The Behavioral Flexibility of *Pongo*: "Mono-Social" Group Living and the Future of Wild Orangutans

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Honors Thesis
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"Hanging around, Orangutans-in-Waiting" by Lone Dröscher Nielsen
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Abstract

Endemic to the islands of Sumatra and Borneo, the orangutan (genus *Pongo*) is endangered and approaching extinction in the wild. *Pongo* requires a large amount of calories and travels across extensive tracts of forest in search of food. Predominately arboreal and reluctant to cross breaks in the canopy, forest fragmentation has confined *Pongo* to smaller patches of forest and forced individuals to interact with conspecifics. This is of particular concern because traditionally *Pongo* has been understood to live a solitary existence. However, research from the last few decades reveals the orangutan social system to be far more multifaceted than previously assumed; orangutans have established relationships and interact with conspecifics frequently. The socio-ecological model explains that female and male population distribution reflects food availability and distribution. Additional evidence suggests that when provided with food, and thus relieved of the pressure to procure food, orangutans exhibit behavioral flexibility and are able to live in close proximity to conspecifics without increased aggression. I propose *Pongo* is a behaviorally flexible primate capable, if provisioned, of living in "mono-social" groups as a radical response to extensive habitat and population loss.

Introduction

The International Union for Conservation of Nature (IUCN) recognizes two extant species of orangutan: *Pongo pygmaeus* and *Pongo abelii,* endemic to the islands of Borneo and Sumatra respectively. When last numerically assessed in 2004, there were roughly 45,000 – 69,000 Bornean orangutans (*Pongo pygmaeus*) and less than 7,300 Sumatran orangutans (*Pongo abelii*), listed as endangered and critically endangered respectively. The Bornean species has experienced a population decrease of 50% in the last 60 years, while the Sumatran population has undergone an 80% decline in 75 years. This drastic drop in population is, in large part, a result of forest fragmentation and loss. Extensive land clearing continues today, and it is reasonable to assume that current numbers are considerably worse than those recorded ten years ago.

An orangutan must daily consume large amounts of calories in order to fulfill his or her energy requirements and consequently travels across extensive tracts of forest in search of food. Primarily arboreal and reluctant to cross breaks in the canopy, an orangutan requires a dense and contiguous forest environment. It is for this reason that the species is highly susceptible to habitat degradation, notably forest fragmentation. *Pongo* is becoming more and more confined to smaller patches of forest, and, therefore, individuals are forced to interact with conspecifics. This is problematic because: 1) orangutans are semi-solitary and thought to be intolerant of conspecifics making them unable to live in groups and 2) conservationists are highly concerned that small patches of forest are unable to adequately support an orangutan's dietary needs.

Socio-ecologists observe the relationship between an organism's behavior and the environment in which the organism lives. Primate socio-ecology explains that "environmental variables (usually food, its seasonality, distribution, and abundance) influence primate group size, composition, and social dynamics" (Parga and Overdorff 2011:12). If food is plentiful and concentrated in one area, then primates are able to live in large groups. If food is scarce and scattered across the environment, then primates benefit from living in small groups, in pairs, or solitarily. Employing the socio-ecological model, *Pongo* is not inherently antisocial, but rather food scarcity has forced the orangutan to adopt a largely solitary existence.

The tropical rainforests of Sumatra and Borneo are, often illegally, logged and cleared for palm oil production. If forest degradation continues, remaining forests may soon become too fragmented to sustain a stable orangutan population. Conservation efforts tend to focus on the preservation of land/habitat, often in the form of governmentally backed nature reserves or wildlife parks. Although highly successful in many parts of the world, securing and maintaining a protected area can be challenging. Economic incentives and government corruption have made it particularly difficult to both secure and protect sections of forest in Indonesia. An alternative approach to orangutan conservation is needed.

While the protection of orangutan-suitable forest *is* essential if orangutans are to survive, the amount of land necessary is far less than currently advocated – recent research suggests that orangutans are not inherently antisocial as was once thought, but are alternatively best described as asocial. They act as if alone (mono) when surrounded up conspecifics (social). I propose *Pongo*, if provisioned, is capable of living in "mono-social" groups as a radical response to extensive population and habitat loss.

