

DEVELOPMENTS IN PRIMATOLOGY:
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Indonesian Primates

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Chapter 4

The Natural History of Sumatran Orangutan (*Pongo abelii*)

Sri Suci Utami Atmoko and Carel P. van Schaik

Introduction

The orangutan is the only great ape of Asia. Its present range is confined to dwindling areas on the islands of Sumatra and Borneo (Rijksen and Meijaard 1999). In contrast to its African relatives, the chimpanzee, bonobo (genus *Pan*), and gorilla (genus *Gorilla*), it is extremely arboreal (the Sumatra species more so than the Borneo as Sumatra still harbors tigers). In fact, it is the largest and heaviest of all predominantly arboreal mammals. Among the diurnal primates, it is, moreover, exceptional in that it is comparatively solitary.

Orangutans are now considered to represent two distinct species, the Sumatran orangutan, *Pongo abelii*, now occurring only in the northern part of Sumatra, and the Bornean orangutan, *Pongo pygmaeus*, still occurring in many scattered parts of Borneo with three subspecies (*P. p. pygmaeus*, *P. p. wurmbii*, and *P. p. morio*; Zhi et al. 1996; Groves 2001; Warren et al. 2001; Steiper 2006; Goossens et al. 2009). Recent work suggests that they are different enough from their Bornean congeners that extrapolation from the Bornean species is risky.

On the basis of two active field sites in the Gunung Leuser National Park, northern Sumatra (Aceh), Indonesia, where wild orangutans are being studied, this chapter focuses on the socio-ecology and behavior of Sumatran orangutans (*Pongo abelii*).

Field Sites

The Ketambe orangutan population is the longest-studied wild Sumatran orangutan population. It has been studied continuously since 1971. Together with Suaq Balimbing population that has been studied since 1991, the long-term data have yielded what we know today about Sumatran orangutan biology. Ketambe (3°41'N,

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97°39'E) is located in the upper Alas valley (a rift valley inside the Barisan mountain range) at an altitude of 350 ± 500 m asl. This study area mainly consists of primary rain forest and was described in detail by Rijksen (1978) and van Schaik and Mirmanto (1985). Suaq Balimbing (3°04'N, 97°26'E) is located in the western coastal plain, some 70 km to the south-west, separated by mountains to over 2,000 m asl with Ketambe, and consists of a variety of floodplain and hill forest habitats.

Life History

Based from 32-years' data at Ketambe and 5.5-years' data at Suaq Balimbing, Wich et al. (2004a, 2009) reported that Sumatran interbirth intervals were longer than those reported for Bornean sites, but that age at first reproduction was similar at 15.5 years. For Ketambe, the mean interbirth interval has been estimated to be 9.3 years (Wich et al. 2004a), while for Suaq Balimbing, estimates are at least 8.2 years (van Noordwijk and van Schaik 2005). The first longevity estimates from the wild (Ketambe) indicate life spans of over 50 years, with no evidence for menopause. Mortality rates were very low for both males and females, with no clear sex difference. These estimates establish the Sumatran orangutan as the nonhuman primate with the slowest life history pace (Wich et al. 2004a).

One of the most unusual features of Sumatran orangutans is the remarkable individual variation in the age at which sexually mature males develop their sexual secondary characteristics (SSC), a phenomenon called bimaturism. This bimaturism leads to the coexistence of two adult, sexually mature morphs: flanged and unflanged males. In Sumatra, SSC development may be delayed 15–20 years after reaching sexual maturity (Utami Atmoko and van Hooff 2004). Although unflanged mature males lack SSCs; they are fertile, sexually active, and are able to sire offspring (Kingsley 1982; Maggioncalda et al. 1999, 2002; Utami Atmoko 2000; Utami et al. 2002; Goossens et al. 2006).

Population Distribution

During the Pleistocene, orangutans could be found from the south in Java up to the foothills of the Himalayas and the Tropic of Cancer in China. This distribution was prehistoric, and the degree to which it has been influenced by humans can be disputed. The reason for the continuous decline in orangutan numbers and distributions is that humans and ape favor the same habitat, namely alluvial plains, peat-swamp forests, and valleys. Now, their habitat has been limited to the island of Borneo and Sumatra (Fig. 4.1).

The Sumatran population is concentrated in the northern part of the island (Aceh and North Sumatra provinces) and is estimated to total ca 6,600 individuals in (yr) (citation). Of the 13 identified populations, only 7 contain more than 500 individuals, the minimum number needed to have some prospects for long-term viability (Soehartono et al. 2007; Wich et al. 2008).



