The Behavioral Ecology and Conservation of the Orangutan (*Pongo pygmaeus*): A Tale of Two Islands

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Orangutans are the only great apes found outside of Africa. At present, they occur only on the two large Sunda-shelf islands of Sumatra and Borneo. Most researchers recognize two separate subspecies, *Pongo pygmaeus abelii* in Sumatra and *P.p. pygmaeus* in Borneo.[1,2] Relative to other primates, they have a variety of unusual features. These large-bodied frugivores are among the most solitary of anthropoid primates.[3–5] They are also highly dimorphic, with the average body mass (78 kg) of males being more than twice that of females (36 kg).[6] Despite its large body size the red ape has more specialized morphological adaptations for arboreality than do the African great apes. Researchers generally recognize sexually mature male orangutans with two physically distinct morphs, a phenomenon described as bimaturism. Males of the relatively smaller morph are known for forcing copulations with adult females.[5,7–9]

In contrast to chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*), orangutans, like bonobos (*Pan paniscus*), have natural histories that are poorly known. Early studies of orangutans were done at a handful of sites, among them Lokan, Ulu Segama, Mentoko, and Renun. Currently, however, and in contrast to the more than a dozen sites across Africa where chimpanzees and gorillas are being studied,[10] there are only four active field sites—Tanjung Puting[3,4] and Cabang Panti[11] in Borneo, and Ketambe[5,12] and Suaq Balimbing[7] in Sumatra (Fig. 1)—where wild orangutans are being studied. Hence, orangutans still present many puzzles, although some tentative solutions are now being explored. First, understanding of their evolutionary origins and successful reconstruction of the habits of their ancestors remain unresolved. Second, although it is clear how postcranial adaptations permit these large-bodied animals to travel through forest canopies,[13] it is not yet known what selective forces drove orangutans to such a pronounced arboreal lifestyle. Third, despite several long- and short-term studies, the orangutan's semi-solitary nature, large home ranges, and extended life history[3–5,7,11,12] make it difficult to acquire the vast amounts of data necessary to understand its social organization. Fourth, despite its high intelligence, often thought to reflect social complexity, the fabled "forest person" lives in a relatively simple social system.[3–5,14–16] Fifth, captive orangutans are expert tool users, whereas, with the exception of a few sites in northwestern Sumatra tool use and manufacture are virtually absent in wild orangutans.[17,18] Finally, while there is recorded variation in behavior and morphology between and among Bornean and Sumatran populations, no hypotheses have been developed to explain the observed differences.

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An understanding of the orangutan's way of living is needed to improve reconstructions of hominid behavioral ecology: Even the best conceptual models need to be tested with hominoids due to their phylogenetic similarity with hominids. Research on orangutans is especially useful in testing models developed for chimpanzees, such as that for the evolution of material culture.[19] Unfortunately, the long-term field studies that might help us to solve these riddles are becoming more difficult because, like many rainforest animals, orangutans are increasingly endangered by habitat loss as a result of logging, fire-aided conversion to plantation estates, and poaching.

Our aim here is to contribute to solving these puzzles and to improve our understanding of the elusive ape by surveying the current state of knowledge about the orangutan, summarizing aspects of its evolutionary

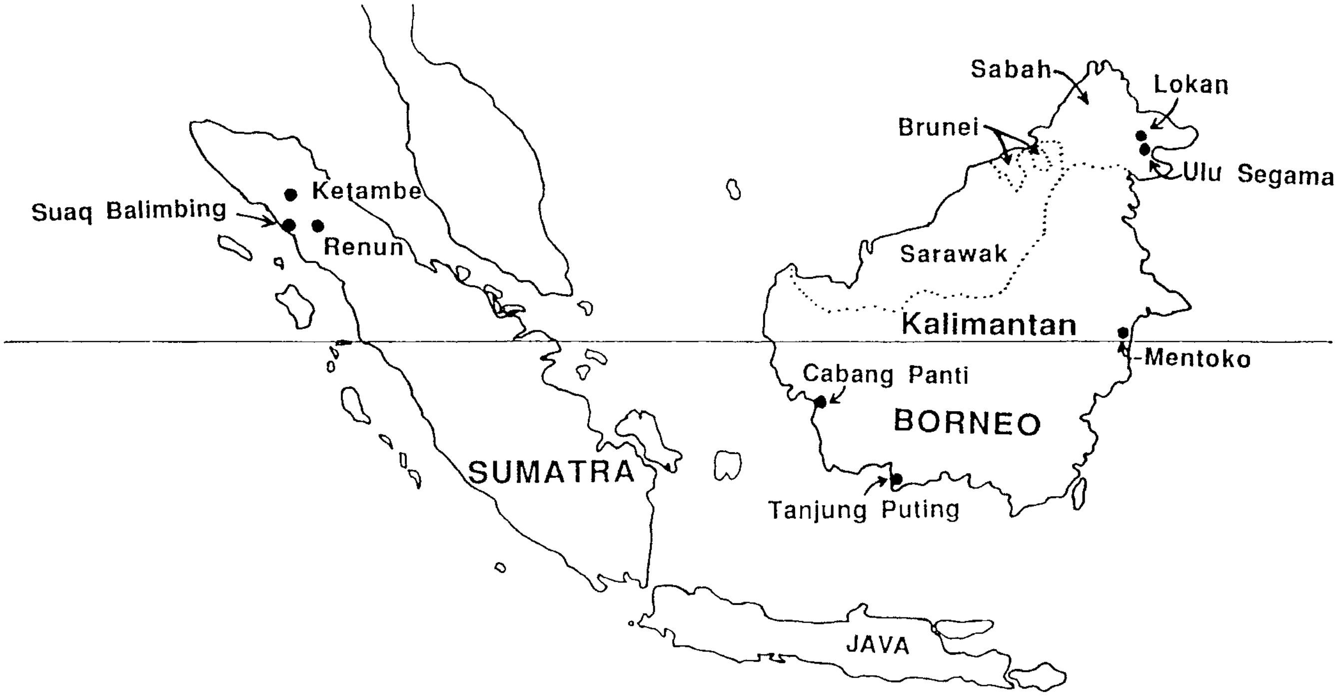

Figure 1. Former and current orangutan study sites. Taken from van Schaik and van Hooff.[109]

history, taxonomy, and behavioral ecology with special emphasis on social organization, reproductive strategies, and recognized inter-island differences. Finally, we hope to raise awareness of conservation efforts to preserve orangutans and their rapidly diminishing habitats.

EVOLUTIONARY HISTORY

The description of the fossilized remains of the Miocene ape *Sivapithecus* (12 to 8 MY) and related taxa from southern Asia, Turkey, and China suggested it as a sister group or possible ancestor to *Pongo*.[20–23] *Sivapithecus'* skull shares with the orangutan a unique dish-shaped face; narrow inter-orbital width; oval-shaped orbits; a tall, narrow, nasal aperture; and flaring cheekbones.[21,23–26] Its dentition also shares several derived similarities with that of *Pongo:* relatively small lateral upper incisors, divergent upper canines, low flat cusps, a robust mandible, thick enamel on the cheek teeth, and crenate, or wrinkled, occlusal surfaces.[20–22] This suite of characteristics suggests that *Sivapithecus* was adapted for diversified feeding on hard nuts, bark, or fruits with hard pits,[26] a diet similar to that of modern orangutans.[27,28]

However, the subsequent discovery of two fossilized humeral fragments challenged the contention that *Sivapithecus* and *Pongo* are closely related.[29] Based on the morphology of these humeri, *Sivapithecus'* locomotor pattern was most likely an intermediate form between that of a quadrupedal primate and that of a climbing or suspensory animal. If *Sivapithecus* and *Pongo* are closely related, then the postcranial features adapted for suspensory behavior shared by extant apes are likely convergences,[29] supporting the belief that the orangutan ancestor was relatively more terrestrial than the modern form.[30] Conversely, if *Sivapithecus* and *Pongo* are less closely related, then their cranial similarities are either convergent traits or shared primitive features[29] (Fig. 2). Presently, there is incomplete information to resolve this question.

Extant orangutans, among which wild adult males may exceed 80 kg, are the largest living forest-canopy animals.

