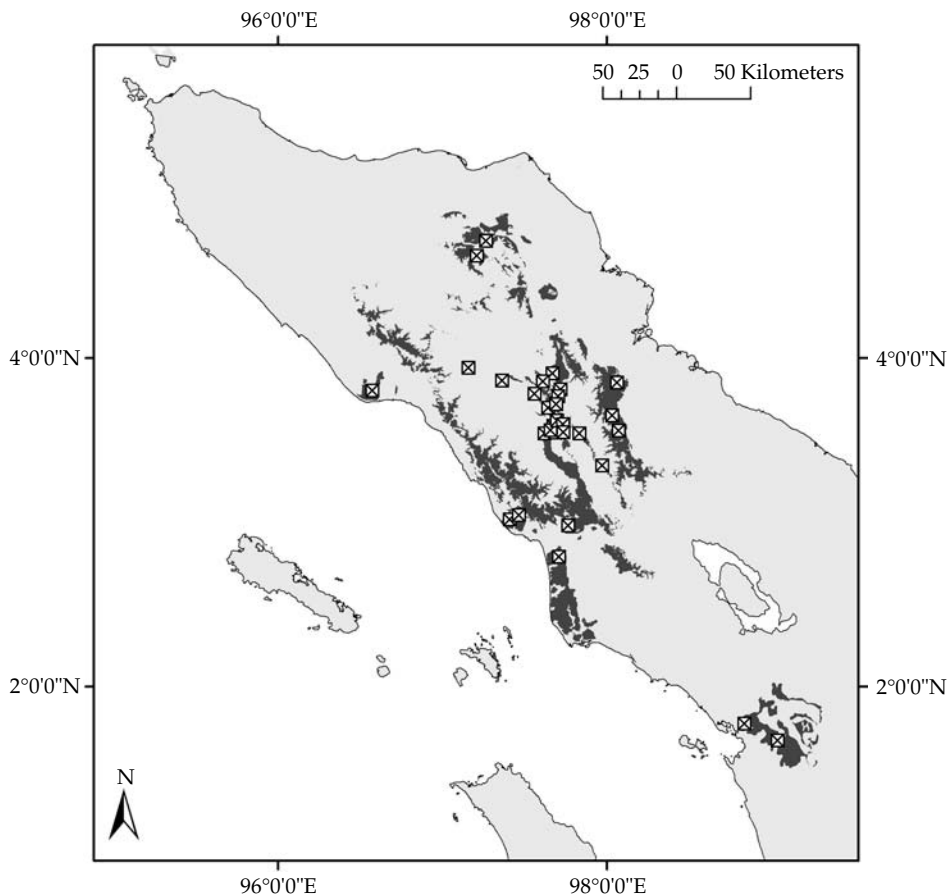


Figure 6.1 Orangutan distribution in Sumatra (dark gray). Surveyed locations included in this analysis are marked with a boxed cross.

nest in Mount Kinabalu National Park was found between 800 and 1300 m asl in forest growing on outcrops of igneous rock at the interface between hill dipterocarp forest and montane forest (Ancrenaz and Lackman-Ancrenaz 2004).

These marginal habitats provide less orangutan food and it seems likely that large expanses of these habitat types are unable to support permanent populations. Where they do occur in marginal

habitats it is likely that they are either dispersing adult males (Delgado and van Schaik 2000) or are able to utilize adjacent prime habitat types in order to meet their nutritional requirements. For example, the karst forests of the Sangkuliarang peninsula are adjacent to mixed dipterocarp forest (Marshall *et al.* 2007) and the montane slopes of Mount Palung rise steeply from the mixed dipterocarp and peat-swamp forests at its base. It is

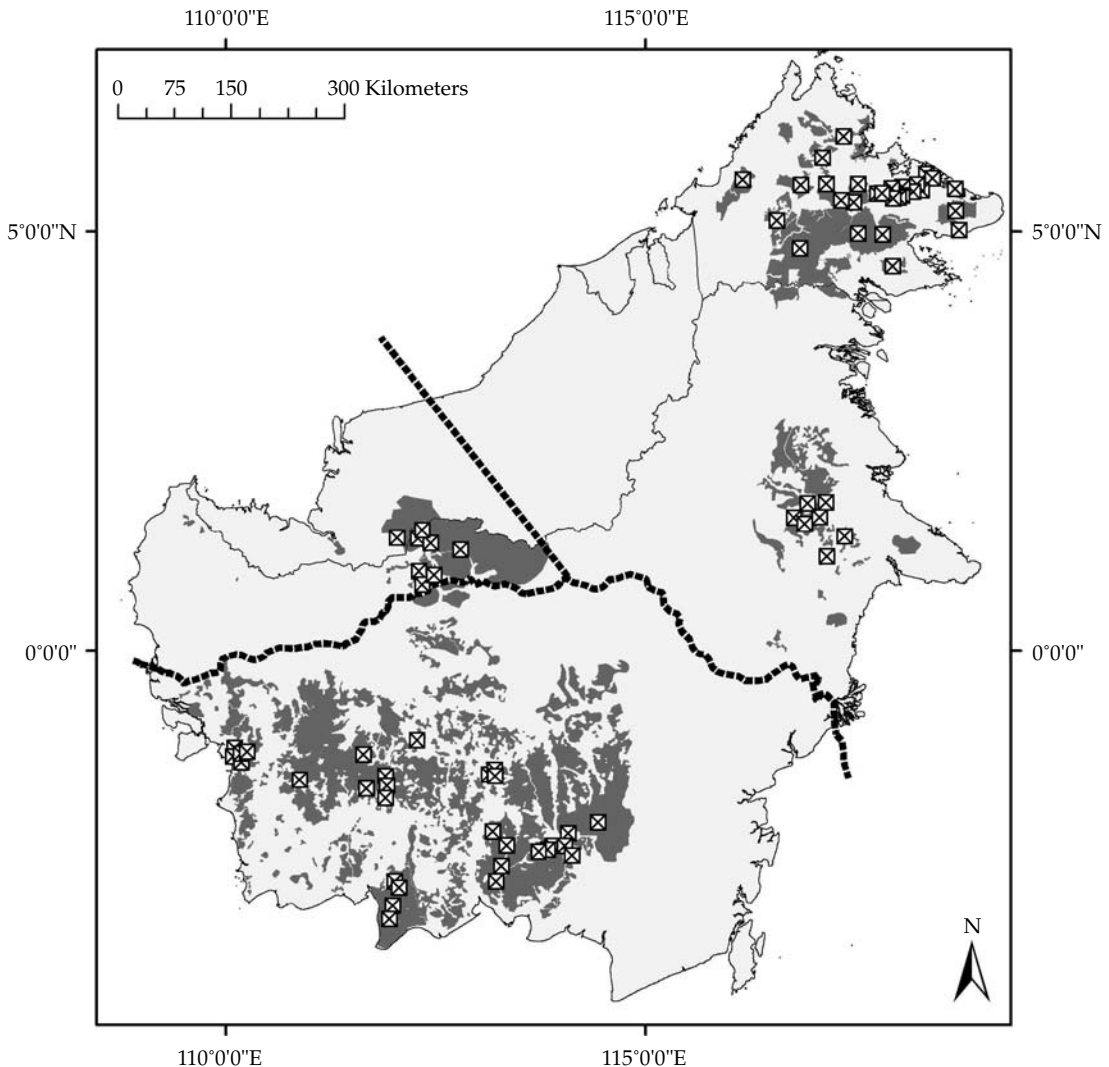


Figure 6.2 Orangutan distribution in Borneo (dark gray). Surveyed locations included in this analysis are marked with a boxed cross. Dashed lines mark the boundaries between subspecies

also possible that interfaces between two habitat types, such as found at high altitudes on Mount Kinabalu, provide suitable conditions for orangutan survival, where either on its own does not.