Studying Primates

Humans study non-human primates for a host of reasons. From an evolutionary lens, as our closest living kin, non-human primates can often serve as a proxy for our more recent human ancestors. Realizing that "identifying our place in nature is by definition a comparative enterprise" (van Schaik 2004:13), non-humans primates provide us with indications as to diet, behavior, tool use, communication and so forth. Forces of natural selection and adaptation can be examined through the extensive and diverse radiation contributing to our understanding of the mechanisms behind variation. Further still, recent developments in "nucleotide sequence data now provide an alternative means to reconstructing phylogenetic relationships and the *timing* [emphasis added] of lineage divergence events" providing time-calibrated phylogenies (Losos and Mahler 2010:384). The animals are also inherently fascinating. As biological anthropologists, primatologists study non-human primates in an attempt to further studies in human origins, to better understand adaptation, and out of an intrinsic interest for the animals.

The Hominidae family is comprised of four genera: *Pan* (chimpanzees), *Homo* (humans), *Gorilla* (gorillas), and *Pongo* (orangutans). Conservation of the non-human great apes is of significant concern because of the primates apes are the most closely related to us and are pivotal in the study of variation and the divergence of *Homo*. The chimpanzee has been researched extensively and received a wealth of public attention. The gorilla, too, attracts public interest and has also been well researched. Jane Goodall and Dian Fossey propelled the chimpanzee and gorilla, respectively, onto both the academic and public radars.

Despite Birutė Galdikas' groundbreaking research in the 1970s and 1980s, the orangutan is undoubtedly the least observed and researched of the great apes (Nystrom and Ashmore 2008; van Schaik 2004).

The Orangutan

A lack of research has not stopped the public from being well aware of and captivated by the orangutan. Former primary advisor to the World Wildlife Fund Malaysia, conservation biologist Junaidi Payne (2008:12) comments:

> People are fascinated by orangutans, perhaps because they seem so similar to us while being so very different; similar in their physical appearance and intelligence, yet different in that they live in an environment that is so foreign to us, up in the trees, without shelter, and often drenched in pouring equatorial rain.

People are right to be intrigued. The orangutan only become a main focus of fieldwork in the last three or four decades. Van Schaik (2004:14) reasons that "orangutans never took center stage because they are the Asian cousins, not part of the main family line. Moreover, they are elusive: hard to find and easy to lose." Although the least related of the non-human great apes to humans, *Pongo* is valuable in the understanding of our own evolution and the development/timing of uniquely human traits. And then there are features – a similar pattern of slow growth and development – that both humans and orangutans share (Galdikas 1999), again shedding light on the mechanisms of variation. The genus merits studying, and its survival *is* worth securing.

Pongo: Species Profile

In Malay 'orang' means person and 'hutang' means forest. The orangutan, then, is the 'person of the forest.' Before delving into a discussion of orangutan behavioral flexibility and sociality, it is imperative that we first place *Pongo* within the primate order, appreciate their distinctive life history, and recognize the factors behind their socio-ecology: morphology, ecology, and, lineage. These factors have shaped the orangutan's ability, or lack thereof, to adapt in times of environmental change and will be referenced throughout the remainder of this paper.

Taxonomy

One of four great apes, the orangutan is a member of the great ape family Hominidae, which further splits into two subfamilies: Homininae and Ponginae. The Homininae subfamily includes the *Gorilla*, *Pan*, and *Homo,* and a number of extinct genera. The Ponginae subfamily encompasses an extensive linage of extinct Eurasian apes and one remaining extant genus: *Pongo*. There are two species: *Pongo pygmaeus* on the island of Borneo and *Pongo abelii* on the island of Sumatra.

The number of *Pongo* (sub) species is subject to debate. There was a shift in the early 21st century from one to two species, as recognized by several preeminent primatologists. Writing in 1999, John Fleagle in *Primate Evolution and Adaptation*, reflecting contemporary thought, recognized one species consisting of two subspecies, one on Sumatra and one on Borneo. However, the Bornean and Sumatran populations have been geographically separated for at least 0.6 million years (Goossens et al. 2009), and the two subspecies were

therefore promoted to species status; Colin Groves reflects this taxonomic shift in *Primate Taxonomy* published 2001.

Promotion of the subspecies to species resulted in a back-and-forth argument over what constitutes a species versus a subspecies. Fischer et al. (2006:1135) sequenced several inter-genetic autosomal regions revealing that the "extent of genetic differentiation among groups of orangutans…lends no support to the notion that [species] are genetically distinct entities," casting doubt on the designation of two species. Supporters of the biological species concept argue *Pongo* to be one species because inter-island populations are able to breed and produce fertile offspring (Goossens 2009). In adherence to Mittermeier et al. (2013) and the IUCN two species will be recognized in this paper.