More recent orangutan evolution is equally unclear. The main fossilized remains of orangutans are isolated teeth from recent cave deposits.[27,31] Modern and subfossil orangutans differ in tooth size, with those dated between 30,000 BP and 40,000 BP having much larger teeth, suggesting that they were either larger than extant forms or of similar size but with larger teeth.[30,31–34] Extant orangutans, among which wild adult males may exceed 80 kg,[35–37] are the largest living forest-canopy animals.[38] In Borneo, large, heavy males are more likely than females to travel on the ground where large terrestrial predators, especially tigers, are absent.[4,39,40] However, Sumatran orangutans are almost exclusively arboreal in both dry-land and swamp forests[5] (C. P. van Schaik, unpublished data). A present-day Sumatran male breaks his support about twice in an average day, crashing to the ground (although there is usually a soft landing). If Pleistocene

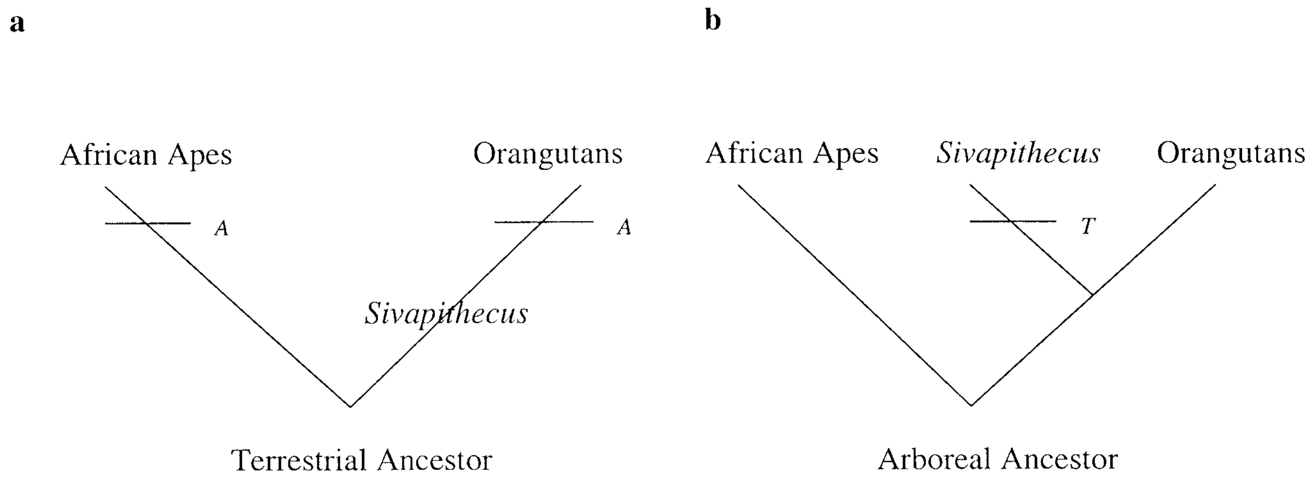

Figure 2. Possible relationships between *Sivapithecus* and *Pongo*. a. If the last common ancestor of great apes was terrestrial, then *Sivapithecus* is likely ancestral to *Pongo* and the postcranial adaptations of African apes and orangutans are convergences. b. Alternatively, if the ancestor was arboreal, *Sivapithecus'* adaptations for quadrupedalism are derived. (A = arboreal adaptations; T = terrestrial adaptations).

orangutans were bigger overall, then they presumably were more terrestrial than modern *Pongo*.[15,30] It is possible that the arboreally adapted postcrania of extant orangutans may be a comparatively recent development[42] that reflects their much-restricted geographic distribution and possible ecological specializations (such as for arboreal travel through swamp forests) as compared to their Pleistocene relatives. Unfortunately, no postcranial remains of Pleistocene orangutans are yet available to test this idea.

Past and Present Distribution

During the Pleistocene, the orangutan ranged throughout both the wet and seasonal tropics, including Java, Sumatra, Borneo, Viêt Nam, and the subtropical regions of southern China, and from lowland to highland localities, as evidenced by subfossil sites (see map, Fig. 3).[27,31,34,42] Pleistocene fossil associations in the westerly parts of southern Asia, including Burma and northeastern India, also suggest that *Pongo* populations lived in those regions.[43] Currently, the orangutan's distribution is restricted to fragmented populations in northern Sumatra and throughout Borneo (Fig. 3).

Two explanations for the collapse of the orangutan's range have been proposed, and include ecological and anthropogenic factors.[15,44–46] The ecological hypothesis is supported by circumstantial evidence from different but related lines of research. First, during the Pleistocene, the orangutan's distribution shifted southward, coinciding with the shifting subtropical and tropical zones in East Asia.[47] Second, rises in mean annual temperature since the last glacial maximum at 18,000 BP would have led to rising sea levels and, consequently, a decline in the availability of suitable habitat for large mammals.[45,46] However, large mammals tend to have very wide habitat tolerances. In fact, a transition from a dry, seasonal forest to a wet, tropical rainforest would have been to the orangutan's advantage as this is a preferred habitat. Third, the ecological hypothesis is supported by default if the alternative hypothesis is rejected. It has been suggested that the human hunting hypothesis cannot explain the present-day occurrence of orangutans on Borneo and Sumatra.[46] The absence of the orangutan would be expected if humans were responsible for exterminating this species.

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Human colonization is likely to have had at least as strong an impact as ecological factors on the range collapse of orangutans. The pattern of human invasion followed by extinction or a massive reduction in distribution is consistent with the "overkill hypothesis."[47] Large, sluggish arboreal animals like orangutans are easy targets to catch, making them exceedingly vulnerable to exploitation, while their slow reproduction makes popu-

Figure 3. Current orangutan distribution and Pleistocene subfossil sites. Note that subfossil sites include locations in Java and south Asia, far beyond the present-day range of orangutans.

lation recovery difficult. The caves at Niah in Sarawak and at Madai in Sabah retained extensive evidence of prehistoric hunting in the form of orangutan remains that had been left behind by tribal hunters.[31,42,45] Seven major gatherer-hunter societies have been identified in historical times and, according to the early ethnographers, the favorite prey of all these tribes were "monkeys and apes," which were hunted with poisoned arrows shot from blowguns, or with dogs and spears.[49] The indications of human habitation and the high frequency of orangutan remains relative to those of other taxa suggest selective targeting of orangutans.[15,45,49,50]

The orangutan's continued presence on Borneo and Sumatra is not inconsistent with the "overkill hypothesis." Human population densities have historically remained low in dense, ever-humid regions such as those found on present-day Borneo and Sumatra, as opposed to the seasonal areas of Java, Indochina, and southern China where orangutans ranged previously.[51] This low human density suggests that refuges must have been available, especially in the extensive malaria-infested swamps, from which animals could recolonize. Interestingly, their current distributions in Sumatra and Borneo still largely reflect the distribution of active hunting of the red ape[52] (C. P. van Schaik, unpublished data). Thus, although ecological factors may have had a strong impact, especially throughout the Pleistocene,[47] humans are highly likely to have shared the responsibility for the orangutan's decline in range and number.

INTER-ISLAND DIFFERENCES AND TAXONOMY

Sumatran and Bornean orangutans differ in many phenotypic features. Flanges, jutting cheek pads made up of fibrous fatty tissue,[53] tend to curve forward in Bornean males whereas the flanges of Sumatran males tend to lie flat against the face, although this difference may reflect individual differences in age and health. The throat sacs of Bornean males tend to be very large and pendulous, while those of Sumatran males are less so. Some researchers suggest that this relates to differences in properties of the male's long call,[1,15] but no quantitative data analyses of long-call properties have been published. Sumatran animals are generally more lightly colored, including their faces, than are Bornean forms,[1] although Rijksen[5] described considerable variation within a localized region of Sumatra where both light and dark morphs have differently shaped faces. Sumatran orangutans also tend to have longer, denser, and fleecier body hair than do Bornean forms, a difference that has been attributed to the generally higher altitude habitats of Sumatran populations.[1] Yet, while orangutans generally reach higher maximum altitudes in Sumatra, they are essentially lowland animals on both islands.[49] A systematic study of the observed morphological differences between the two subspecies is needed to clarify these reports.

Traits related to differences in the general appearance, behavior, and biochemistry of the Bornean and Sumatran populations have been examined to determine the extent of divergence between the two islands and to identify taxonomic distinctions. Populations on the two islands have been geographically and reproductively isolated for at least 10,000 years[1] and perhaps much longer due to the presence of large rivers on the Sunda shelf during the last major glaciation.

Taking into consideration chromosomal and biochemical differences, some researchers have proposed that each subspecies should be elevated to species status.[54–56] In addition to an island-specific pericentric inversion that occurs at chromosome 2, results from isozyme and two-dimensional gel electrophoresis indicate greater differences between Bornean and Sumatran orangutans than between species of gibbons (*Hylobates concolor* and *H. lar*) or chimpanzees.[54] These same data also suggest a divergence time between Bornean and Sumatran orangutan populations of at least 1.13 ma,[54] much longer than inferred from the available biogeographic data.