6.3 Density

6.3.1 Hypotheses

6.3.1.1 *Habitat differences*

Simple ecological theory suggests that a species' density is positively correlated with the amount of food available to it, and more specifically that density of slow-reproducing species (such as orangutans) are limited by the frequency and duration of periods of food shortage (Cant 1980; Marshall and Leighton 2006). In support of this, Marshall *et al.* (Chapter 7, using data from 12 sites) found that Sumatran forests were better orangutan habitat than Bornean forests, and that orangutan density was positively correlated with fruit abundance during periods of low-fruit availability, indicating that sites which experience less extreme periods of food shortage can support higher densities. Here we suggest basic hypotheses that arise from Marshall *et al.*'s conclusions, and test whether they hold true for the larger sample of sites presented here.

Hypotheses 1: Sumatran orangutans are found at higher densities than Bornean orangutans. Published orangutan densities in Sumatra are consistently higher than estimates from comparable habitat in Borneo (Rijksen and Meijaard 1999; Singleton *et al.* 2004) and this is generally assumed to result from higher levels of plant productivity, and hence greater availability of orangutan food, on Sumatra's more fertile volcanic soils (Rijksen and Meijaard 1999). In Chapter 7, Marshall *et al.* find that Sumatran forests have a higher proportion of stems bearing fruit; are more often in periods of high-fruit availability; have higher densities of some of the orangutan's preferred foods; and experience shorter periods of low-fruit availability, than in comparable habitats in Borneo. These findings are all consistent with, and provide support for, the assumption stated above. Hence we test the hypothesis that Sumatran forests support higher densities of orangutans.

Hypotheses 2: Orangutan density declines with increasing altitude.

Density is reported to decline with altitude (van Schaik *et al.* 1995; Rijksen and Meijaard 1999; Johnson *et al.* 2005b) and this is believed to be a consequence of lower food availability at higher altitudes, particularly of fleshy-pulp fruits (Djojosudharmo and van Schaik 1992).

Hypotheses 3: Peat-swamp forest supports higher densities than other habitat-types, followed by dry forest and karst forest.

Marshall *et al.* (Chapter 7) conclude that the highest orangutan densities are found at sites with shorter, less frequent and less extreme periods of low food availability. This implies that peat-swamp forests should support higher densities than dry forest types, as dry forests experience extreme temporal fluctuations in food availability owing to the mast-fruiting phenomenon (Leighton and Leighton 1983; Knott 1998a), which exhibits peaks of synchronized fruit production followed by several years of reproductive inactivity (Medway 1972; Ashton *et al.* 1988). In contrast, peat-swamp forest displays consistent reproductive productivity (Cannon *et al.* 2007), and so we hypothesize that orangutan densities are highest in this habitat type. We expect karst forests to support the lowest densities, owing to their relatively low tree species diversity and more limited productivity (Marshall *et al.* 2007).

Hypotheses 4: 'Mosaic' sites support higher orangutan densities than single habitat types.

A further category of habitat in which we may expect overall fruit availability to be high and periods of low-fruit availability to be short are 'mosaic' habitats. These are defined as areas in which all or most individuals in a population have access within their home ranges to two or more different types of habitat, e.g. dry, dipterocarp-dominated, forest with accumulations of peat in depressions, or peat-swamp forest margins that are seasonally inundated with river floodwater. In such areas one habitat may be more productive overall but the other have a more stable, year-round supply of food (Cannon *et al.* 2007), so that the orangutan population can exploit different habitats at

different times of year (Singleton and van Schaik 2001). Alternatively, the species composition of each habitat may be different, with preferred food species fruiting at different times of the year in the two habitat types. In either case, from an orangutan's perspective, there are likely to be fewer periods of low-fruit availability in 'mosaic' habitats than in areas with only one type of habitat.

Hypotheses 5: Densities of *P. pygmaeus morio* are lower than the other subspecies of *P. p. pygmaeus* and *P. p. wurmbii*.

Eastern Borneo experiences long periods of drought (MacKinnon *et al.* 1996; Walsh and Newbery 1999) and so we expect that forests in this region show greater seasonality of food availability, and hence longer periods of extreme food shortage, than elsewhere in Borneo. Thus, we hypothesize that densities of *P. p. morio* will be lower than those of the other two subspecies of Bornean orangutan, unless the local populations have evolved special adaptation to food scarcity (Taylor 2006a; Chapter 2).

6.3.1.2 Impacts of disturbance

Human disturbances complicate our analyses in a number of ways. By felling and removing large trees, logging theoretically lowers the availability of food and hence carrying capacity (Johns 1988; Grieser Johns and Greiser Johns 1995), but also affects the behavior, diet and ranging patterns of a species (Johns 1986; Marsh *et al.* 1987; Rao and van Schaik 1997; Meijaard *et al.* 2005). Additionally, logging operations provide increased opportunities for hunting (Rijksen and Meijaard 1999) which can have strong negative impacts on orangutan populations (Leighton *et al.* 1995; Marshall *et al.* 2006).

Hypotheses 6: Orangutan density is negatively correlated with the intensity of logging damage.

Logging damages forest structure through the removal of commercial timber species, incidental damage to other trees, lianas and figs and the construction of logging access routes. This inevitably reduces the number of fruit-bearing trees, and thus is likely to reduce the carrying capacity of the habitat and orangutan density. Although the

majority of studies that have directly examined the effect of logging on orangutan density support this hypothesis (Rao and van Schaik 1997; Felton *et al.* 2003; Morrogh-Bernard *et al.* 2003; Johnson *et al.* 2005b), some studies find no obvious relationship (Marshall *et al.* 2006), or that undisturbed areas of habitat support similar densities to partly disturbed areas (Ancrenaz *et al.* 2004b), or that populations can recover to pre-logging density in a relatively short-period of time (Knop *et al.* 2004). We test to see if densities in unlogged forest are significantly higher than those in logged forest.

Hypotheses 7: There is a degree of logging damage that can be tolerated by orangutans.

Little, or no, difference in orangutan density between unlogged areas and areas of 'light' logging have been found in some studies (Ancrenaz *et al.* 2004b, 2005; Marshall *et al.* 2006). The most prized timber species are those from the Dipterocarpaceae family, which are not regarded as important food for primates, including orangutans (Chivers 1980; Chapter 9). Therefore a well-managed, selective-logging operation that only removes those species of trees and does minimal damage to the surrounding forest may not significantly alter the forest structure and food availability from an orangutan's perspective. We test to see if there are differences in density between four classes of logging disturbance.

Hypotheses 8: Logging operations lead to inflated orangutan densities in neighboring, unlogged habitat.

MacKinnon (1971) first observed that orangutans exposed to disturbance move out of the local area, returning once the disturbance is over. This displacement of orangutans leads to what has been described as 'refugee crowding', i.e. an overshoot of the carrying capacity in forested areas that neighbor areas where logging is active. Inflated densities in such areas have been reported in a number of studies in Borneo (Russon *et al.* 2001; Morrogh-Bernard *et al.* 2003; Ancrenaz and Lackman-Ancrenaz 2004; Marshall *et al.* 2006) although this has not been observed in Sumatra where at least adult females are unwilling to leave their home ranges (van Schaik *et al.* 2001).

6.3.2 Density estimates and accuracy of standardization

Estimates of orangutan density were collated from studies in which nest-count survey methods were used (Box 6.1) and standardized for differences in study design (Box 6.2).

Standardized density estimates were in the range 0.06 individuals per square kilometer (ind km⁻²) to 9.58 ind km⁻² with a median of 1.93 ind km⁻²

and 50% range 0.91–3.09 ind km⁻². All estimates are presented in Table 6.2. It should be noted that many study sites have been purposefully chosen in areas of high density, and lower-density sites, such as upland areas, non-mosaic peat-swamps and karst forests, are under-represented in our sample. Therefore the median density of our sample is likely to be higher than the overall median orangutan density across the species full range. The standardization process resulted in higher

Box 6.1 Survey methods

Survey data from a combination of published papers, survey reports and unpublished data are collated here. These are from 110 locations in 42 forest blocks, including 29 locations in 11 forest blocks for *P. abelii*; 9 locations in 3 forest blocks for *P. p. pygmaeus*; 37 in 16 forest blocks for *P. p. morio* and 35 in 12 forest blocks for *P. p. wurmbii*. All surveys were carried out since 1993.