Sumatran orangutan (*Pongo abelii*) (Photo by Jeff Oonk)

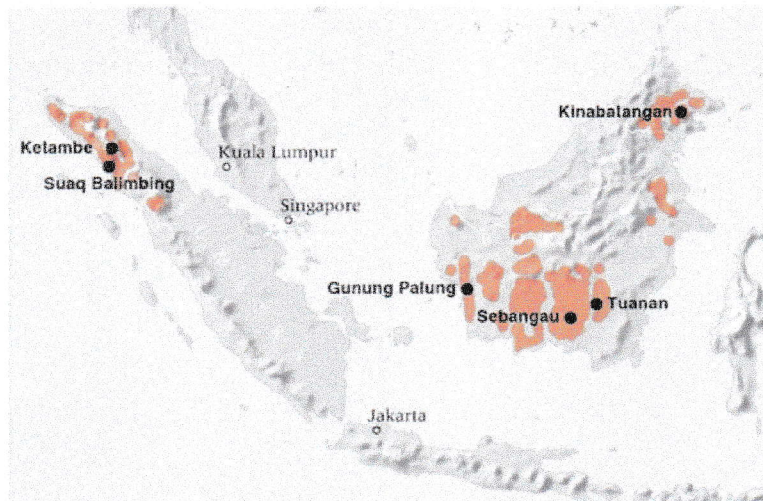


Fig. 4.1 Research study sites of Ketambe and Suaq Balimbing at Gunung Leuser National Park, Aceh, Indonesia (map by Perry van Duihoven)

Sumatran orangutans are found at higher densities (Ketambe 3–5 ind/km²; Suaq Balimbing 7 ind/km²) than most Bornean orangutans, although densities decline with increasing altitude in both species (Rijksen 1978; Djojosoedharmo and van Schaik 1992; van Schaik 1999; Rijksen and Meijaard 1999; Husson et al. 2009). Because the orangutan is a frugivore, studies suggest that orangutan densities are related to the proportion of soft pulp in a given area (Djojosoedharmo and van Schaik 1992; van Schaik et al. 1995; Buij et al. 2002) and the density of large strangling figs, at least on dry land (Wich et al. 2006). Lower densities at higher altitudes are probably a function of decreasing fruit availability.

Behavioral Ecology

Sumatra lies at the edge of a currently active subduction zone between two tectonic plates. The resulting recent and ongoing mountain building and volcanism lead to relatively intense erosion that provides continued mineral deposition in the lowland regions. As a result, a much higher proportion of Sumatran soils are productive and suitable for agriculture. In general, then, Sumatra is the product of recent geological processes, and, therefore, the soils of Sumatra tend to be higher in plant nutrients than those of Borneo (van Schaik et al. 2009c).

The implications of these island differences for fruit availability are probably the most important for orangutans. Fluctuations of food-fruit availability in Southeast Asian rain forest are particularly pronounced in lowland forests. As Wich et al. (2006) showed, there is very little systematic influence of fruit availability on Sumatran orangutan diets. At Ketambe, this might be due to the relatively high density of strangling figs and the general high productivity of the area. The figs' fruiting patterns are not strongly seasonal, which ensures that there are always a few huge fig trees in the area with abundant fruit in which orangutans can gather to feed (van Schaik 1986; Sugardjito et al. 1987; Utami et al. 1997).

As a result, Sumatran orangutans always have a high percentage of fruit in their diet; in this they differ from their cousins in Borneo, who must turn to leaves and bark as fallback food resources during low fruit availability. In Gunung Palung, on Borneo, orangutans suffered negative energy budgets during periods of prolonged low fruit availability after mast fruiting, as shown by ketones in their urine (Knott 1998; see Table 4.1). In Ketambe, however, we found no ketones in orangutans' urine and so no evidence of negative energy budget (Wich et al. 2006). These and other analyses of geographic variation in orangutans support the view that the Sumatran forests are generally better habitat for orangutans than Bornean forests (Marshall et al. 2009).