Until more data are collected that include systematic sampling from all geographic populations and more complete genetic information, a revision of orangutan taxonomy is premature. Hence, we agree with Groves, who rejects the notion of two orangutan species based on the extent of morphological variation within and between recognized subspecies.

Although, morphologically, it is not too difficult to distinguish among the recognized subspecies in cranial metrics,[57] intra-island variation is as great, or greater, than inter-island variation for facial features, at least in Borneo.[1] Additionally, an examination of postcanine tooth morphology demonstrates population differences among Bornean study sites as great as differences between Bornean and Sumatran populations.[58] Indeed, the available data indicate at least three morphologically and geographically distinct populations across Borneo and Sumatra.[1,58,59] Orangutan populations from western Borneo are separated from populations in southwestern Borneo by the Kapuas river; both of these are separated from populations in northern and eastern Borneo by the central mountain ranges of the island.[49] On Sumatra, geographic features such as the Barisan mountains, which stretch along the western half of the island, and the Alas river are possible barriers to dispersal.[49] Because the major morphological separations may not coincide with between-island differences (and thus with current subspecies designations), and because genetic sampling of Bornean individuals may have been geographically uneven, any arrangement with two groupings, be they into species or subspecies, may not optimally represent the extensive variation in orangutans. Until more data are collected that include systematic sampling from all geographic populations and more complete genetic information, a revision of orangutan taxonomy is premature. Hence, we agree with Groves,[60] who rejects the notion of two orangutan species based on the extent of morphological variation within and between recognized subspecies.

MORPHOLOGY AND LIFE HISTORY

Orangutans have long forelimbs with hook-like hands and long, curved phalanges, but short thumbs. Their intermembral index value is 139, the highest among extant apes and comparable to that of the large-bodied gibbons,[26] indicating specialization for suspensory behavior. Their hindlimbs are short and they have hand-like feet with curved phalanges and shortened, though highly opposable big toes. These postcranial traits, coupled with an extremely mobile hip, allow large-bodied orangutans to traverse the forest easily via quadrumanous scrambling.[38]

Females

Orangutans follow the general ape pattern of having slow life histories. In captivity, females reach sexual maturity at approximately seven years of age,[61] but field workers estimate that they do so between 11 and 15 years of age in the wild.[62,63] First breeding, however, may not occur until several years later.[62] Females do not have conspicuous sexual swellings that advertise ovulation, but do develop labial swellings anywhere from two weeks to over a month after conception.[64,66] Gestation is estimated to approach a nine-month term (260 to 270 days) in the wild,[66,68] but there is considerable variation. Data from captive populations give an approximate length of 244 days.[68] Females care for dependent offspring for at least six years.[3,5] The interbirth interval in both Borneo and Sumatra is about eight years,[1,63,70] the longest among extant nonhuman primates. Slow growth and development also contribute to long life spans, a maximum of 57 years for females and 58 years for males in captivity and an estimated 45 years in the wild.[63] The unfortunate consequences of this pattern are low population growth and slow recovery rates following crashes resulting from events such as habitat destruction, intense hunting, or disease.

Males

Orangutans exhibit extreme sexual dimorphism in body size,[38] and researchers generally recognize two sexually mature male morphs. The two morphs are distinguished by both morphological features and behavioral traits. Flanged[71,72] adult males are twice the size of adult females; express secondary sexual characteristics such as a well-developed throat sac, wide cheek pads, and long, dense cape-like hair; and emit periodic loud vocalizations known as long calls.[15] Unflanged adult (subadult) males lack the large size and secondary sexual characteristics common to flanged males but are normally as large as, or larger than, adult females.[8] So great are the physical differences between the two male morphs that early naturalists considered them to be either separate races[73] or sympatric species.[74] The two morphs have been described as "adult" and "sub-adult"[15,75] or "developed" and "undeveloped"[76] males.

In captivity, males reach sexual maturity at roughly eight to ten years of age, although they probably do so later in the wild.[63] Unflanged males may maintain their relatively smaller body size (35 to 50 kg) for as long as ten to 20 years in the wild[8,11] or for up to 18 years in captivity,[71] but ultimately acquire the full suite of secondary sexual characteristics diagnostic of flanged adults. Hence, the two morphs are most likely developmental phases rather than alternative pathways. Leigh and Shea[77] have presented male orangutan growth curves and suggested that sexual dimorphism in orangutans is a result of indeterminate growth by males, although this pattern of weight gain without skeletal growth may reflect a tendency to become obese in captivity. Adult male bimaturism cannot be understood in this species without detailed knowledge of ontogeny. In the absence of growth curves from the wild and without additional data derived from measures other than body mass, research will be necessary in order to understand how male orangutan bimaturism develops. Growth curves for captive orangutans further imply that the concept of "arrested development" is questionable and more likely reflects a long and highly variable maturation period for males.[77]

Male-male sociality in the wild is limited, but it is possible that auditory signals mediate socio-endocrine interactions affecting male development.

The mechanism for the large variation in the length of the period during which male orangutans acquire secondary sexual characteristics is not well understood, but several ecological and social factors have been proposed. These include nutritional deficiencies, pheromonal or auditory cues from flanged males, and chronic stress resulting from aggression received from flanged males.[78] The nutritional-deficit hypothesis has been discounted because arrest is observed in captivity where the diet of growing males is monitored and optimized.[78] In addition, hormonal studies conducted in captive settings have eliminated the chronic stress hypothesis because "arrested" males have an endocrine profile that includes low stress-hormone levels.[79] The observed hormone profiles support either the pheromone or auditory-signal hypothesis. Male-male sociality in the wild is limited, but it is possible that auditory signals mediate socio-endocrine interactions affecting male development.[78,79] Future captive or field studies combining techniques from behavioral endocrinology with experimental playbacks may provide insight into the factors influencing delayed maturation among orangutan males.

ACTIVITY BUDGET AND DIET

Body size, age or sex class and, for females, reproductive status largely determine the proportion of time that orangutans engage in different activities. Both Rodman[28] and Knott[76] have provided summaries of data collected from several studies. Compiling both summaries indicates that, on average, orangutans spend 43% of their active time feeding, 41.5% resting, 13.5% traveling, and 2% in other activities that include nest-building, vocalizing, socializing, and mating. These numbers vary between sites and individuals over time due to variations in local demography, active day length (time between night nests), fruit availability, and individuals' reproductive status.

Orangutans are selective feeders that require large amounts of food because of their body size. They prefer big loads of easy calories from food items with high energy content. Orangutans are primarily frugivorous, eating almost exclusively fruit when fruit is abundant and having a strong preference for fruits with soft pulp[80] in large crops.[81] Apart from fruit, orangutans eat substantial amounts of young leaves and shoots, seeds, buds, flowers, the inner bark of some trees and lianas, and small quantities of insects and mineral-rich soil.[4,15,28,81,82] On occasion, orangutans may eat meat acquired through opportunistic hunting.[83,84] In orangutans, this behavior has a female bias, perhaps a result of sex differences in foraging technique.[84]

Because orangutans require large amounts of fruit, they must respond to seasonal and inter-annual declines in fruit availability. During periods of food abundance, orangutans seem to be efficient at storing large amounts of energy as fat, which allows them to subsist on lower quality foods in environments with unpredictable fruiting.[63,81,85] However, longer periods of food scarcity, which impose negative energy balance and mobilization of the stored fat,[85] should force animals to change their foraging strategies. One option is to modify their ranging patterns. During periods of fruit scarcity, individuals are known to concentrate in areas within their home range that have relative fruit peaks.[86] Many researchers have commented on the episodic appearance of large numbers of orangutans in areas with locally high fruit abundance[15,86,87] (C. P. van Schaik, unpublished data). These fluctuations in fruit availability may also help explain the seasonal influx of transient or "nonresident" animals and the disappearance of well-habituated individuals from long-term study sites.[86,87] Alternately, this influx of transients and the disappearance of residents might be explained by the large home ranges, which exceed most study areas. At present, there are no data to indicate how orangutans know where distant food sources are located.