At all sites orangutan density was estimated by counting orangutan nests (sleeping platforms) along straight-line transects, with the exception of sixteen sites in Sabah which were surveyed by helicopter. In the latter method the resulting aerial nest-counts were related to absolute nest density by calibrating with nest counts from concurrent ground surveys (see Ancrenaz *et al.* [2005b] for full details). In all cases the effective transect width was calculated using the Distance software program (Thomas *et al.* 2006) and nest density (DN) estimated accordingly. Nest densities are converted to orangutan density using the formula: $DOU = DN / (p \times r \times t)$ where: p = proportion of nest-builders in the population, r = number of nests built per day per individual, and t = nest decay time in days.

Each survey location was classified for the following variables:

- *Species/subspecies*: Following the revised classification of Groves (2001) and Brandon-Jones *et al.* (2004).
- *Dominant habitat type*: Three broad habitat types are described: (1) peat-swamp forest: forest growing on peat deposits, including both ombrotrophic ('true') peat-swamps (the only external source of water and nutrients is via aerial deposition from rain, aerosols and dust) and minerotrophic peat-swamps (which receive external supplies of water and nutrients from surface run-off, groundwater flow or seasonal inundation of river water);

(2) limestone–karst forest: dipterocarp-dominated forest growing on limestone bedrock, often with a dramatic landscape of pinnacles, sinkholes, caves and cliffs; (3) dryland forest: typically dipterocarp-dominated mast-fruiting forests on a wide range of soils, found in lowland plains and foothills, hilly regions and mountainsides.

- *'Mosaic' habitat*: whether more than one habitat type is present at or near to the study site.
- *Altitude*: in meters above sea level.
- *Logging disturbance*: each site was classed as either logged or unlogged. We further subdivided logged sites into lightly logged, logged or heavily logged, for cases where these divisions are made explicit in the literature, and recorded whether active logging was present in contiguous habitat adjacent to, but not in, each survey site. Classifications of logging intensity between sites in a single study is largely based on measurements of tree density, canopy disruption and stump density, and/or the visual determination of canopy structure and forest condition, although no empirical data exist to compare logging intensity between studies and thus there remains the possibility of bias.

These habitat characteristics are necessarily limited to broad definitions and thus we can only test for the presence of correlations without being able to identify the reasons for differences in density. Including more detailed site-specific variables, for example stem density, stand biomass and fruit availability, would greatly increase the power of our analyses, but these data are only available for a handful of sites, some of which are considered separately in Chapter 7. Nevertheless, we can assess whether the conclusions of Chapter 7 and other similar studies support or contrast with trends from this larger dataset.

Box 6.2 Standardization of density estimates

In order to properly compare densities between different habitat types and locations, these results have been standardized to control for the effects of different survey techniques. There is much variation in the values used for the nest-life history parameters and so we have recalculated densities using standardized values. These values are shown in Table 6.1. p has been estimated by direct observation at six sites and is similar at all sites, so the mean value of 0.89 is used. r has been estimated by direct observation at the same six sites and is distinctly higher in Sumatra compared to Borneo.

A lower r value was estimated at Lower Kinabatangan than at the three sites in southern Borneo, reflecting a higher-than-normal incidence of nest reuse at Lower Kinabatangan (Ancrenaz *et al.* 2004a). This may be common to the *P. p. morio* sub-species or could have arisen in Lower Kinabatangan owing to heavy habitat disturbance and consequent overcrowding of the population there, meaning that there are relatively few potential nest sites. In the absence of data from other sites in *P. p. morio*'s range we have decided to use the value of 1.0 nests/day/individual for Lower Kinabatangan only and a mean value of 1.16 for all other sites in Borneo. For Sumatra a mean value of 1.80 is used.

There is greatest inter-site variation in t , the nest decay time. The time taken for a nest to decay is likely to (a) be positively correlated with climatic factors such

as temperature, rainfall, humidity and wind (van Schaik *et al.* 1995; Mathewson *et al.* 2008); b) depend on nest building-time and complexity (night nests last longer than day nests, which are generally built more quickly and are thus less sturdy); and (c) depend on the wood density of the trees used to build the nest (harder/denser wood, such as that of the Dipterocarpaceae family, decays slower; Ancrenaz *et al.* 2004a; Mathewson *et al.* 2008). Soil pH is thought to be a good proxy for wood density (Buij *et al.* 2003), as wood is denser and thus stronger on acidic soils (van Schaik and Mirmanto 1985). One study has suggested that nest decay rates are positively correlated with altitude in Sumatra (van Schaik *et al.* 1995) although others in Sumatra (Buij *et al.* 2003; Wich unpublished data) and Borneo (Johnson *et al.* 2005b; Marshall *et al.* 2006) have not found this relationship. Altitude correlates with temperature, and thus to some degree tree species composition and humidity, but not with other abiotic factors. While it may be possible to build a model to estimate t that incorporates all of these factors, these parameters are not known for most of the sites surveyed and the size of their effect on t is not fully understood. Therefore, for our purpose of standardizing density estimates, we control only those factors for which we have a good understanding, i.e. shorter decay rates in Sumatra compared to Borneo (higher incidence of day-nest construction in Sumatra), longer decay rates in

Table 6.1 Nest 'life history' parameters estimated at eight sites in Sumatra and Borneo

Island	Site	Habitat	p	r	t
Borneo	Gunung Palung	DF	0.89 ¹	1.16 ¹	259 ¹
	Gunung Palung	PSF	—	—	399 ¹
	Lower Kinabatangan	DF	0.85 ²	1.00 ²	202 ²
	Sabangau	PSF	0.89 ³	1.17 ³	365 ⁴
	Mawas—Tuanan	PSF	0.88 ⁵	1.15 ⁵	—
	Muara Lesan	DF	—	—	602 ^{*6}
Sumatra	West Leuser—Ketambe	DF	0.90 ⁷	1.70 ⁷	170 ⁸
	Kluet—Suag	PSF	0.90y ⁹	1.90 ⁹	199 ¹⁰

Habitat: DF, Dry forest; PSF, Peat-swamp forest.

* Markov chain analysis.

¹Johnson *et al.* 2005b; ²Ancrenaz *et al.* 2004a; ³Morrogh-Bernard unpublished data; ⁴Husson unpublished data; ⁵van Schaik *et al.* 2005a; ⁶Mathewson *et al.* 2008; ⁷van Schaik *et al.* 1995; ⁸Wich unpublished data; ⁹Singleton 2000; ¹⁰Buij *et al.* 2003 (mean of backswamp and transit-swamp values).

continues

Box 6.2 continued

acidic peat-swamp forests than other habitat-types and longer decay rates on the east coast of Borneo—which has lower rainfall and is more drought-prone than the rest of the island (MacKinnon *et al.* 1996; Walsh and Newbery 1999).

t has been estimated at seven sites by following a cohort of nests from construction to disappearance. For Sumatra, values of 170 days for dryland forests and 193 days for peat-swamp forest are used. For Borneo peat-swamp forest, the value from Sabangau of 365 days is used in favor of that from Gunung Palung as the latter is based on a much smaller sample (35 nests vs 908 nests). For Borneo dryland forest, the value from Gunung Palung of 259 days is used in favor of that from Lower Kinabatangan as the latter is from a shorter period of study (2 years 4 months vs 5 years). Nest decay rates in dry forest sites in East Kalimantan are very slow, however (Mathewson *et al.* 2008), which can be attributed to lower annual rainfall on the east coast of Borneo compared to the rest of the island, and thus we use a value of 602 days for sites in East Kalimantan.