Activity Patterns

A general trend across sites shows that Sumatran orangutans divide their time among feeding (>50%), resting (22–42%), traveling (9–19%), with the remaining time spent on socializing and nest building (Table 4.2). Thus, orangutans in

Table 4.1 The comparison of fruit availability in Ketambe, Sumatra and Gn. Palung, Borneo (Wich et al. 2006; Knott 1998)

Condition	Ketambe (Sumatra)	Gn. Palung (Borneo)
Average monthly % of OU food trees fruiting	9.6 (sd=3.6, range=6.3–14.3)	6.1 (sd=2.8, range=2.5–12.5)
Minimum number of OU food trees fruiting/month	6.3%	2.5%
Minimum monthly % of fruit in the diet	50%	20%
Maximum monthly % constitute of cambium	5.3%	37%
Soil nutrients	More (volcanic origins)	Less

Table 4.2 Comparison of activity patterns in Ketambe and Suaq Balimbing (Wich et al. unpubl and van Schaik et al. unpubl cited in Morrogh-Bernard et al. 2009)

Site	Unflanged male			Flanged male			Sexually active female			Non-sexually active female		
	F	R	T	F	R	T	F	R	T	F	R	T
Ketambe	52.6	33.5	13.0	48.3	41.9	9.2	55.4	32.0	12.1	59.3	28.7	11.8
Suaq Balimbing	53.6	25.7	17.9	48.0	34.9	14.9	54.9	25.9	16.9	55.7	22.1	19.6

Sumatran forest have a high proportion of fruits in their diet year-round, which enables them to feed for more than 50% of their active period. They also restless and travel more than Bornean orangutans, at least Borneans that range in mixed-dipterocarp forest (Morrogh-Bernard et al. 2009).

In summary, non-sexually active females feed the longest and rest the least, flanged males rest the longest and feed/travel the least, and unflanged males travel the longest in Ketambe, while non-sexually active females travel the longest in Suaq. Because flanged males are larger than other sex-age classes, they can more easily satisfy their energy needs with foods that are harder and can, therefore, be harvested with less travel (Gaulin and Sailer 1985 in van Schaik et al. 2009b). Flanged males can also eat the same food items faster than other age-sex classes because of their larger body size, especially larger food items (e.g., in a giant strangler figs; see Utami et al. 1997).

Diet

Table 4.3 shows a comparison of diet composition, as measured by percentage of total feeding time. It appears that at both Ketambe and Suaq Balimbing, individuals show little variation in the time feeding on fruits, even though those at Ketambe have a slightly higher proportion of fruit in the diet. Wich et al. (2006) attributed this difference to the high density of large strangling fig trees at Ketambe. Strangler figs produce fruit year-round, thus are fed by orangutan constantly throughout the

Table 4.3 Orangutan diet composition at Ketambe and Suaq (percentages of total feeding time) (Morrogh-Bernard et al. 2009)

Site	Fruits	Leaves	Bark	Invertebrates	Other
<i>Ketambe</i>					
Mean	67.5	16.4	2.7	8.8	4.8 (inc. fl)
Low–high fruit	64.2–70.7	17.5–15.2	3.0–2.5	8.7–8.8	6.7–3.0
<i>Suaq Balimbing</i>					
Mean	66.2	15.5	1.1	13.4	3.8 (inc. fl)
Low–high fruit	62.7–69.6	18.3–12.7	0.8–1.4	14.6–12.2	3.6–4.1

year (Sugardjito et al. 1987). Figs are normally considered a fallback food that can be relied on when nonfig fruits are not available (Wich et al. 2006).

Meat Eating

Predation by orangutans on vertebrates is rare, considering the many hours of observation in the wild. However, occasionally at Ketambe and Suaq Balimbing, they catch slow loris, either by grabbing them directly or by quickly killing them by a bite to the head, after a short pursuit onto the forest floor. This qualifies as the stumble-upon-and-capture type of predation, and in this respect, it differs from the hunting that has been described for chimpanzees. So, capture of slow loris does not qualify as pursuit hunting (Utami Atmoko 1997; van Schaik et al. 2009b).

At Ketambe, no males have ever been seen to catch slow loris. Two females are loris capture specialists: their capture rate is higher than all other local orangutans (Utami and van Hooft 1997; Hardus et al. in preparation). At Suaq Balimbing, only three cases of loris capture have been observed, by three different individuals: two adult females, and one flanged male. There is therefore no evidence for a male bias in vertebrate capture among orangutans, as there is in chimpanzees (Boesch 1994a, b; Stanford et al. 1994a, b). If anything, the available data suggest a bias toward females, this could owe to the fact that catching loris typically takes place in the context of insect foraging (van Schaik et al. 2009c).