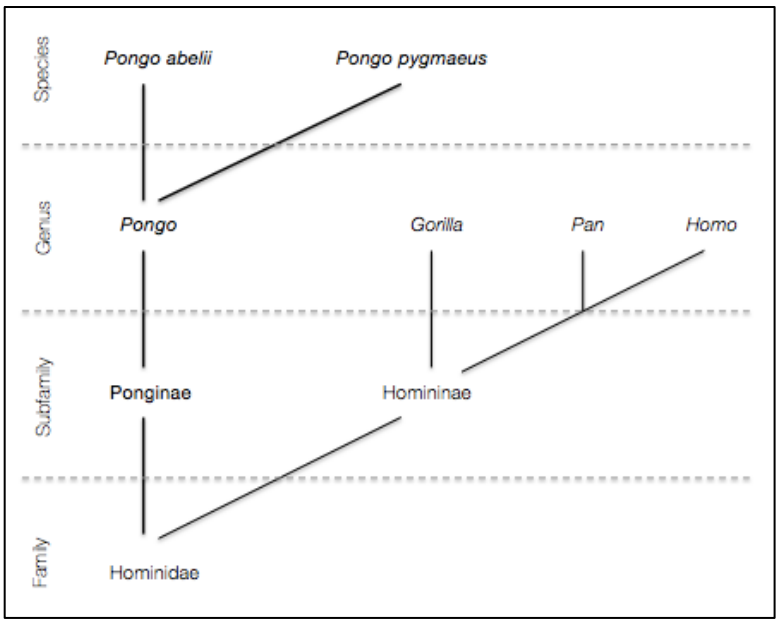


Figure 1:
Phylogenetic tree of Hominidae family, emphasis on Ponginae subfamily.

The species debate forces us to consider how similar or different the two species are. Research strongly supports that species differences are strictly biological – small differences

in morphology – as opposed to behavioral (van Schaik 2004). Subsequently, all extant *Pongo* species and subspecies will be treated as a single taxon in this paper.

Life History

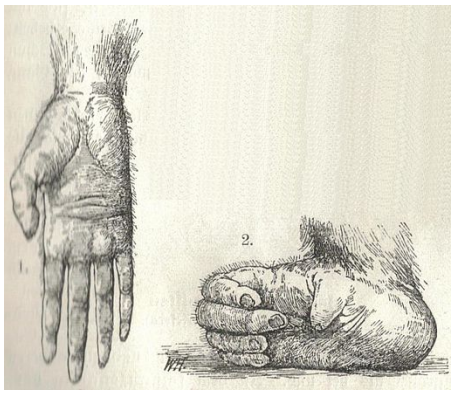
The orangutan has a distinctively slow life history. A female matures between ages eight and 11, but age at first reproduction is 15 (Wich et al. 2009). A male orangutan matures, becoming sexually active, around age eight. Between the ages of 20 and 30 the male might (not all males do) undergo a second maturation. At this time the male develops a throat sac, cheek flanges (fibrous tissue pads), his hair becomes long and thick, and he doubles in size becoming twice the size of a female (Delgado and van Schaik 2000). This phenomenon, known as bimaturism, results in two "morphs" of male orangutan: sub-adult/unflanged and adult/flanged. Orangutans display extreme sexual dimorphism, with fully developed males weighing on average 120kg and females less than half that at 40 – 60kg (Fleagle 2013; OFI 2015).

Among primates, orangutans experience the longest period of dependency. Up until age five a juvenile relies heavily on his or her mother to procure food, cross gaps in the forest, build sleeping nests, etc. (Galdikas 1999). In contrast to the other great ape taxa, in which a female has several young in her care, an orangutan mother has only one offspring in her care at a single time (twinning is an extremely rare occurrence). Offspring leave their mother when they mature, and orangutans, therefore, have an inter-birth interval of eight years. A female is only able to produce four or five offspring in her lifetime. At 24.4 years, *Pongo* has the slowest generation time among primates (Wich et al. 2009). A slow life history is of concern as van Schaik (2001:29) explains:

Slow life history means that it takes decades for orangutan populations to build up numbers again after decimation of the population. It also makes them very vulnerable to exploitation. A simulation study showed that even minute increases in adult female mortality rates in the order of 1 to 3%, for instance due to hunting, can drive orang-utan populations into extinction.