Once density estimates were standardized for differences in parameter values, they were corrected further for differences in survey technique. Surveys in which a transect is surveyed twice by different teams of observers obtain higher nest counts and higher nest density estimates than surveys in which transects are surveyed once only. Five separate studies indicate that densities obtained using the repeat survey method are higher by factors of 1.10–1.22 (Johnson *et al.* 2005b; van Schaik *et al.* 2005; Marshall *et al.* 2006; Husson unpublished data; Simorangkir unpublished data). Two studies have shown that nest densities obtained by counting nests in plots are higher by a factor of c. 1.25 than repeated line transect surveys (van Schaik *et al.* 2005; Husson unpublished data), and orangutan densities estimated this way closely approximate ‘real’ densities (van Schaik *et al.* 2005). Hence, a mean correction factor of 1.18 was applied to all data obtained by single surveys (including aerial survey data that was calibrated against single surveys on the ground), and a further correction factor of 1.25 applied to all data.

estimates than the original value in 83 cases and lower estimates in the remaining 27. The standardized density was within 30% of the original estimate in 35 of the 110 cases, and was over 80% higher than the original estimate in 12 cases.

In order to judge the effectiveness of the nest survey method and this standardization process, these estimates were compared to the actual density at those sites where long-term studies have taken place. Density estimates generated in this study closely approximate those estimated from long-term studies at five of the six sites where comparable data are available (Table 6.3). The exception is Ketambe in West Leuser, at which orangutan densities exceeding 5 ind km⁻² are regularly reported by long-term researchers (Rijksen 1978; van Schaik *et al.* 1995, 2001) even though recent nest-survey density estimates are invariably lower (Buij *et al.* 2003; Wich *et al.* 2004a).

This difference is unlikely to be due to either survey error (the survey teams in Ketambe are very experienced) or the standardization process

(which increased the published estimate). It seems more likely that the Ketambe study site, a very fertile area with high densities of strangling figs (an important fallback food resource; Wich *et al.* 2006a), attracts large seasonal aggregations of apes (Rijksen 1978; Sugardjito *et al.* 1987). If orangutans make biased use of their home range to spend as much time as possible in the Ketambe study site during periods of high-fruit abundance, then the estimate of annual average density for this site will exceed the actual density for the wider Ketambe region. Nest counts along long, straight-line transects are more likely to give a better estimate of density in areas where there is markedly biased use of home ranges, as randomly sited transects are predicted to pass through both preferred and non-preferred areas with equal frequency.

We must raise a note of caution before proceeding. Although we show here that, in the majority of cases, density estimates generated from nest count surveys and this standardization closely match ‘real’ densities at a number of sites, it must

also be noted that the estimation of parameters has been most thorough at these same sites. Assigning parameter values from one site to another, particularly the nest decay time t , remains the largest source of potential error (e.g. Mathewson *et al.* 2008). The plot method has not been validated for habitats other than peat-swamp forest, and thus the correction factor may not apply equally across all habitats. The uncertainties generated by these sources of error have led some researchers to calculate nest density only. While this is perfectly valid for comparisons within a site, nest densities are affected by nest construction rates and decay rates, so we have deemed it better to try and identify differences in these parameters instead of ignoring them. Nevertheless there is still more that can be done to improve our estimates of t , in particular the need to factor in effects of altitude, pH and rainfall. At present, adequate data on these are lacking.

6.3.3 Results of analysis

Before proceeding with the analyses, we log + 1 transformed all density values as these were highly skewed. To compare absolute densities for a single independent variable we used independent-samples t-tests or one-way ANOVA followed by Tukey HSD post-hoc tests. All our tests are one-tailed as our hypotheses are directional, and all P-values are presented as such, with the exception of non-directional hypothesis H5 for which two-tailed P-values are presented.

Hypotheses 1: The first hypothesis, that densities in Sumatra are higher than in Borneo, was supported when comparing all sites on the two islands ($t = 2.22$, $df = 108$, $p = 0.014$). This difference was especially strong when comparing peat-swamp forest sites only ($t = 3.20$, $df = 21$, $p = 0.002$), but was much reduced when comparing non-karst dry forest sites ($t = 1.42$, $df = 81$, $p = 0.080$). The difference in density between the two islands appears to be strongly influenced by higher densities in Sumatran peat-swamp forest compared to Bornean peat-swamp forest.

Hypotheses 2: We found no correlation between density and altitude when comparing all sites ($r = -0.11$, $n = 110$, $p = 0.135$), all dry forest sites ($r = -0.04$, $n = 83$, $p = 0.353$), all Sumatran sites

($r = -0.24$, $n = 29$, $p = 0.103$) or all Sumatran dry forest sites ($r = 0.57$, $n = 26$, $p = 0.783$). We found a strong significant negative correlation between density and altitude when comparing all Bornean sites ($r = -0.38$, $n = 81$, $p < 0.0005$) and all Bornean non-karst dry forest sites ($r = -0.39$, $n = 57$, $p = 0.002$). Therefore we find that density declines significantly with increasing altitude in Borneo but not in Sumatra.

Hypotheses 3: We hypothesized that densities would vary between habitat types, with peat-swamp forests expected to support the highest densities, and karst forests the lowest. With all sites included, mean values were in the expected order of peat-swamp > dry forest > karst. Karst forest supports significantly lower densities than both peat-swamp and dry forest but there is only a very weak difference between peat-swamp and dry forest ($F_{2,107} = 7.13$, $p = 0.001$; peat-swamp > karst, $p = 0.001$; dry forest > karst, $p = 0.005$; peat-swamp > dry forest, $p = 0.052$). Within each island the rank order remained the same (there are no Sumatran karst sites in our sample), although in Sumatra peat-swamp density was significantly higher than density in dry forest ($t = 2.94$, $df = 27$, $p = 0.003$). Differences in Borneo mirrored those for the full sample.

Hypotheses 4: Our hypothesis that mosaic sites support higher densities than non-mosaic sites was strongly supported for all sites ($t = 5.91$, $df = 108$, $p < 0.0005$), Sumatra only ($t = 2.70$, $df = 27$, $p = 0.006$) and Borneo only ($t = 6.25$, $df = 79$, $p < 0.0005$). It seemed plausible that high densities in mosaic habitats were strongly influencing our previous test comparing between habitat types, and so we reassigned each mosaic site to one of three new habitat categories: (1) Peat-mosaic: predominately peat-swamp with dry or freshwater habitats (essentially minerotrophic peat-swamps); (2) Dry lowland-mosaic: predominately dry forest with riverine/swamp habitats; (3) Hillside-mosaic: dry forest sites with sharply changing altitudes (essentially mountainsides).

Re-running the comparison showed significant differences between habitat types ($F_{5,104} = 9.85$, $p < 0.0005$) and clearly separated the six habitat-types into two groups, mosaic (mean values: peat-mosaic > dry lowland-mosaic > hillside-mosaic)

Table 6.2 Density estimates and site descriptions of 110 locations used in this analysis