A second tactic by which orangutans cope with declines in fruit availability is to alter their diet.[4,85] In times of severe fruit scarcity, orangutans rely on the inner cambium layer of bark as one of their keystone resources, particularly at sites throughout Borneo, including Kutai in Eastern Borneo,[82] Tanjung Puting[3] in Central Borneo, and Gunung Palung[11] in western Borneo. Specialized features of a species' dentition often reflect adaptations to the food eaten during periods when its preferred foods are scarce. Rodman[28] suggested that orangutan dental morphology, particularly the broad central incisors, the small lateral incisors, and short maxillary canines, may be related to bark opening and stripping. Specifically, use of the canine to penetrate the bark leads to unusual wear on the lateral maxillary incisors, posing a possible selection pressure for reduction in size.[28]

Orangutans also have thick enamel on their cheek teeth and this is thought to be an adaptation for feeding on hard objects.[88,89] Although the soft pulp of fruit is preferred, it is relatively scarce in most habitats except during a mast, so orangutans feed regularly on hard unripe fruits and seeds.[81] When orangutans eat seeds, processing may vary by seed age[28]: Mature seeds are either swallowed whole[90] or eaten (E. A. Fox, personal communication; C. D. Knott, personal communication), but immature seeds tend to be crushed and digested.[81,82] Another uncommon dental trait found in orangutans that might be related to hard-object feeding is the crenate occlusal surfaces on molars, which might act as micro-grips that prevent food items from slipping.[91] Additionally, the associated enamel microstructure might lessen the risk of having a tooth shatter from the high pressure of biting through a seed.[92] Only one other primate radiation, the New World pithecines, expresses this trait, and they, too, are hard-object feeders.[93,94] These adaptations suggest that the availability of soft fruits is often insufficient. In the case of orangutans, this is in part due to their large body size and in part to the low productivity of Southeast Asian rain forests.[95,96]

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In the humid and largely maritime climates of Southeast Asia, seasonal variation in forest phenology is generally muted as compared to other tropical rainforest regions. However, unique to Southeast Asia is the phenomenon of mast fruiting: Long periods of very low fruit production are punctuated by brief periods of excessively high fruit availability at intervals anywhere between two and ten years.[97] During masts, up to nearly 90% of canopy species in rainforests produce fruit.[98,99] Orangutans will feed exclusively on fruits during masts but, during nonmast periods, fruit abundance is low and animals diversify their diet.[85] Once the mast is over and fruit becomes scarce once again, the diet may comprise low-quality food items such as bark (up to 37% at Gunung Palung),[76] with opportunistic feeding on leaves, insects, and fruits. Thus, these inter-annual fluctuations strongly affect orangutan dietary patterns.

Diet also has important consequences for females and reproduction. As nonseasonal breeders with long lactation periods, like other Southeast Asian primates such as *Macaca fascicularis,*[100] female orangutans probably have high condition thresholds for resuming ovarian activity.[85] During poor fruit periods, changes in dietary composition result in major differences in nutritional intake.[11,85] Consequently, these differences in caloric intake, especially between masting and nonmasting years, may affect whether or not females continue cycling.[11] The high fruit season provides enough nutrients for females to cycle and, as this period also coincides with higher levels of social-

TABLE 1. Island Differences in Average Orangutan Density with Standard Deviation (inds/km^2) Across Habitat Types from Undisturbed Sites*

Habitat	Borneo	Sumatra
Flood plains and peat swamp	2.9 (0.4)	6.1 (1.2)
Alluvial lowlands	2.3 (0.6)	3.9 (1.1)
Uplands	0.6 (0.4)	1.4 (0.5)
(Sub) Montane	n.d.	0.8 (0.3)

*Data are taken from Rijksen and Meijaard.[49]

ity among orangutans, may promote increased mating opportunities for both males and females.[101,102] Indeed, more females tend to conceive in the wake of masting periods, both in Borneo[11] and Sumatra.[100]

HABITAT AND DENSITIES

Orangutans range within the mosaic habitats of tropical rain forests in Borneo and northern Sumatra that include lowland dipterocarp forest, heath forest, peat swamp forest, alluvial flats, and mountain slopes up to 2000 m.[38,80,103,104] Orangutans are most commonly found close to streams and rivers, and in swamps. In the absence of hunting, the greatest densities are in nonmasting habitats such as alluvial forest patches in lowland river valleys and in the freshwater and peat swamp forests in floodplains (Table 1).[49] Orangutan densities decline steeply with increasing altitude and tend to be higher in Sumatra than in Borneo in similar habitats.[49,80]

What are the major determinants of orangutan density? Findings from northern Sumatra demonstrate that orangutan densities vary closely with the amount of soft pulp of fruit available.[80,104,105] Because the production of soft, fleshy fruits declines with altitude, this explains the strong relationship between orangutan density and altitude.[80] The Sumatran result also helps explain the variability in orangutan densities at a given altitude. Forests on relatively more fertile soil tend to have a higher proportion of plant species that produce soft-pulp fruits. This probably explains why riverine alluvium and some swamp forests have remarkably high densities of orangutans.[105] In forests that are not swampy, strangling figs are important food sources because they produce large crops of easily harvested and easily digested soft-pulp fruits.[103] The density of large stranglers increases with soil pH,[106] which in turn is a good predictor of forest productivity,[107] another reason for the high orangutan densities in alluvial forests. Finally, alluvial and swamp forests tend not to show masting because, on average, they contain a lower proportion of mast-fruiting species.[106] Accordingly, there is a higher abundance of fruiting trees in any given year and, thus, higher orangutan density (C. P. van Schaik, unpublished data). Masting habitats might be expected to support high orangutan densities, but masting also means that there is lower productivity during nonmast years and that such habitats will not provide a reliable source of soft-pulp fruits.[98,99]

SOCIAL ORGANIZATION

The orangutan's social system is unique among diurnal anthropoids, and still is not well understood despite several long-term studies. All observers agree that individuals are semisolitary, although the degree of solitariness varies between sites and over time within sites.[4,5,7,15,16,102] However, higher social units are likely to be recognized by examining association patterns.

Parties

Fruit is not regularly available, either spatially or temporally, in large enough concentrations to permit orangutans to be permanently gregarious.[28,87,101] Nonetheless, orangutans sometimes will form parties. MacKinnon[15] speculated, and Mitani and coworkers[101] confirmed, that orangutans encounter each other more frequently than would be expected by chance and often coordinate travel during times of uneven food distribution, although mean party size remains small, less than 1.1 individuals in Borneo (Fig. 4).[104]

Orangutan parties come in two types. In large fruiting trees, they form feeding aggregations that are often the result of attraction to large food sources.[4,5,14,86,87,101] Individuals tend to arrive and leave independently. The second type of party is a travel band, in which individuals coordinate travel between food sources.[86,87] There is variation across sites in the proportion of time that orangutans spend in feeding aggregations and travel bands. At sites such as Ketambe, where there are many large strangling figs, estimated party sizes involve many aggregations and relatively few travel bands.[86] At Suaq Bal-

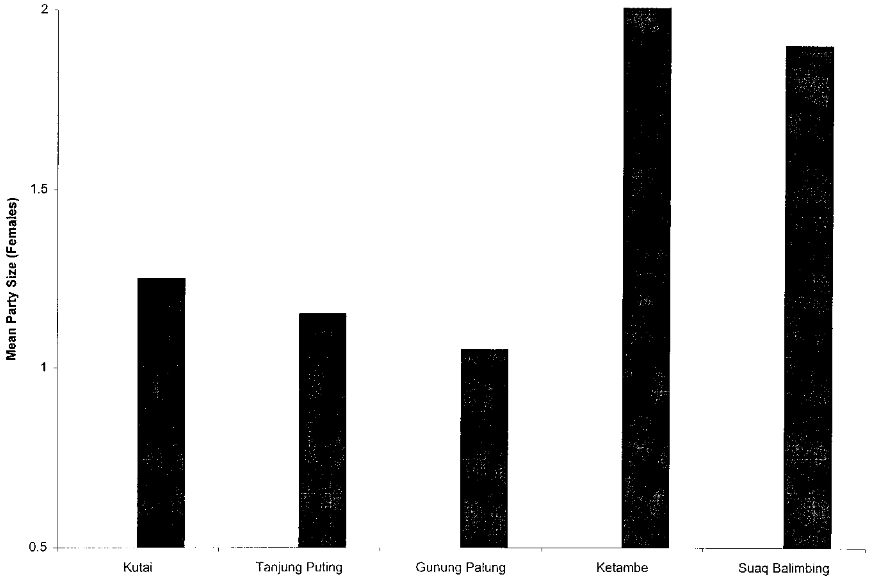


Figure 4. Mean party size for adult females across sites (from van Schaik[102]). Bornean sites: Kutai, Tanjung Puting, and Gunung Palung; Sumatran sites: Ketambe and Suaq Balimbing.