Morphology

Orangutans are almost exclusively arboreal. Spending more than 95% of their time in the canopy, the orangutan's limbs are highly specialized for suspensory life (OFI 2015). They have long forelimbs and hind limbs with flexible shoulder and hip joints. The hand is narrow with exceptionally long fingers allowing the orangutan to securely wrap its hand around a branch in suspension – the pollex is reduced and in line with the hand so as to not get in the way. Often used like a third or forth hand, the foot also has long toes with a short, tucked hallux and is "hook-like." Individuals move through the forest using a form of locomotion known as quadrumanous scrambling (Mittermeier et al. 2013, OFI 2015). An orangutan moves slowly from one branch to the next and therefore struggles to navigate large gaps in the canopy: *Pongo* requires a dense forest environment.



"Orangutan Hand and Foot" by Walter Heubach
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Ecology

Habitat. *Pongo* is endemic to the Southeast Asian islands of Borneo and Sumatra, which form the north and west boundaries of the Java Sea. Borneo is divided between the countries

of Brunei, Malaysia and Indonesia, while Sumatra is a part of Indonesia. Orangutan ranges can be found throughout the Indonesian sector of Borneo, Kalimantan in English, and northern Sumatra (Husson et al. 2009). Tropical rainforests cover the hilly topography of both islands, and "orangutans seem to prefer upland rather than lowland forest areas" (Fleagle 2013:158). Within lowland environments, orangutans gravitate towards the canopies of dense old growth alluvial and peat-swamp forests (Husson et al. 2009; Morrogh-Bernard et al. 2013). These waterlogged forest habitats do not boast as many species of soft-pulp producing fruit trees as do montane regions, but are rich in year-round fruit producing tree species (van Schaik 2001). This minimizes the effects felt during periods of low fruit production.

Diet. The orangutan is a frugivore, favoring ripe, pulpy fruits and hard seeds – the eating of seeds, granivory, is often categorically separated from frugivory, but in discussions of *Pongo* ecology no distinction is made and granivory is considered synonymous with frugivory. Long-term field studies have found seeds to constitute 24% of the diet and fruit 38% (Conklin-Brittain et al. 2001). Individuals select high-energy fruits and avoid fruits rich with tannins. A soft, sugary fruit, melaka (*Tetramerista glabra*) is a favorite of orangutan, but figs from the strangler fig tree (*Ficus viens*) are a clear staple (Fleagle 2013; Taylor 2009). Small amounts of "young leaves and shoots, invertebrates, occasionally mineral-rich soil, and sometimes even the odd vertebrate, such as slow loris" are eaten (van Schaik 2004:30). During periods of low fruit production the orangutan is forced to feed on fallback foods such as unripe fruits, larger amounts of leaves, epiphytes, lianas, and bark (Taylor 2009; Wich et al. 2006).

Energy Needs. One of the largest primates, *Pongo* must consume a huge number of calories daily. The energy an individual requires is calculated using the relationship between

body weight and activity level. A healthy adult human needs roughly 40 kcal/kg/day. Applying this model, Peter Rodman (1984) calculates an adult female orangutan weighing 37.8kg to require 1512 kcal/day and an adult male weighing 83.6 to require 3344 kcal/day. In line with Rodman's estimates, Bruce Wheatley (1982) substitutes basal metabolic rate for bodyweight, and calculates 2333 kcal/day for an orangutan weighing 55 kg. Caloric intake fluctuates with periods of growth, reproduction, and maintenance (Nutrient Requirements of Nonhuman Primates 2003), and "none of these figures take account of additional energy requirements for pregnant or lactating females" (Knott 1998:1075). In order to reproduce, upon which species survival is dependent, females must have access to large amounts of calories/food.

Lineage: the Initial Factor

When compared to that of *Pan* or *Gorilla*, the evolutionary history of *Pongo* is relatively well established. Fleagle (2013:338) is almost joking when he writes: "there seems to be an overabundance of fossil orangutan relatives from the Miocene of Asia and possibly Europe." The orangutan is thought to have derived from one of the following extinct Ponginae genera: *Ankarapithecus*, *Lufengpithecus*, *Gigantopithecus*, and notably *Sivapithecus* and *Khorapithecus*. From the early and middle Miocene of Pakistan, *Sivapithecus* is the genus most commonly designated as the orangutan predecessor (Fleagle 2013; van Schaik 2004). Recent finds, however, suggest *Khorapithecus,* a descendent from *Sivapithecus*, as a good model for a direct ancestor of the modern orangutan. From the middle and late Miocene of Thailand, *Khorapithecus* displays all of the traits joining the genera listed here and shares several derived traits observed in *Pongo* today.