Habitat unit	Region name	Reference	Survey date(s)	Reported density (ind/km ²)	Standardized density (ind/km ²)	Species	Mean altitude (m)	Dominant habitat	Mosaic	Logging status	Neighbouring logging
Sumatra											
Batang Toru	Batang Toru	1	2003	1.14	2.08	<i>P. abelii</i>	500	1	0	2	0
Batang Toru	Teluk Nauli	1	2003	1.26	2.30	<i>P. abelii</i>	850	1	0	2	1
East Leuser–Kapi and Upper Lesten	Aunan	2	1995–2001	1.63	3.26	<i>P. abelii</i>	1036	1	0	1	0
East Leuser–Kapi and Upper Lesten	Balailutu	2	1995–2001	0.57	1.16	<i>P. abelii</i>	916	1	0	1	0
East Leuser–Kapi and Upper Lesten	Kapi 1	2	1995–2001	0.52	0.97	<i>P. abelii</i>	1236	1	0	1	0
East Leuser–Kapi and Upper Lesten	Kapi 2	2	1995–2001	0.61	1.14	<i>P. abelii</i>	1266	1	0	1	0
East Leuser–Kapi and Upper Lesten	Marpunga 1	2	1995–2001	2.62	4.45	<i>P. abelii</i>	925	1	0	1	0
East Leuser–Kapi and Upper Lesten	Marpunga 2	2	1995–2001	2.79	4.74	<i>P. abelii</i>	1122	1	0	1	0
East Leuser–Kapi and Upper Lesten	Marpunga 3	2	1995–2001	0.30	0.62	<i>P. abelii</i>	1100	1	0	1	0
East Leuser–Lawe Sigala-gala	Batu 200	2	1995–2001	0.28	0.57	<i>P. abelii</i>	1283	1	0	1	0
East Leuser–Lawe Sigala-gala	Seledok	2	1995–2001	0.23	0.43	<i>P. abelii</i>	1205	1	0	1	0
East Leuser–Sikundur-Langkat	Bohorok	2	1995–2001	0.88	1.79	<i>P. abelii</i>	500	1	0	1	0
East Leuser–Sikundur-Langkat	Sikundur	2	1995–2001	1.04	1.79	<i>P. abelii</i>	50	1	0	1	0
East Leuser–Sikundur-Langkat	Tankahan	2	1995–2001	0.79	1.58	<i>P. abelii</i>	350	1	0	1	0
East Middle Aceh	Samarkilang 1	2	1995–2001	1.14	2.09	<i>P. abelii</i>	250	1	0	1	0
East Middle Aceh	Samarkilang 2	2	1995–2001	0.41	0.79	<i>P. abelii</i>	750	1	0	1	0
Tripa swamp	Tripa	3	1993	2.85	4.20	<i>P. abelii</i>	10	2	2	3	0
Trumon-Singkil swamp	Trumon-Singkil	3	1993	4.00	5.90	<i>P. abelii</i>	10	2	2	3	0
West Leuser–East Mount Leuser/Kemiri	Agusan	2	1995–2001	5.99	10.18	<i>P. abelii</i>	1186	1	0	1	0
West Leuser–East Mount Leuser/Kemiri	Kedah	2	1995–2001	3.79	6.44	<i>P. abelii</i>	1456	1	0	1	0
West Leuser–East Mount Leuser/Kemiri	Kemiri	2	1995–2001	3.12	4.49	<i>P. abelii</i>	1183	1	0	1	0
West Leuser–Kluet highlands	Suaq Hills	4	1997	1.57	2.32	<i>P. abelii</i>	50	1	0	1	0

West Leuser–Kluet swamp	Suaq Swamps combined	5	1997	4.00	7.44	<i>P. abelii</i>	10	2	2	1	0
West Leuser–Mamas-Bengkung	Bengkung	2	1995–2001	1.07	2.10	<i>P. abelii</i>	700	1	0	1	0
West Leuser–Mamas-Bengkung	Ketambe 2	2	1995–2001	2.03	3.24	<i>P. abelii</i>	705	1	1	1	0
West Leuser–Mamas-Bengkung	Ketambe 3	2	1995–2001	0.95	1.65	<i>P. abelii</i>	1270	1	0	1	0
West Leuser–Mamas-Bengkung	Mamas 1	2	1995–2001	1.66	2.65	<i>P. abelii</i>	421	1	1	1	0
West Leuser–Mamas-Bengkung	Mamas 2	2	1995–2001	2.03	4.00	<i>P. abelii</i>	770	1	1	1	0
West Leuser–Mamas-Bengkung	Mamas 3	2	1995–2001	0.89	1.84	<i>P. abelii</i>	1293	1	0	1	0
Borneo											
Arut	Arut heavy logging	6	2003	0.64	0.81	<i>P. p. wurmbii</i>	100	1	0	4	0
Arut	Arut secondary	6	2003	1.54	1.94	<i>P. p. wurmbii</i>	100	1	0	4	0
Arut	Arut unlogged	6	2003	3.45	4.34	<i>P. p. wurmbii</i>	100	1	0	1	1
Batang Ai	Batang Ai	7	2005	1.14	1.43	<i>P. p. pygmaeus</i>	350	1	0	4	0
Belantikan	Belantikan unlogged	6	2003	2.65	3.34	<i>P. p. wurmbii</i>	110	1	1	1	0
Belantikan	Mendahan river	8	2005	3.34	4.40	<i>P. p. wurmbii</i>	125	1	1	1	0
Betung Kerihun	BK Embaloh 1	9	2005	1.01	1.47	<i>P. p. pygmaeus</i>	340	1	0	3	0
Betung Kerihun	BK Embaloh 3	9	2005	0.58	0.81	<i>P. p. pygmaeus</i>	230	1	0	3	0
Betung Kerihun	BK Potan	9	2005	0.65	0.92	<i>P. p. pygmaeus</i>	150	1	0	3	0
Betung Kerihun	BK Sibau	9	2005	0.27	0.35	<i>P. p. pygmaeus</i>	200	1	0	3	0
Bongaya	Bongaya	10	2002–2003	0.18	0.28	<i>P. p. morio</i>	250	1	0	4	0
Bukit Baka	Bukit Baka	11	2003	0.43	0.60	<i>P. p. wurmbii</i>	400	1	0	1	0
Bukit Perai	South Rongga-Perai	11	2003	0.46	0.64	<i>P. p. wurmbii</i>	140	1	0	3	0
Crocker range	Crocker range	12	2002–2003	0.20	0.31	<i>P. p. morio</i>	1000	1	0	1	0
Danau Sentarum	DS lowland	12	1997	1.80	2.07	<i>P. p. pygmaeus</i>	50	1	0	3	1
Danau Sentarum	DS peat heavy logged	12	1997	0.43	0.37	<i>P. p. pygmaeus</i>	50	2	0	4	0
Danau Sentarum	DS peat logged	12	1997	3.29	2.86	<i>P. p. pygmaeus</i>	50	2	0	3	0
Danau Sentarum	DS peat partly logged	12	1997	4.09	3.55	<i>P. p. pygmaeus</i>	50	2	0	2	1
Gunung Gajah	Corridor	13	2001–2004	5.66	2.63	<i>P. p. morio</i>	345	1	0	3	1
Gunung Gajah	Ex-Gruti	13	2001–2004	2.26	1.05	<i>P. p. morio</i>	296	1	0	2	0
Gunung Gajah	Gunung Gajah	13	2001–2004	2.98	1.39	<i>P. p. morio</i>	341	1	3	2	0
Gunung Gajah	Sungai Gie	13	2001–2004	0.53	0.25	<i>P. p. morio</i>	300	1	0	1	0
Gunung Palung	GP buffer zone	14	2001	2.50	3.97	<i>P. p. wurmbii</i>	50	2	2	4	1
Gunung Palung	GP disturbed lowland	14	2001	3.00	3.75	<i>P. p. wurmbii</i>	50	1	1	3	0
Gunung Palung	GP disturbed peat	14	2001	3.20	4.37	<i>P. p. wurmbii</i>	50	2	2	3	0
Gunung Palung	GP Lowland hill	14	2001	2.60	3.41	<i>P. p. wurmbii</i>	200	1	0	2	1
Gunung Palung	GP mid-elevation	14	2001	2.77	3.97	<i>P. p. wurmbii</i>	550	1	3	1	0
Gunung Palung	GP montane	14	2001	2.43	3.76	<i>P. p. wurmbii</i>	900	1	3	1	0
Gunung Palung	GP primary lowland	14	2001	3.22	4.03	<i>P. p. wurmbii</i>	50	1	1	1	1

Table 6.2 (cont.)