TABLE 2. Orangutan Densities and Estimated Home Ranges Across Field Sites. Bornean Sites: Lokan, Kutai, and Tanjung Puting. Sumatran Sites: Ketambe and Suaq Balimbing

	Core Study Area	Female Home Range	Male Home Range	Density	Duration of Study
Lokan[118]	380ha	64ha	~500ha	2.1/km^2	1 year
Kutai[101,103]	300ha	>150ha	n.d.	2.0/km^2	2 years
Tanjung Puting[4]	2000ha	500–600ha	>600ha	3.0/km^2	3 years
Ketambe[67]	400ha	>300ha	>800ha	5.5/km^2	3 years
Suaq Balimbing[117]	520ha	700–900ha	1000–4000ha	7.0/km^2	5 years

imbing, in contrast, feeding aggregations are uncommon because large strangling figs are very rare.[102] At these two Sumatran sites, parties are larger, including about two independent individuals (Fig. 4).[86,109] Although juvenile and adolescent offspring are included in counts, they account for a small proportion of the associations.[102] At Suaq Balimbing, focal animals formed parties in nearly 68% of all full-day follows.[102] For Sumatran orangutans, this figure might help to dispel the long-held belief that orangutans are solitary.

The benefits of party formation are likely to be largely social rather than ecological. Potential benefits of grouping include access to mates[101,102]; for females, protection from male coercion[5,7]; and for youngsters, socialization, including the transmission of cultural information such as the ability to manufacture and use tools.[102,109] Ecological benefits are less likely. Independent individuals have a low predation risk, and coalitions over food have never been observed.[4,102,110]

Gregariousness is energetically costly. Orangutans require much food, and if multiple individuals use the same food source, per capita intake by subordinates could be reduced.[111] Animals can respond to high costs of grouping in two different ways: They can form parties only when the costs are reduced by an abundance of fruit or they can form parties when they can pursue benefits such as, for males, consorting with a female whenever the opportunity to do so arises, sometimes at a considerable cost.[102] Both patterns are observed. At both Ketambe and Cabang Panti, the size of orangutan travel bands increases in direct proportion to overall fruit abundance,[87,112] whereas at Suaq Balimbing this relationship is weak, and travel distance increases with party size.[102] Other studies also have shown that individuals who associate in travel parties increase time spent traveling and decrease time eating[4] or resting.[113]

Costs fall most heavily on the age-sex classes with the greatest needs[113] and on those with the most deviant foraging schedules (for example, the longest patch residence times).[11] Flanged males and females with small infants are the least gregarious.[15,16,75,101,102,114] The amount of time necessary for foraging and resting limits the time that flanged adult males can spend traveling closely with females,[4,101,113] especially in Borneo, but does not necessarily preclude long-lasting associations among similar age-sex classes or among individuals of relatively small body size. Consistent with this idea are the observations that the most commonly observed parties do not involve flanged males.[4,102]

Dispersal

Unlike the pattern predominating among the African great apes and humans,[115] orangutan dispersal patterns may be considered a variation of female philopatry. Several studies suggest that females tend to settle in ranges that overlap with or are near those of their mothers.[5,14,113,116] It has been noted that physically similar and presumably related females form clusters with a high degree of range overlap,[4,117] which tend to be reproductively synchronized.[15,117] Conversely, males tend to disappear at maturity and most new or unfamiliar individuals entering or passing through an area are males.[5,15,16,110] This suggests a male bias for long-distance dispersal or even a nomadic phase at some stage of adulthood.[117]

Social Units

Adult females tend to have highly overlapping home ranges of up to 900 ha, with the greatest overlap occurring in areas of high density (Table 2).[5,16,116–118] Flanged males do not actively defend territories, but use long calls as a site-independent spacing mechanism. Their home ranges are larger than those of females and may exceed 2,000 to 3,000 ha (Table 2); these ranges also have extremely high overlap.[116] Variations in male ranging patterns are likely tied to fluctuations in the availability of fruit and receptive females, and the presence of other, more dominant males.[15,38,86,87,101,102]

The amount of time necessary for foraging and resting limits the time that flanged adult males can spend traveling closely with females, especially in Borneo, but does not necessarily preclude long-lasting associations among similar age-sex classes or among individuals of relatively small body size.

Unlike all other anthropoids, orangutans do not have easily recognizable social units. Individuals are often solitary, but associate in parties on a regular basis for social benefits. However, mean party size tends to remain small because of the high costs of feeding competition.[101,102,110] Behavioral observations further suggest individualized relationships between different animals.[110] Together, they form a network of loose associations characteristic of individual-based fission-fusion societies (for example, those of chimpanzees and spider monkeys).[15,86,102] These associations most likely are organized around the locally dominant flanged male,[15] which is the preferred mating partner of the area's females.[7,119,120] The other flanged males and probably most unflanged males visiting an area form a separate class covering several such loose communities.

Already well accepted as serving a spacing function between adult males,[15,121–123] long calls are also the most likely mechanism by which individuals maintain associations within this loosely knit community. Long calls tend to be given by the dominant resident male three to four times a day, although there is variation between individuals and between sites that are likely dependent on local population density[122] (C. P. van Schaik, unpublished data). These calls carry long distances in the forest and are audible to human observers on the ground up to 800 m away.[122] Long calls enable dispersed female or juvenile parties to remain in spatial contact with the dominant male of the area.[15] Long calls may also act as a coordinating signal for orangutan populations: Coordinated seasonal movements of whole "communities" over several km have been noted[86,87] and could be guided by a male's long calls. Future behavioral studies involving simultaneous follows of multiple adult individuals will be able to detect these coordinated community movements.

Among males, experimental playback studies and behavioral studies have shown individual-specific responses to long calls based on dominance relationships[122,123] in which adult males ignore, avoid, or threaten the caller, depending on their relationship with the vocalizer. These behavioral responses suggest individual recognition based on the vocalizations alone or at least some criteria for the assessment of long-call properties which may include, but are not limited to, the rate and duration of those calls. Flanged males emit long calls not only in responses to disturbances, but as they move through their home ranges and when resting.[15,110,118] Adult females may also avoid, approach, or ignore these calls, depending on their reproductive condition and social context, but this hypothesis remains to be tested more rigorously. Both male and female responses are likely to be relationship-dependent but more field experiments are needed to further understanding of the role of long-distance vocalizations in interindividual communication and social organization.

In Borneo, both flanged and unflanged males force copulations with females, although unflanged males do so with greater frequency. In Sumatra, flanged males hardly ever resort to using forced copulations when mating with females.

SOCIOSEXUAL BEHAVIOR

In Borneo, both flanged and unflanged males force copulations with females, although unflanged males do so with greater frequency.[8,9,75] In Sumatra, flanged males hardly ever resort to using forced copulations when mating with females.[7,119,120] The vulnerability of orangutan females to this form of sexual coercion is due to the lack of allies and the tremendous disparity between adult males and females in terms of size and strength.[125] Paradoxically, females do not have conspicuous sexual swellings or other visual markers that advertise a short receptive period and that might minimize the threat of harassment.[110,119] However, females can easily avoid flanged males by keeping track of their long calls, and there is some evidence that they do.[114,118] Unflanged males are not as easily avoided and harass lone females by often associating with them to force copulations. As a consequence, females suffer reduced foraging efficiency.[7]

Flanged males and females normally mate within the context of a consortship.[5,7,66,126] These consortships are often initiated by females who, at the time of presumed fecundity, usually seek out dominant flanged males with which to copulate.[7,12,128] Thus it appears that females express mating preferences for and against certain males either by initiating consortships or resisting mating attempts, suggesting individualized relationships.[66,110,114,119,124] Paired mate-choice experiments conducted in captivity are consistent with this hypothesis. Using free-access and restricted-access tests with animals of the opposite sex, Nadler[127,128] demonstrated that it is the female that restricts mating to the presumptive periovulatory period, whereas the male initiates matings at all other times. (In this series of tests, females were presented with a single flanged male. Future studies should provide the female with a choice between a flanged and unflanged male or among several flanged males in order to determine what criteria females rely on when choosing their mates).

Solitary females with overlapping ranges might suggest "roving male promiscuity" as the most effective mating system for male orangutans because of the males' inability to defend exclusive access to females.[38,110] However, where female mating preferences can be expressed (perhaps more so at Sumatran sites?) the orangutan mating system is not properly described as one in which males search for and find passive females. Hence, in order to understand the orangutan mating system, and indeed its social system, we must understand the adaptive significance of these pronounced female mating preferences.