Tool Use

Orangutans at Suaq used tools in two main foraging contexts: extracting honey or social insects from nests hidden in tree holes and extracting the lipid-rich seeds from mechanically and chemically protected *Neesia* fruits. Use of seed extraction tools is somewhat biased toward females, but only because flanged males (and larger unflanged ones) are strong enough to open the fruits before they dehisce and before the protective stinging hairs have matured, so they can pick out the seeds

with their fingers. Once fruits have opened, all individuals use tools at virtually all visits (see van Schaik and Knott 2001 for details; van Schaik et al. 2003, 2009b).

At Ketambe and Agusan (some 30 km to the North), orangutan use leaf gloves as tools to handle spiny fruits or spiny branches, or as seat cushions in trees with spines. Orangutan in Ketambe also use tools for sexual stimulation (auto-erotic), both female and male, and as young as two years of age (van Schaik et al. 2003, 2009b; Utami Atmoko et al. 2009a; Fox and bin Muhammad 2002).

Social Relationships

A local area contains a dominant flanged male, a number of unflanged males, adult females, often with offspring, and adolescent males and females, along with various males that pass through regularly. The flanged male is intolerant towards other fully flanged males that intrude into his vicinity, and is supposed to be the focal element around whom the other units are organized (van Schaik and van Hooff 1996; Utami Atmoko 2000; Utami Atmoko et al. 2009a).

Individual orangutans live in large home ranges (Table 4.4). Perhaps more on ranging in Sumatran OU's, e.g., larger ranges than in Borneo and why, ranging responses to seasonal fruit scarcities.

Table 4.4 shows in both sites that male home ranges are larger than those of females, even if no estimates were possible. This is consistent with the expectation that males competing for access to females maximize their access to females by ranging more widely. As a result, male home ranges overlap extensively (Utami Atmoko et al. 2009a). That local resident dominant males have smaller ranges may be because dominance allows them to monopolize the females in the area where they reside. Other males, instead, must always be looking for females not monopolized by local dominants, and this forces them to range much more widely.

The ranges of several individuals of both sexes overlap considerably. Females appear to be philopatric; among males, some flanged ones remain in a relatively small area (called "resident") while others range over greater regions (called "non-resident") (Singleton and van Schaik 2001, 2002; Goossens et al. 2006; Knott and Kahlenberg 2007). Patterns of male residency are not permanent, because resident males may be forced out by non-resident or resident challengers (Utami and Mitra Setia 1995).

Two major factors are known to affect the tendency to associate: food availability and mating opportunities (Sugardjito et al. 1987; te Boekhorst et al. 1990; van

Table 4.4 Home range estimates of Sumatran orangutans (Singleton and van Schaik 2001; Utami Atmoko et al. 2009a)

Sites	Study area size (ha)	Female HR (ha)	Flanged male HR (ha)	Unflanged male HR (ha)
Ketambe	450	300–400	>females	>females
Suaq Balimbing	500–2,000	≥850	≥2500 ^a	≥2,500

^aThe locally dominant male ("resident") had a smaller home range than other flanged males, although it was still larger than the females' ranges.

Schaik and van Hooff 1996). Both the large size of orangutans and consequently, the high cost of their almost exclusively arboreal locomotion explain why they keep on their own. There is circumstantial evidence that living with others would impose to high costs in terms of the time and energy, budget because of the competition involved (te Boekhorst et al. 1990; van Hooff 1988; van Schaik and van Hooff 1996). This is indicated by the fact that on rare occasions, namely under conditions of ecological affluence, orangutans do congregate in groups and may even stay and travel together for several days (Sugardjito et al. 1987; Utami et al. 1997; Utami Atmoko 2000). However, this idea is not supported by the fact that the average party size at each site is not linked to the average fruit abundance at that site (van Schaik 1999; Utami Atmoko 2000; Wich et al. 2006). It is likely that Ketambe and Suaq orangutans, associate for rare benefits like mating and the transmission of social and foraging skills, that was suggested to be important in orangutans (Wich et al. 2006; van Schaik and Knott 2001; van Schaik et al. 2003). It seems that orangutans in Sumatra are able to maintain relatively high mean party size without bearing much cost on fruit availability due to the high density of large strangling fig trees in Ketambe compared to other areas (Rijksen 1978; Wich et al. 2004b) and these figs are less seasonal in their fruiting patterns than other fruiting trees in Ketambe (van Schaik 1986). This also explains why Sumatran orangutans tend to be more often found in groups than their Bornean counterparts (see the following section).