Habitat unit	Region name	Reference	Survey date(s)	Reported density (ind/km ²)	Standardized density (ind/km ²)	Species	Mean altitude (m)	Dominant habitat	Mosaic	Logging status	Neighbouring logging
Gunung Palung	GP primary peat	14	2001	4.09	5.59	<i>P. p wurmbii</i>	50	2	2	1	1
Katingan floodplains	Kat Kajang Pamali	15	2003	1.95	1.92	<i>P. p wurmbii</i>	10	2	2	2	0
Katingan floodplains	Kat Kaluruan	15	2002	0.94	0.93	<i>P. p wurmbii</i>	10	2	0	4	0
Katingan floodplains	Kat Perigi	15	2002	2.94	2.89	<i>P. p wurmbii</i>	10	2	2	1	0
Katingan floodplains	Kat Tarantang	11	2003	1.69	1.66	<i>P. p wurmbii</i>	10	2	0	3	0
Kuamut	Kuamut	10	2002–2003	0.06	0.09	<i>P. p. morio</i>	500	1	0	3	0
Kulamba	Kulamba	10	2002–2003	2.50	3.85	<i>P. p. morio</i>	100	1	1	3	1
Lower Kinabatangan	Gomantong FR	16	2002–2003	3.80	3.23	<i>P. p. morio</i>	100	1	1	1	0
Lower Kinabatangan	Lower Kinabatangan Lot 1	16	2002–2003	6.00	4.95	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 10a	16	2002–2003	1.80	1.83	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 10b	16	2002–2003	2.40	2.30	<i>P. p. morio</i>	100	1	1	4	0
Lower Kinabatangan	Lower Kinabatangan Lot 2	16	2002–2003	5.00	7.04	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 3	16	2002–2003	1.90	1.83	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 4	16	2002–2003	3.10	2.73	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 5	16	2002–2003	2.10	2.00	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 6	16	2002–2003	2.10	1.95	<i>P. p. morio</i>	100	1	1	3	0
Lower Kinabatangan	Lower Kinabatangan Lot 7	16	2002–2003	1.30	1.20	<i>P. p. morio</i>	100	1	1	4	0
Lower Kinabatangan	Lower Kinabatangan Lot 8	16	2002–2003	0.70	0.58	<i>P. p. morio</i>	100	1	1	4	0
Lower Kinabatangan	Lower Kinabatangan Lot 9	16	2002–2003	1.60	1.32	<i>P. p. morio</i>	100	1	1	4	0
Lower Kinabatangan	Pangui FR	16	2002–2003	2.60	2.27	<i>P. p. morio</i>	100	1	1	1	0
Mangkutup	Block B Main Canal	15	2001	0.67	0.78	<i>P. p wurmbii</i>	20	2	0	3	1
Marang-Baai	Baai	13	2001–2004	1.74	0.81	<i>P. p. morio</i>	435	3	0	4	0
Marang-Baai	Marang	13	2001–2004	0.39	0.18	<i>P. p. morio</i>	125	3	0	4	0

Mawas	Tuanan	17	2003	2.77	3.84	<i>P. p wurmbii</i>	20	2	2	4	0
Muara Lesan/Gunung Nyapa	Gunung Nyapa	13	2001–2004	0.63	0.29	<i>P. p. morio</i>	256	3	0	2	0
Muara Lesan/Gunung Nyapa	Muara Lesan	13	2001–2004	6.36	2.96	<i>P. p. morio</i>	160	1	0	2	1
Pinangah	Pinangah	10	2002–2003	0.23	0.35	<i>P. p. morio</i>	1000	1	0	4	0
Sabangau	LAHG LPF 1996	18	1996	0.96	1.12	<i>P. p wurmbii</i>	10	2	0	1	0
Sabangau	LAHG MSF 1996	18	1996	2.01	2.35	<i>P. p wurmbii</i>	10	2	0	3	0
Sabangau	LAHG TIF 1996	18	1996	2.13	2.49	<i>P. p wurmbii</i>	10	2	0	1	0
Sabangau	Paunggulas	15	2004	2.70	3.16	<i>P. p wurmbii</i>	10	2	2	3	1
Sabangau–Kahayan	Block C Kalamangan	15	1999	0.42	0.49	<i>P. p wurmbii</i>	10	2	0	3	1
Sabangau–Kahayan	Block C Pilang	15	2000	1.13	1.31	<i>P. p wurmbii</i>	10	2	0	3	1
Samba–Kahayan uplands	N Kecubung	15	2003	0.72	1.18	<i>P. p wurmbii</i>	150	1	0	2	0
Samba–Kahayan uplands	N Kecubung a	8	2005	1.10	1.59	<i>P. p wurmbii</i>	178	1	0	3	0
Samba–Kahayan uplands	N Kecubung b	8	2005	0.06	0.08	<i>P. p wurmbii</i>	88	1	0	3	0
Samba–Kahayan uplands	S Kecubung	8	2005	1.06	1.48	<i>P. p wurmbii</i>	92	1	0	3	0
Segama	Danum Valley	10	2002–2003	1.04	1.60	<i>P. p. morio</i>	250	1	0	1	0
Segama	Segama–Production forests	10	2002–2003	1.30	2.00	<i>P. p. morio</i>	250	1	0	3	0
Silabukan	Silabukan	10	2002–2003	0.58	0.89	<i>P. p. morio</i>	250	1	0	3	1
Tabin	Tabin	10	2002–2003	1.26	1.94	<i>P. p. morio</i>	100	1	1	3	0
Tanjung Puting	TP Camp Leakey	19	2003	1.96	2.72	<i>P. p wurmbii</i>	10	2	2	1	0
Tanjung Puting	TP disturbed dry forest	19	2003	1.59	2.21	<i>P. p wurmbii</i>	10	1	0	3	0
Tanjung Puting	TP disturbed swamp	19	2003	1.99	1.96	<i>P. p wurmbii</i>	10	2	0	3	0
Tanjung Puting	TP good dry forest	19	2003	2.09	2.90	<i>P. p wurmbii</i>	10	1	0	1	1
Trus Madi	Trus Madi	10	2002–2003	0.41	0.63	<i>P. p. morio</i>	1000	1	0	3	0
Ulu Kalumpang	Ulu Kalumpang	10	2002–2003	0.30	0.46	<i>P. p. morio</i>	250	1	0	2	0
Ulu Tungud	Ulu Tungud	10	2002–2003	0.04	0.06	<i>P. p. morio</i>	1000	1	0	4	0
Upper Kinabatangan	Deramakot	10	2002–2003	1.50	2.31	<i>P. p. morio</i>	500	1	0	2	0
Upper Kinabatangan	Lokan	10	2002–2003	1.19	1.83	<i>P. p. morio</i>	500	1	0	2	0
Upper Kinabatangan	Tangkulap	10	2002–2003	0.62	0.95	<i>P. p. morio</i>	500	1	0	4	0
Upper Kinabatangan	Tawai	10	2002–2003	0.07	0.11	<i>P. p. morio</i>	500	3	0	1	0

1, Wich and Geurts unpublished; 2, Wich *et al.* 2004a; 3, van Schaik *et al.* 2001; 4, Buij *et al.* 2003; 5, Singleton 2000; 6, Simorangkir unpublished; 7, Gumal unpublished; 8, Brassey unpublished; 9, Ancrenaz 2006; 10, Ancrenaz *et al.* 2005; 11, Hearn and Ross unpublished; 12, Russon *et al.* 2001; 12, Marshall *et al.* 2006; 14, Johnson *et al.* 2005b; 15, Husson; Morrogh-Bernard; McLardy and D'Arcy unpublished; 16, Ancrenaz *et al.* 2004; 17, van Schaik *et al.* 2005a; 18, Morrogh-Bernard *et al.* 2003; 19, Galdikas *et al.* unpublished.

Dominant habitat: 1, dry forest; 2, peat-swamp forest; 3, limestone–karst forest.

Mosaic: 0, single habitat-type; 1, dry-lowland mosaic; 2, peat mosaic; 3, upland mosaic.

Logging status: 1, unlogged; 2, lightly logged; 3, logged; 4, heavily logged.

Neighboring logging: 1, present; 0, absent.

Table 6.3 Comparison between orangutan densities estimated from (a) counts of animals and (b) standardized nest surveys

Site	'Actual' density	Source	Standardized density	Difference (%)
Kluet swamp Suaq Balimbing	7.0	van Schaik (1999)	7.20	+3
Tanjung Puting Camp Leakey	3.0	Galdikas (1988)	2.72	-9
Mawas Tuanan	4.25-4.5	van Schaik <i>et al.</i> (2005a)	3.84	-10 to -15
Upper Kinabatangan Lokan	2.1	Horr (1975) ^a	1.83	-13
Sabangau LAHG MSF	2.3	Ley-Vela (2005) ^b	1.93 ^c	-15
West Leuser Ketambe	5.0	Rijksen (1978)	3.05	-39

^aLokan has been selectively logged since Horr's study.

^bline transect estimate, N, 18; distance surveyed, 151.5 km.