Mating preferences generally result in either indirect or indirect benefits for the choosy sex. Under the good-genes hypothesis, female orangutans should selectively mate with flanged males, or perhaps with the dominant resident flanged male in her community, because the status of these males is an indirect reflection of overall genetic fitness. This hypothesis assumes that such fitness has high heritability.[129] The good-genes hypothesis is consistent with the observed female resistance against mating attempts by unflanged males and preference for consorting with flanged males. (Utami[12] recently showed that males in voluntary consortships are most likely to father offspring.) Evidence against the good-genes hypothesis comes from observations that demonstrate changes in female allegiance following a takeover by a new male even though the formerly dominant male remains in the research area[120] and that females initiate consortships with large unflanged males during periods of unstable male ranks.[12] At this stage, the good-genes hypothesis does not provide a convincing explanation for female mate choice among orangutans.

If the good-genes hypothesis is not considered adequate, then how can we explain such strong mating preferences? Association with the dominant flanged male may instead provide females with phenotypic benefits. Among these phenotypic benefits, only protection against harassment or infanticide seem to be potentially relevant to orangutans. Flanged males appear to protect females from harassment indirectly. Association with the flanged male reduces the success rate of mating attempts by unflanged males, although it does not reduce the overall rate of forced matings that occur due to increased sexual interest by unflanged males.[7] However, this does not explain why females need to be protected from harassment in the first place. To explain that, we need to postulate other benefits from having offspring sired by dominant flanged males.

Indeed, mate choice by female orangutans might be explained by protection against infanticide. Although the lack of published reports of infanticide by male orangutans makes this hypothesis highly speculative, the threat of infanticide by new immigrant dominant males might still act as a strong selective pressure for loose associations between females and flanged males.[130–132] Females have the opportunity to track flanged males by homing in on their conspicuous long calls, whereas other flanged and unflanged males, typically those subordinate to the caller, are kept away by these calls.[121–123] As a result, a vocalizing male creates a sphere of relative safety for females within his immediate area. A flanged male's strength and ability as a good protector might be reflected in properties of his long call such as its duration, frequency, loudness, or rate of vocalization.[120,133] Counterintuitively, females will often ignore long calls. However, a vocal signal is likely to be responded to only when the vocalization has some value to the receiver. Anecdotal reports indicate that females will travel quickly toward long-calling males when being harassed by unflanged males[7] (C. P. van Schaik, unpublished data). Thus, females may selectively react only under motivational conditions that are associated with sexual proceptivity[124] or when there is a real or perceived threat.[7]

. . . ironically, despite the absence of reported cases of infanticide among orangutans, the patterns in female sexual behavior, at least in Sumatra, are consistent with an infanticide-avoidance hypothesis.

In order to acquire protection against infanticide, females should concentrate paternity into the dominant flanged male by initiating and maintaining consortships during estrus, as has been observed.[7] They should also avoid insemination by nonpreferred subordinate males, flanged or unflanged, by resisting their mating attempts, as has been reported.[5,7–9] Females should immediately change allegiance upon takeovers of top dominance in the area, as was seen in Ketambe.[120] Finally, they should become actively promiscuous when no locally dominant male can be recognized. Researchers extrapolating from date of birth concluded that most offspring are conceived during consortships with adult males.[5,62,66,119] However, during periods of instability, both flanged and unflanged males engaged in matings and females' degree of resistance to forced copulations was reduced.[12]

Thus, ironically, despite the absence of reported cases of infanticide among orangutans, the patterns in female sexual behavior, at least in Sumatra, are consistent with an infanticide-avoidance hypothesis. Moreover, it is not clear what other hypothesis would explain the same set of observations. Further study of male-female sociosexual interactions is needed to understand male and female reproductive strategies and the inter-island variation we have uncovered here. Table 3 summarizes our current insights into female and male reproductive strategies.

COGNITION

Orangutans are highly intelligent: Their scores on various cognitive tasks are consistently among the highest for primates.[134] They share with other great apes a variety of cognitive abilities not known to be displayed by other primates, such as causal and logical reasoning, mirror self-recognition, role reversal, planning, intentional deception, and proto-language.[135,136] Captive orangutans in rich environments readily demonstrate habitual manufacture and use of tools in a variety of tasks.[17] However, until recently only rare instances of tool use and manufacture by wild orangutans had been observed.[137–139] The only known natural populations of habitually tool-making and tool-using orangutans exist in the swamps of northwestern Sumatra[18,140] (C. P. van Schaik, unpublished data). Orangutans at Suaq Balimbing have a tool kit and adjust tool features to current needs. Their tool use occurs exclusively in the trees and primarily in two foraging contexts: extracting insects or honey from tree holes and prying seeds from hard-husked fruit. De-

TABLE 3. Individual Reproductive Strategies of Adult Orangutans*

Adult females:	Prefer mate with highest resource-holding potential, usually the locally dominant flanged male. Initiate consortships at times of high ovarian activity. Resist matings by unflanged males and subordinate flanged males unless there is little or no cost. When lactating, possibly keep track of familiar flanged males by their long calls for protection against infanticide
Unflanged males:	Seek and attempt matings with adult females, despite restricted access due to high proportion of flanged males, infrequent encounters, and high costs of association. When females resist, force copulations.
Flanged males:	Given female preference for high resource-holding potential, attain locally dominant status and broadcast presence using long calls. Attempt to exclude all other males from receptive females, and maximize length of consortships commensurate with the energetic costs of association. If not locally dominant, force copulations with females.

*Modified from van Hooff.[124]

tailed consideration of geographic variation in these skilled behaviors supports the conclusion that these behaviors are cultural,[141] as with chimpanzees.[142,143]

The absence of habitual tool use and manufacture at other sites is most likely due to the lack of suitable conditions for social transmission.[109,137,141] At Suaq Balimbing, the greater gregariousness of individuals and the degree of social tolerance make tool use and social transmission more likely and are direct reflections of higher habitat productivity. Tolerant gregariousness during extractive foraging also explains variation in the size of the tool kits among chimpanzee populations and may therefore explain the first thrust toward improved technology among hominids.[109]

If cognition is intimately tied to social complexity, as some researchers have suggested,[144] then orangutan intelligence seems paradoxical. Arguments that rely on ecological determinants such as extractive foraging are also unconvincing in explaining the cognitive abilities of orangutans, although technically complex processing of food is harder to refute.[145] The idea that arboreal quadrumanous scrambling, by selecting for self-awareness, also produced cognitive abilities[146] is difficult to test. Because most great apes show a comparable level of cognitive abilities,[135,145] it is perhaps best to look for more general explanations. For now, their life-history patterns, particularly the extended period of development and long life spans, perhaps linked with prolonged learning, might best explain the cognitive capacities of great apes.[135]

CONSERVATION

Since prehistoric times, hunting by humans has resulted in greatly reduced populations of orangutans. Today, some indigenous cultures still hunt orangutans for food but a far greater problem is habitat loss due to logging and conversion to agriculture. Orangutans do not cope well with the effects of habitat exploitation by humans. First, they are old-growth specialists, which makes them sensitive to forest disturbance such as selective logging, and they disappear altogether from heavily logged forests or cleared land.[44,147] Orangutans simply cannot survive in deforested areas because they require such large home ranges and depend on a large diversity of tree and liana species. Second, their dependence on forest and reluctance to travel across open areas makes the fragmentation effects of logging and development more serious for them than for virtually any other forest species. Finally, logging, and especially conversion, tend to be concentrated in habitats such as alluvial flats that are preferred by orangutans.

As little as four decades ago, Borneo and Sumatra were almost completely covered by tropical forests. Deforestation has changed the landscape dramatically, leaving only isolated pockets of protected habitats suitable for orangutans. Initially, logging was restricted to accessible lowland areas, but excessive logging has pushed the frontier into hitherto inaccessible swampy and steep, hilly terrain in remote regions. This logging has traditionally been highly selective, focusing on only a small number of valuable export species. However, selectively logged areas have almost invariably been converted into agricultural areas by burgeoning local populations or, increasingly, as part of an integrated program of transmigration and large-scale agricultural plantations. As a result of these developments, Rijksen and Meijaard[49] estimate that orangutan numbers in Borneo and Sumatra had fallen to approximately 25,000 individuals, by the late 1990s, less than 8% of those estimated almost a century earlier (Fig. 5).

If cognition is intimately tied to social complexity, as some researchers have suggested, then orangutan intelligence seems paradoxical.