Given these costs of association, it is clear that consort formation affects travel behavior in both classes of males; on average, flanged males traveled less than unflanged males when traveling alone, but did not differ significantly when they were in consort with a female (Utami Atmoko and van Hooff 2004). When consorting, flanged males had to increase their travel to keep up with female they accompany, whereas consorting unflanged males slowed down. The females' travel behavior did not change when they were consorting. In other words, the males adjusted to the females (van Schaik 1999; Utami Atmoko 2000; Utami Atmoko and van Hooff 2004).

Male–Male Relationships

Given the large size and high overlap of home ranges as well as the dense vegetation, it would seem impossible for flanged males to monopolize access to potentially reproductive females effectively, especially since orangutan females do not show visible signs of ovulation. Among orangutans, there is ample evidence for male-male contest competition for access to fertile females, as well as alternative male mating strategies driven by this contest, suggesting that multiple males can easily locate females (Utami Atmoko et al. 2009a).

Both in Ketambe (Utami Atmoko 2000; Utami Atmoko and van Hooff 2004; Wich et al. 2006) and in Suaq Balimbing (van Schaik et al. 2009a), the differences between the two male classes were as predicted based on their difference in social strategy. We found ecological differences between flanged and unflanged males that are direct expressions of the large difference in mobility (time spent moving,

travel speed, day journey length). The greater mobility of unflanged males allowed them to feed more selectively, and thus have shorter feeding bouts. Flanged males may have supported their more sedentary life style by eating more fruit, in longer feeding bouts, and perhaps by spending more time on eating vegetable matter. Only the latter difference between the two male classes might also be linked to body size per se. To the extent that females differ significantly from any of these values, the sex difference is a product of multiple processes (reproduction, size, male socio-ecology) (van Schaik et al. 2009a).

Male–Female Relationships

Orangutans at the two Sumatran sites are more gregarious than Bornean orangutans (mean adult female party size 1.5–2.0 in Sumatra vs. 1.05–1.3 in Borneo; Mitra Setia et al. 2009). Sumatran orangutans occasionally congregate when they meet in large fruit trees. At Ketambe, for instance, large strangler figs often attract multiple adult orangutans simultaneously, and up to 14 individuals have been seen in or near a single tree (Mitra Setia et al. 2009).

Flanged males advertise their location by giving long calls. Long calls play a role in male spacing, by which relationships are communicated within the dispersed society, but their primary function in Sumatra is probably coordination of range use with adult females, and attraction of fertile females; unflanged males, in contrast, do not long call so they have to travel through an area to locate potentially fertile females (Delgado and van Schaik 2000; Mitra Setia et al. 2009; Utami Atmoko et al. 2009b). Females' responses to long calls suggest that they are trying to maintain earshot associations with the locally dominant male. The function of these loose associations is almost certainly that they allow females to seek refuge with the flanged males, especially dominant ones, if they are being harassed by other males. This evidence indicates the existence of loose communities in Sumatran orangutans, organized around dominant flanged males (MacKinnon 1974; Mitra Setia et al. 2009).

Female–Female Relationships

Among the Sumatran females, mean female party sizes at Ketambe and Suaq Balimbing are comparable in size, but associations at Ketambe involve fewer travel parties (van Schaik 1999). In Suaq, we found evidence for clusters of females, who may well be related, and whose ranges share similar boundaries with considerable overlap. Within these clusters they also show a tendency toward reproductive synchrony, as they have infants of similar ages, and preferential association with each other, even if home range overlap is taken into account (Singleton and van Schaik 2002).

Another example of female philopatry also found in Ketambe, where the daughters and granddaughters of the reintroduced rehabilitant Binjai all settled in the study

area and they have more tolerant relationships, meet more often, show less aggression and feeding tolerance (Mitra Setia et al. 2009), except during lowest fruit availability (Utami Atmoko et al. in preparation). With mix female population (wild and ex-rehab) in Ketambe, displacements between adult females occurred even in large fig trees. They were unidirectional, with one exception. The females in the study area could be ordered in a nearly linear dominance hierarchy. Although the test for linear hierarchy showed only a trend, the displacement data had a high directional consistency, and it seems justified to claim that a hierarchy indeed exists. With the acquisition of more data, this could become significant (Utami et al. 1997).