^cDensity estimate from 2005, post-logging.

and non-mosaic (mean values: peat-swamp > dry forest > karst). Post-hoc tests showed no significant pairwise comparisons within either group. Between groups, peat-mosaic habitat supports significantly higher densities than all non-mosaic sites (peat-mosaic > peat-swamp, $p = 0.001$; peat-mosaic > dry forest, $p < 0.0005$; peat-mosaic > karst, $p < 0.0005$); dry-lowland mosaic supports significantly higher densities than dry forest ($p = 0.002$) and karst ($p = 0.001$) sites; and hillside-mosaic supports significantly higher densities than karst forest ($p = 0.010$). Comparisons using solely Bornean sites yielded comparable patterns; sample sizes were too small to permit an analysis using solely Sumatran sites.

Hypotheses 5: We tested to see if densities differed between the three subspecies of *Pongo pygmaeus*. When all sites were included in the analysis, observed densities were in the rank order *P. p. wurmbii* > *P. p. pygmaeus* > *P. p. morio*, and the difference between *P. p. morio* and *P. p. wurmbii* was significant ($F_{2,78} = 4.14$, $p = 0.020$; *P. p. wurmbii* > *P. p. morio*, $p = 0.020$). No peat sites were surveyed in *P. p. morio*'s range, however, and no karst sites surveyed in either of the other two subspecies' range. Removing these habitat types from the analysis resulted in a change of rank order to *P. p. wurmbii* > *P. p. morio* > *P. p. pygmaeus* although none of these differences were significant ($F_{2,54} = 2.11$, $p = 0.132$). As altitude is shown to be negatively correlated with density in Borneo we ran a density/altitude

regression for all non-peat or karst sites and then conducted a one-way ANOVA between subspecies on the residuals. Again, this was not significant ($F_{2,54} = 1.69$, $p = 0.195$) so we find no evidence for densities varying between subspecies on Borneo.

To identify those factors which explain the most variance in population density, we conducted an ordinary least squares (OLS) regression with orangutan population density as the dependent variable, coding both species and the presence/absence of a mosaic of habitats as dichotomous variables and habitat type as a block of dummy variables. The significance of these dummy variables was assessed as a set using the F test for r^2 change. We examined a scatterplot of the standardized residuals against the standardized predicted values which confirmed that assumptions of linearity and homogeneity of variance were met.

In this test both mosaic and species were highly significant correlates of orangutan density (presence of mosaic > absence of mosaic; *P. abelii* > *P. pygmaeus*) whereas altitude was not (whole model: adjusted $r^2 = 0.36$, $F_{5,104} = 13.44$, $p < 0.0005$; Mosaic: $\beta = 0.47$, $t = 5.65$, $p < 0.0005$; Species: $\beta = 0.35$, $t = 3.54$, $p < 0.0005$; Altitude: $\beta = -0.12$, $t = -1.04$, $p = 0.151$). Habitat-type was also a significant predictor of density (r^2 change = 0.05, F -change_{2,104} = 3.84, 2-tailed $p = 0.025$) although peat-swamp forest density was not significantly higher than dry forest density ($\beta = 0.13$, $t = 1.46$, $p = 0.074$). Both peat-swamp and dry forest habitats had significantly

higher density than karst forest (peat > karst, $\beta = 0.23$, $t = 2.73$, $p = 0.003$; dry > karst, $\beta = 0.17$, $t = 2.21$, $p = 0.015$).

Hypotheses 6: To test the effect of logging on density we conducted an OLS regression with mosaic, altitude, habitat-type and logging (coded as a dichotomous variable: 1 = unlogged, 0 = logged) as the independent variables. We excluded Sumatran sites from this analysis as there are very few logged Sumatran sites in our sample. In this analysis logging was a weakly significant predictor of orangutan density with logged sites having a lower density than unlogged sites (whole model: adjusted $r^2 = 0.42$, $F_{5,75} = 12.73$, $p < 0.0005$; Logging: $\beta = 0.16$, $t = 1.79$, $p = 0.039$).

Hypotheses 7: To test for differences between categories of logging intensity we ran the same OLS regression, this time with the four categories of logging intensity coded as dummy variables. Logging intensity is a significant predictor of density (whole model: adjusted $r^2 = 0.46$, $F_{7,73} = 10.73$, $p < 0.0005$; r^2 change = 0.07, F -change_{3,73} = 3.51, 2-tailed $p = 0.019$). Logged sites had a lower density than both unlogged and lightly logged sites, and a higher density than heavily logged sites, but this difference was not significant. There was very little difference between unlogged and lightly logged sites. Heavily logged sites had significantly lower density than both unlogged and lightly logged sites. (unlogged > heavily logged, $\beta = 0.29$, $t = 2.74$, $p = 0.004$; lightly logged > heavily logged, $\beta = 0.26$, $t = 2.65$, $p = 0.005$).

Hypotheses 8: Testing our last hypothesis, that logging causes overcrowding in neighboring areas of unlogged habitat, is problematic as this factor cannot be determined by a brief visual inspection of a site only. We could only confirm that overcrowding has occurred at sites where we have density estimates from both before and after logging. A gross analysis of our sample reveals that densities in areas where neighboring logging is reported were higher than densities elsewhere ($t = 2.04$, $df = 108$, $p = 0.022$), and that this was a strongly significant predictor of density when incorporated into the regression model created for H7 (whole model: adjusted $r^2 = 0.51$, $F_{8,72} = 11.18$, $p < 0.0005$; Neighboring logging: $\beta = 0.23$, $t = 2.75$, $p = 0.004$).

6.4 Discussion

6.4.1 Natural variation in orangutan density

In this chapter we have presented the first large-scale quantitative comparison of orangutan densities between Sumatra and Borneo and between different habitat types. We show that densities in Sumatra are higher than in comparable habitat in Borneo, providing support for Marshall *et al.*'s conclusion (Chapter 7) that Sumatran forests are more productive than Bornean forests and hence provide better habitat for orangutans. This is largely influenced by the very high densities found in the Kluet, Singkil and Tripa swamps where peat soils are regularly inundated by rivers and run-off from adjacent hills that bring minerals from the Leuser mountains. This must be as close to the optimum habitat that remains in the orangutan's range (similar conditions are exceedingly rare in Borneo). Within Borneo we find no significant differences in density between the three subspecies of *P. pygmaeus*, suggesting that *P. p. morio* has evolved special behavioral and anatomical adaptations to food scarcity in eastern Borneo and therefore occurs at a similar density as the other two subspecies (Taylor 2006a; Chapter 2).

We provide support for Marshall *et al.*'s second conclusion (Chapter 7), that sites with less extreme periods of fruit shortage support higher densities, by demonstrating that sites with a mosaic of habitats support significantly higher densities than those areas with a single habitat-type present. We also show that peat-swamp forests support higher mean densities than dry forest habitat, however, this difference was not significant in our analysis, contrary to our prediction. We generated this hypothesis from knowledge of a few, seasonally inundated (mosaic) peat-swamp forests where orangutan density is high, but our analysis shows that non-mosaic peat-swamps support much lower densities. Peat-swamp forest structure and diversity depends on peat thickness, hydrology, chemistry and organic matter dynamics (Page *et al.* 1999), with the lowest tree biomass, canopy height and plant diversity occurring in poorly drained areas of deep peat (Page *et al.* 1999). Therefore we conclude that all peat-swamps are not equal and very poorly drained peat areas (such as the Sabangau low pole

forest) support very low densities. Additionally, it is possible that orangutans maintain similar densities in peat-swamp and dry forest habitats by adopting a different foraging strategy in each. Morrogh-Bernard *et al.* (Chapter 8) show that Bornean orangutans allocate their activity budgets differently in dry forest compared to peat-swamp forest, and suggest that this is in response to different temporal patterns of fruit production in the two habitats.