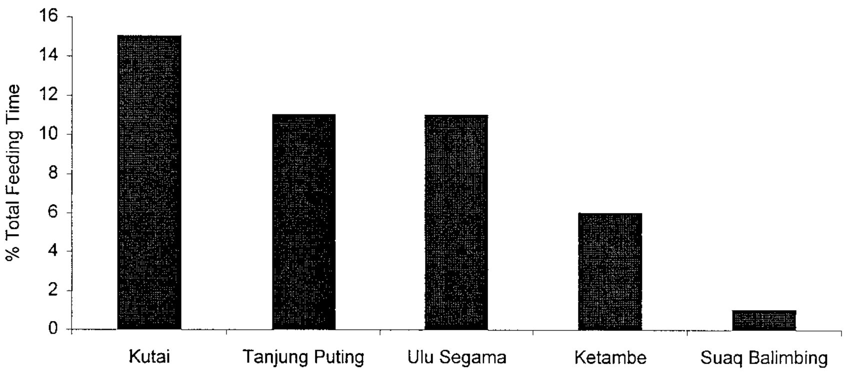
Activities that damage or destroy natural forests have increased with the growing population and economies of Southeast Asia. The main orangutan concentration in Sumatra is within the Leuser Ecosystem in the northern part of the island. Recent estimates indicate that logging and clearing for agricultural plantations in Leuser have led to a 45% decline in orangutan numbers over the past seven years alone.[150] The current wave of illegal logging, brought about by the anarchy following the fall of the Suharto regime, is increasing the pace of this already steep decline. Matters would have been even worse if the massive forest fires of 1997 and 1998 had not missed the orangutan's range in Sumatra. Nonetheless, the total estimated number in Sumatra has now fallen well below 10,000.

Borneo was less fortunate, however.

Box 1. Inter-Island Differences Revisited

Densities of orangutans on Sumatra are approximately twice as high as in similar habitats on Borneo (Table 2); the biomass of primates and other mammals is also higher on Sumatra.[44,107] The orangutan's altitudinal range appears to be much higher in Sumatra. Sumatran orangutans tend to spend more of their feeding time eating fruit and insects and less on the cambium growth layer of some trees (Fig. 1).[109] Together with the greater gregariousness of Sumatran orangutans, these differences suggest that Sumatran forests are more productive than are Bornean forests.[104] Although a thorough inter-island comparison of soil types and productivity is needed, the ecological factors underlying the differences may well be tied to divergent geologic histories that included extensive uplift and volcanism in Sumatra, producing much higher soil fertility.[104] Higher soil fertility generally results in higher productivity and, consequently, a higher density of orangutans.[102,104,105] Both habitat productivity and orangutan density, then, are likely to influence behavioral traits such as long-call rates, rates of encounter, costs of association, and, therefore, the reproductive tactics of both sexes (Fig. 2). Future work should establish whether this contrast between the islands is true for all populations, and thus taxonomically based, or simply due to the nature of the sites sampled. In the latter case, areas should occur where the pattern associated with the other island is seen.

a) Cambium Feeding



b) Insect Feeding

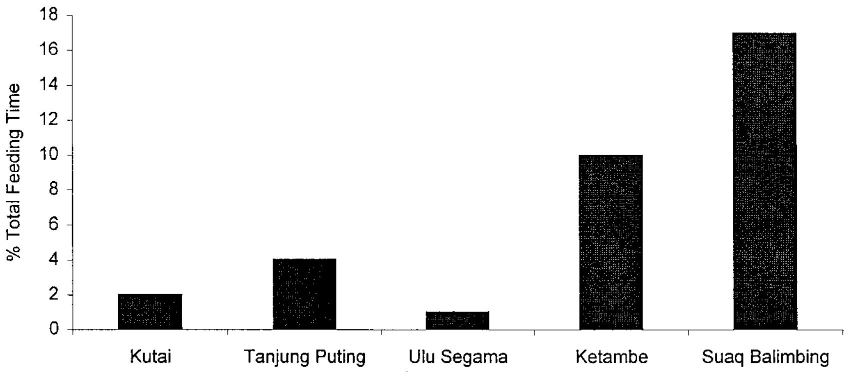


Figure 1. Site-specific differences in diet composition. Note that Bornean sites have a higher proportion of cambium feeding (a), whereas Sumatran sites have higher insect feeding (b). Bornean sites: Kutai, Tanjung Puting, and Ulu Segama; Sumatran sites: Ketambe and Suaq Balimbing. Modified from van Schaik and coworkers.[108]

Adult male reproductive tactics vary between Bornean and Sumatran populations, particularly among subordinate flanged and unflanged males. Flanged males in Borneo engage in short consortships and use both forced and unforced copulations when mating with females, with the majority of forced copulations performed by either small or low-ranking males.[9] Bornean flanged males are also more than ten times as likely (~24%) to force copulations than are their Sumatran counterparts (2.3%), though still far less likely to do so than are unflanged males.[7–9,75,119] In contrast, subordinate flanged males in Sumatra rarely achieve matings, but both the dominant flanged male and unflanged males can maintain long consortships with females.[7,12] This difference may be a consequence of systematic differences in habitat quality between the Bornean and Sumatran sites. Bornean males, living in relatively poor habitats and more limited by energetic constraints than Sumatran males, are able to sustain only brief consortships.[101] Low habitat quality also results in lower densities and less frequent rates of association. As a consequence, males probably have little or no knowledge about the females they encounter and are likely to be more aggressive in their mating attempts. In contrast, Sumatran males, living in richer habitats at higher densities, encounter females more often and are capable of maintaining longer consortships and sustained associations with females likely to be fecund.[7,66,102]

Box 1. (Continued)

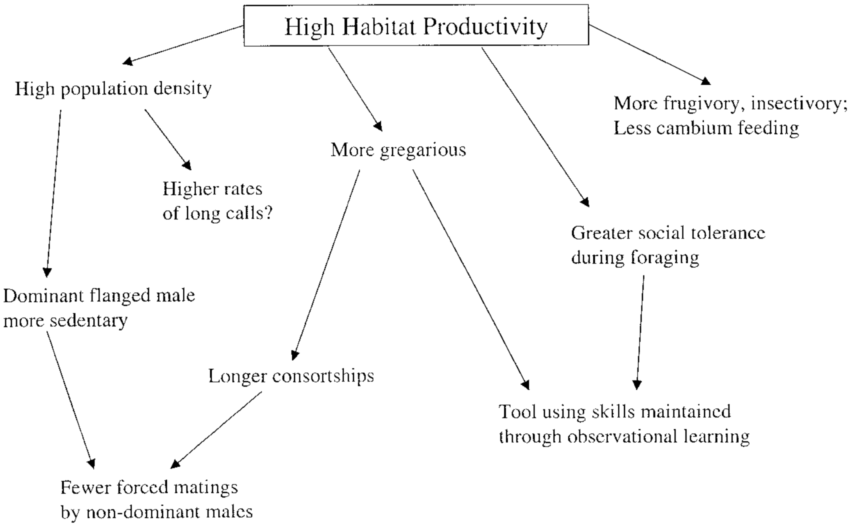


Figure 2. Inter-island differences are likely due to habitat differences in productivity.

Unflanged males on both islands actively seek and follow females and engage in consortships that often involve forced copulations.[8,119] A striking difference, however, is that 90% of the matings between unflanged males and adult females in Borneo involve forced copulations,[8,9] whereas forcing characterizes only about 45% of the matings in Sumatra.[7,119] On both islands, these males tend to be more constrained in the length of their consortships by social factors such as the presence of flanged males.[8,9,121] In Sumatra, it is possible that the difference reflects a greater degree of monopolization of females during their fecund period by the resident dominant flanged male. This restricted access is more likely in habitats with high productivity, where preferred flanged males can maintain longer consortships, making forced matings less likely. (An alternative explanation for the island difference would be that Sumatran females display a lower degree of resistance as a result of higher encounter frequencies or lower mating costs).

Another remarkable difference concerns the relative proportion of flanged males. Although the adult sex ratio is near parity across all sites in Borneo and Sumatra, in Borneo, on average, there are 1.6 times as many flanged males as there are unflanged males.[8,9,11,16] In Sumatra, on the other hand, there are nearly twice as many unflanged males as there are flanged males.[19,87] Perhaps Sumatran males are more susceptible to socially induced delay in acquisition of secondary sexual characteristics. This possibility is not inconsistent with the greater density of flanged males (C.P. van Schaik, unpublished data).[49] Such a response could be adaptive in light of the greater monopolization of females by dominant flanged males in Sumatra, making the reproductive success of nondominant flanged males close to zero.