Mating Strategies

Flanged and unflanged males differ in their mating strategies. Flanged males, and especially dominant individuals, often establish consortships with potentially reproductive females and are usually preferred by females (Utami Atmoko 2000). Unflanged males engage in consortships comparatively rarely, but often try to copulate with females, even when they resist and resulting forced copulation (Galdikas 1979; MacKinnon 1974; Mitani 1985; Rijksen 1978; Schurmann and van Hooff 1986).

Despite their semi solitary nature, behavioral and experimental evidence suggests that individualized sexual relationships exist in orangutans (van Schaik and van Hooff 1996; Delgado and van Schaik 2000). The majority of sexual interactions in Sumatra were cooperative and occurred during a consort relationship. Females select their sexual partners and choose when to consort and mate cooperatively, i.e., females show clear preferences for or aversions to particular males (Utami Atmoko 2000; Fox 2002; Utami Atmoko et al. 2009b). The reproductive success of flanged males is made possible by the females' preference for flanged over unflanged males. The dominant flanged male in an area may be able to exclude other flanged males from his immediate ranging area, but he certainly does not exclude all unflanged males. Female preference then sets the scene for male-male competition; if females had no preferences at all, unflanged males would be much more successful than flanged males due to their higher mobility (Utami Atmoko et al. 2009a). At least in Sumatran, subordinate flanged males do not seem to be successful at all (Utami Atmoko et al. 2009a; van Schaik 2004). Whether this is also true for Borneo needs to be assessed in future work.

On the basis of the long term behavioral data and genetic paternity studies at Ketambe, Utami et al. (2002) hypothesized that the two male morphs represent coexisting male reproductive strategies, "sitting, calling, and waiting" for flanged males vs. "going, searching, and finding" for unflanged males. The unflanged males travel faster and roam more widely, and can also endure longer associations because they lack SSCs and flanged males are more tolerant toward these smaller males. They are therefore better able to gain access to some potentially fertile females by following consort pairs closely and engaging in sneak mating sometimes by harassing the females and by engaging in voluntary consorts with nulliparous females

who are less attractive to the flanged males (and with whom they may achieve their greatest siring success). Thus, only when a male is likely to achieve dominance in an area would the mating benefits of developing the full set of SSCs outweigh its costs. It is possible that a male may need to wait for a long time for such an opportunity to arise, which would explain the development arrest.

Conservation

Orangutans are of great scientific interest, representing a branch of great ape evolution distinct from the African great apes, and relevant to management of forest. They are regarded as “flagship” species that provide a symbol to raise conservation awareness to ensure survival of the forests that contain many other organisms.

The number of wild orangutans has declined continuously with the rapid loss of forest habitat, particularly in the lowland forests with their many timber trees species. The 2007 edition of the IUCN Red List (IUCN 2007) species recognized the Sumatran orangutan as Critically Endangered, whereas the Bornean orangutan has been listed as Endangered.

Orangutans everywhere cannot survive the conversion of forest into plantations, but on Sumatra, orangutans do not seem to cope well with selective logging. More research is needed to determine whether certain levels of extraction are compatible with orangutan conservation (Wich et al. 2008). Although the rate of forest loss in some areas remains high, in other areas there has been a decrease in forest loss rates and hence also a likely reduction in rates of orangutan decline. For instance, in recent years, annual forest loss in the Leuser Ecosystem in Sumatra decreased to 0.6% (Griffiths pers. com. in Wich et al. 2008). Recovery could be helped by retaining soft-pulp fruit bearing trees and climbers (especially *Ficus sp.* for Sumatran population) and strictly enforcing antipoaching laws (Rijksen and Meijaard 1999; Robertson and van Schaik 2001; Wich et al. 2008). However, habitat protection is most important as this is a key to orangutan survival.

Conclusions

Orangutans have been the subjects of long term field study at a number of different sites. Given their extended life span and slow development and the long-term cycles in affect their habitat, long-term studies like these are essential to document their behavior and life history. Only after more than 30 years of research are we beginning to understand orangutan life history to a certain extent, but we need much longer to complete the picture.

It is well appreciated that logging has a negative effect on orangutan density: on both islands orangutan density decrease after logging. Researchers have noted that the logging induced decrease in orangutan density seems less severe on Borneo than

on Sumatra. Although this ability to endure habitat damage might enable Bornean orangutans to survive in the short-term, it is largely unknown how logging affects long-term survival of orangutan populations. As habitat protection has become the foremost issue in orangutan conservation, we should continue long-term studies in part to monitor the long-term effects of logging on Sumatran orangutans and to their long-term survival, as part of efforts to save Sumatran orangutans.

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