We report a strong negative correlation between orangutan density and altitude for Borneo, as predicted, but not for Sumatra. Density is expected to decline with altitude in Borneo because fruit availability declines along the same gradient (Cannon *et al.* 2007), but Djojosedharmo and van Schaik (1992) find the same relationship between fruit availability and altitude in Sumatra. We do not discount the possibility of an altitude–density relationship in Sumatra, but instead put forward a number of reasons to explain why we do not find this. First, there are very few lowland dry forest sites in our Sumatran sample, mainly because most of these forests have already been cleared for development. Second, the situation in Sumatra is complicated by the *Massenerhebung* effect, caused by the Barisan mountain chain (Rijksen and Meijaard 1999). This results in an upwards shift of altitudinal vegetation limits in those parts of northern Sumatra where high peaks are found, but this effect does not act in a uniform manner throughout the Leuser ecosystem. Therefore forests at the same altitude may have very different floral compositions and hence different carrying capacities for orangutans. Third, the nest-degradation time is expected to vary considerably in upland areas, where mountain peaks, ridges, steep uphill gradients and plateaus are likely to cause large variations in rainfall, exposure and soil types over relatively small distances. For the standardization process we assigned nest decay times estimated from low-elevation dry forests to high-elevation sites. As a result we could have under- or over-estimated densities at high-elevation sites by a wide margin. This is less of a concern in Borneo, where dipterocarp-dominated hill forests generally support very low orangutan densities, but could be significant in northern Sumatra where very high nest counts are

recorded at high altitudes. Further examination of the factors affecting nest decay rates are urgently required across the orangutan's range, and particularly in the Leuser ecosystem.

6.4.2 Impacts of disturbance on density

Our analyses show that densities are lower in moderately to heavily logged forest than in unlogged areas of comparable habitat, in accordance with the majority of studies already published on this subject. This is primarily attributed to the loss of large trees and consequent reduced level of fruit availability (Rao and van Schaik 1997; Wich *et al.* 2004a). Increased energetic costs owing to a break-up of canopy structure are also implicated in the observed decline (Rao and van Schaik 1997). Sumatran orangutan densities are reported to decline by 50% (van Schaik *et al.* 1995) to 60% (Rao and van Schaik 1997) post-logging, and southern Bornean orangutan (*P. p. wurmbii*) densities are reported to decline by 21% (Felton *et al.* 2003) to 30% (Morrogh-Bernard *et al.* 2003).

The size of the decline depends on a number of factors. First is the degree to which orangutans can survive in logged forest. Meijaard *et al.* (2005, 2008) suggest that a species ability to persist in logged habitat depends on their degree of dietary flexibility, in common with Johns (1997) who suggests that the most successful species are those which can survive on a largely folivorous diet even if they are considered frugivorous in primary forest. During periods of low-fruit abundance orangutans change their diet to include more leaves and cambium (Knott 1998a) and a shift from frugivory to folivory following logging was recorded at Ketambe in northern Sumatra (Rao and van Schaik 1997). Bornean orangutans have more dietary flexibility than Sumatran orangutans (Wich *et al.* 2006a), probably evolved as a response to longer periods of low-fruit abundance on Borneo than Sumatra (Wich *et al.* 2006a, b), and this may be why Bornean orangutans appear to be more resistant to logging than their Sumatran counterparts. Within Borneo, *P. p. morio* has more dietary flexibility than the other two subspecies (Chapter 8) and thus may explain why *P. p. morio* seems to cope extremely well with logging (Ancrenaz *et al.* 2004b;

Marshall *et al.* 2006) compared to the other subspecies of *P. pygmaeus*.

Second, the type and intensity of logging has an impact. We found that orangutan density was dependent on the intensity of logging, with heavily logged forests having the lowest density, and unlogged and lightly logged forests the highest. This is in agreement with Ancrenaz *et al.* (2004b, 2005) who found that densities at a number of sites in Sabah were not significantly different between unlogged and sustainably logged areas but significantly lower in heavily logged areas. While it was difficult to empirically compare logging intensity between all the sites included in this study, sites with well-managed selective-logging operations were typically classed as lightly logged, and those subjected to uncontrolled illegal logging as heavily logged. Most traditional logging operations target only a small number of valuable tree species, especially dipterocarps which do not produce fruit important to orangutans (Chapter 9) and the density of which is negatively correlated with orangutan density (Chapter 7). Illegal logging targets a much greater number of tree species, including many food-trees (twelve of the twenty most-eaten species were cut illegally at one peat-swamp forest study site, compared to only three cut by the previous legal logging concession; Morrogh-Bernard unpublished data) and is thus expected to have a much more severe effect on orangutan density. Other studies have noted differences between mechanized logging and hand logging. Mechanized logging, in which roads are constructed and all trees are removed by vehicles, causes far more structural and incidental damage to the forest than hand logging, in which felled timber is dragged from the forest on greased rails, or floated out of peat forests along small canals. Felton *et al.* (2003) found that hand-logging in Gunung Palung left the middle canopy relatively unscathed, whereas Johns (1988) found that mechanized logging in West Malaysia affected all tree size classes equally.

Third, the opening up of the forest to logging increases opportunities for hunters, and hunting has a serious negative impact on orangutan populations above and beyond that caused by habitat degradation (Leighton *et al.* 1993). In areas where hunting is prevalent, the effects of hunting

may outweigh the effects of logging (Marshall *et al.* 2006) and may be the main factor determining the survival of orangutans in exploited forests (Ancrenaz *et al.* 2004b).

Fourth, the time elapsed since logging is important. As discussed above, orangutans show dietary flexibility and this can delay an observed decline in density, sometimes for several years. In one study at Sabangau in southern Borneo, localized changes in orangutan distribution were recorded following the onset of logging activities but no decrease in overall numbers was recorded until four years later when a sudden and large decline of 30% was estimated over the course of a year (Husson *et al.* unpublished data). At the other end of the scale, one study showed that orangutan density at a site in Sumatra had recovered to its pre-logging density after a period of twenty years (Knop *et al.* 2004).

As well as long-term reductions in density, several studies report high densities of orangutans in old-logged and unlogged forest neighboring areas where logging is active (Russon *et al.* 2001; Morrogh-Bernard *et al.* 2003; Ancrenaz *et al.* 2004b, 2005). This is attributed to localized changes in distribution caused by orangutans moving away from logging disturbance, resulting in overcrowding and an overshoot of the carrying capacity in these refuge areas. For example Husson *et al.* (unpublished data) show that the density of an actively logged area declined to one-sixth of its pre-logging level while the density in a neighboring area of less-optimal habitat doubled over the same time period. This behavior is reported for other non-territorial primates including *Colobus spp.* and *Cercopithecus diana* (Martin and Asibey 1979), *Indri indri* (Petter and Peyrieras 1976) and *Presbytis melalophos* (Johns 1986) and in our analysis we find further evidence for overcrowding in Bornean orangutan populations. In Sumatra, by contrast, overcrowding has not been reported at either Ketambe or Suaq Balimbing, even though neighboring forest at each site has been logged and cleared, both prior to and during surveys (van Schaik *et al.* 2001). Sumatran females are believed to have stable, possibly fixed, home ranges (Singleton and van Schaik 2001) which may explain their reluctance to move during or after logging.

6.4.3 Implications for conservation

Both species of orangutan are endangered and effective forest conservation and management programs are required to save them from extinction in the wild. The results presented in this chapter have several implications for their conservation. First, sites with the highest density of orangutans should be prioritized for conservation (together with the largest remaining populations), and we show these to be sites with a mosaic of habitats. It is therefore essential to preserve this habitat heterogeneity, in particular by protecting riverine forest that is at most risk of conversion and by preventing peatland drainage. Second, we show that orangutan density decreases with increased logging intensity, but that orangutans are resistant to light-logging disturbance. In areas where orangutans coexist with legal logging operations we encourage sustainable logging management, that restricts the type and size of trees removed and retains patches of pristine forest. Third, the standardization process produced density estimates that were in the most part an increase on published estimates and closely matched estimates of density from long-term studies. It is therefore possible that the total number of orangutans remaining exceeds the most recent estimate of population size. Nevertheless we must stress that the destruction of orangutan habitat in Borneo and Sumatra is continuing at a rapid pace, and that the downward

trend in orangutan numbers which has been documented over the past twenty years has not been stopped or slowed.

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