A recent survey suggests that massive fires alone caused a 33% loss of the remaining population of orangutans on that island.[49] We can only guess what the current wave of illegal logging and mining is doing to their numbers on this island, but people have now invaded the Tanjung Puting National Park, one of the orangutans main refuges in Borneo, while Kutai National Park, a former stronghold, has all but disappeared. With the exception of orangutans within the Gunung Palung reserve, the remaining animals are scattered over numerous forest fragments, almost all of which may prove too small to retain viable populations.

The relationship between orangutans and their habitats is one of interdependence.[40] Orangutans act as seed dispersers and predators that help maintain the species diversity of the forests they inhabit. For this reason, the presence of orangutans is a good indicator of the biological diversity of Southeast Asian rainforests. If orangutans are present at normal densities, then the area is likely also to contain at least five other species of primates, at least five species of hornbills, at least 50 different fruit-tree species, and 15 liana species.[49] Thus, orangutans are an excellent "umbrella species" for rainforest conservation. This species' requirements with regard to area and habitat are wide enough that if orangutans were made a focus of protective management, the biodiversity of species within its range would also automatically be preserved.[49] Furthermore, it is extremely important to conserve as much habitat as possible to maintain variability within and between orangutan populations so that we can better understand inter-island differences and study cultural variation, which may be rapidly eroding.[149]

National and international conservation organizations have responded to threats to orangutans by setting up rehabilitation centers for confiscated animals and by establishing protected areas. The development of rehabilitation centers that reintroduce confiscated and formerly captive orangutans into the wild has been one attempt to preserve viable populations. Initially, the task of such centers was to squelch the trade in pets, and they released animals into forests with existing orangutan populations. In addition, these centers have become the basis for ecotourism programs that encourage the viewing of

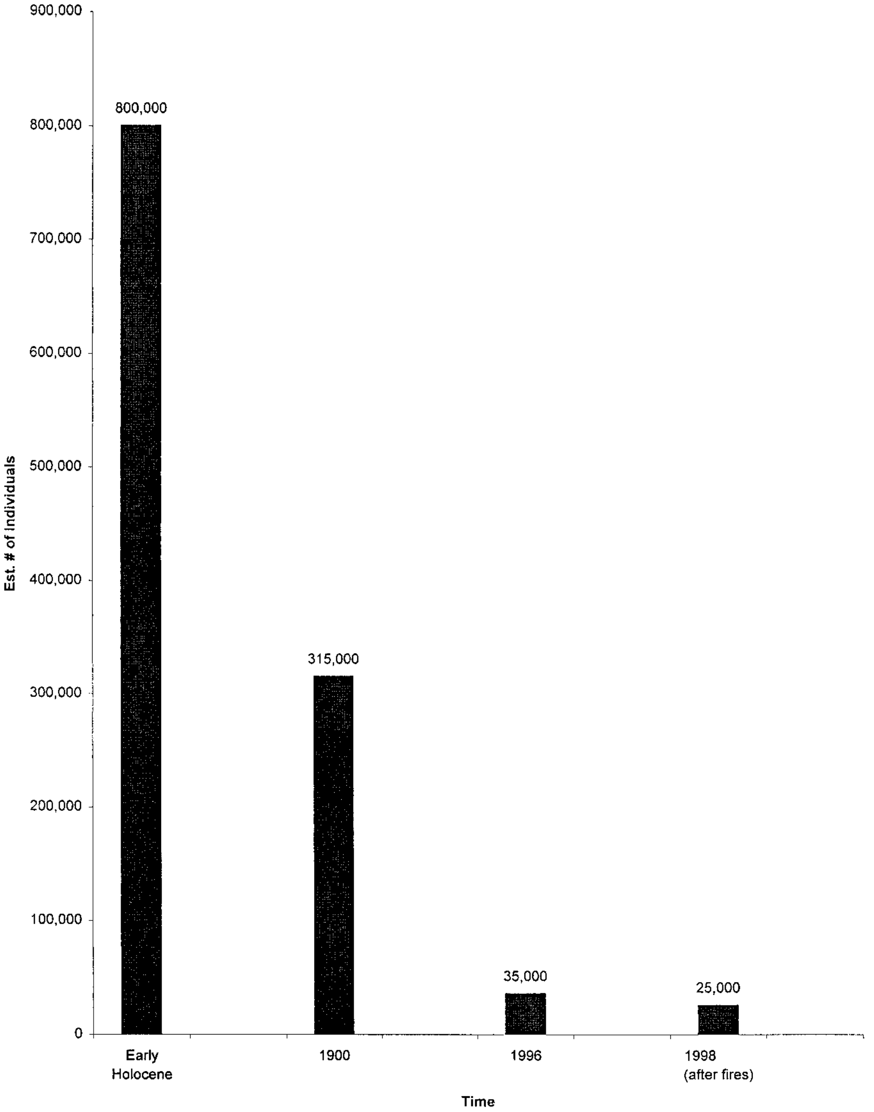


Figure 5. Total estimated orangutan populations since the early Holocene. Data are taken from Rijksen & Meijaard.[48]

wild orangutans. Ecotourism can produce revenues to continue and improve conservation efforts and provide local people with economic incentives not to destroy the extensive forest tracts that sustain orangutans and sympatric species. More recent attempts at reintroduction have focused on returning animals, increasingly displaced by forest conversion or driven out by forest fires, into suitable but currently unoccupied forests.[150]

Various national parks are in place in regions of Borneo and Sumatra where orangutans range. However, the protection of these parks is inadequate,[151] and the recent lawlessness has made it harder to defend the orangutan's key habitats. In the absence of effective enforcement of existing conservation policies, including the tight regulation of logging, orangutan populations are currently slipping from endangered to critically endangered.[152] This problem is compounded where one country contains species found nowhere else: Indonesia contains over 90% of the world's wild orangutans.

Any further losses may spell the end of a variety of endangered species, including the wild orangutan. In order to prevent these extinctions, uncontrolled and unplanned logging and clearing must be brought to a halt. Only in well-protected old-growth forests does the wild orangutan have a realistic hope of long-term survival. And only through continued field studies on wild orangutans can we hope to understand those as yet unsolved puzzles we outlined in the introduction and develop realistic models of hominid behavioral ecology, as well as the evolution of many unique human behaviors.

CONCLUSIONS

1. The evolutionary history of orangutans, including their ancestral locomotor patterns, remains uncertain. *Sivapithecus* remains the best candidate for an orangutan ancestor, but postcranial fossils from the late Miocene and Pleistocene of Southeast Asia are needed to test current hypotheses.
2. The prehistoric decline in numbers of orangutans and the collapse of their ranges are best explained by human hunting, although ecological factors may have also played a role.
3. There is considerable morphological and genetic variation both among and between Bornean and Sumatran populations such that the current scheme of classification does not capture the full range of variation.
4. The orangutan's social organization remains puzzling, though an individual-based fission-fusion system is consistent with behavioral observations. A network of loose associations within a greater open community, centered around a dominant long-calling male, is the most likely social unit.
5. The evolution of this system is potentially explained by the infanticide-avoidance hypothesis, but further research, including field experiments, is needed to test this hypothesis.
6. Demographic and behavioral variation between the islands populations, including density, the incidence of tool use, male reproductive tactics, and perhaps susceptibility to developmental slow-down in males, is best explained by habitat productivity.
7. Conservation is of the utmost importance for assuring the orangutan's survival and for increasing our under-

standing of hitherto unexplained aspects of their socioecology, sociosexual behavior, and cognition.

ACKNOWLEDGMENTS

We thank the Indonesian institute of Sciences, LIPI, for granting us permission to do research in Indonesia, and Universitas Indonesia in Depok and Universitas Syiah Kuala in Banda Aceh for sponsoring the projects. The directorate general of Nature Conservation and Forest Protection, PKA, gave permission to do the work in Gunung Leuser National Park. Fieldwork by van Schaik on orangutans at Suaq Balimbing receives long-term support from the Wildlife Conservation Society (formerly New York Zoological Society). Additional support came from the L.S.B. Leakey Foundation. We thank Mike Griffiths, Kathryn Monk, Yarrow Robertson, S. Poniran, the late Sayed Mudahar, and especially Perry van Duynhoven for various kinds of support, and Asril, Beth Fox, Tatang Mitrasetia, Dolly Priatna, Herman Rijksen, Ian Singleton, and Suci Utami for discussion. Maria van Noordwijk, Cheryl Knott, John Mitani, Peter Rodman, Rich Kay, and Todd Yokley gave useful comments on the manuscript. This paper is dedicated to the memory of Idrusman (Yus): friend, naturalist, and conservationist.

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