During the Miocene, the tropical rainforests of modern-day Indonesia extended north and west into the areas of Thailand and Pakistan. Extinct pongids, from one of which *Pongo* is a descendant, "evolved within a tropical habitat similar to where [modern orangutans] are found today" (Nystrom and Ashmore 2008:183). The Ponginae subfamily experienced an *extended* period of co-evolution in a *stable* environment. Reflective of this co-evolution, orangutans are decidedly adapted to their respective habitat: an arboreal frugivore that requires a dense and contiguous peat-swamp forest environment. *Pongo* is unable to cope with substantial environmental change.

Under Threat

Orangutan populations are rapidly dwindling. *Pongo pygmaeus* is endangered and *Pongo abelii* is critically endangered, approaching extinction in the wild (IUCN 2015). Rijksen and Meijaard (1999) contend that the combined number of Bornean and Sumatran orangutans was 25,000 in the late 1990s, reflecting a 92% population decline in under a century. While prone to many threats, like hunting by humans and wildfires, the orangutan is most severely threatened by habitat fragmentation and loss in the forms of land clearing for agricultural production and selective logging.

Home Range Size

Range size is determined by the spatiotemporal distribution of resources. A primate's range must yield the food products necessary to fulfill his or her daily caloric and nutritional requirements. Fleagle (2013:38) comments: "primates live in a complex environment with many constantly changing variables. One way groups of primates deal with this complexity is to restrict their activities to a limited area of forest they know well." A primate inherently leans toward as small a range as is resource possible.

It has been established that *Pongo* requires a large number of calories daily. Fruit, while considered a high calorie food, is a relatively low-calorie per unit food and orangutans must, therefore, consume a large quantity in order to fulfill their daily energy needs. Additionally, they require a certain amount of macronutrients (carbohydrate, protein, and fat) and micronutrients (vitamins and minerals). In order to fulfill these needs, orangutans consume

a diverse range of species of fruit. Singleton and van Schaik (2000:899) found that "low species richness in the [peat-swamp forests] force orangutans to use larger areas to maintain an adequate diet." Orangutans consistently move around the forest in search of different species of fruit and, consequently, have extensive individual ranges. This is not to say that orangutan ranges do not overlap, because they do heavily overlap.

In discussion, range can be defined in varying ways. *Day range* or daily path length is "the distance an individual or group moves in a single day" (Fleagle 2013:39). *Home range* encompasses the day ranges utilized over a longer period, such as a month or year, of time (Fleagle 2013; Singleton and van Schaik 2000). This includes travel outside of the *core range* (sometimes referred to as core area) or "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943:351).

Orangutans have extensive home ranges. Conducting a four-year study from the Suaq Balimbing Research Station in the Kluet region of the Leuser Ecosystem, Singleton and van Schaik (2000) calculated the home ranges of *Pongo.* They observed female orangutans to have long-term home ranges of roughly 850 hectares, while males have home ranges of well over 2500 ha. Within the 850 ha, a female spends the majority of her time in a core area of 400-500 ha. Males also have core ranges, but these have yet to be estimated. Additionally, Singleton and van Schaik (2000:908) surmise:

> much larger areas than often assumed are needed to support even small orangutan populations. A single female may require a minimum of 150 ha to support herself and her offspring, and males may require up to 4000 ha or even more.

Reluctant to, and often unable to due to morphological restrictions, negotiate gaps in the forest canopy, and requiring a large home range to fulfill its caloric and nutrient needs, an orangutan needs an extensive tract of *contiguous forest*. Unfortunately for the orangutan, sizable patches of contiguous, peat-swamp forest are becoming increasingly rare.

Habitat Degradation

The tropical forests of Sumatra and Kalimantan, Borneo are subject to some of the highest rates of forest clearing in the world (Broich et al. 2011; FWI/GFW 2002). Home to the largest populations of *Pongo*, lowland peat-swamp forests are easily accessed and are most subject to clearing and fragmentation (Campbell-Smith et al. 2011a).

Forest Loss. As recently as 1950, Indonesia was densely forested with over 162 million hectares of tropical rainforest. In 2000, only 98 million hectares of forest remained, a 40% decrease in 50 years (FWI/GFW 2002). Examining forest lost in in the Bukit Barisan Selatan Forest Landscape (BBSFL), Gaveau et al. (2006) recorded a 50% decline in 692,850 hectares between 1972 and 2002. Rates of forest fragmentation have only increased: "1 million ha per year were cleared in the 1980s, rising to about 1.7 million ha per year in the first part of the 1990s. Since 1996, deforestation [has] increased to an average of 2 million ha per year" (FWI/GFW 2002:xi). A recent publication by Broich et al. (2011:1) revealed "the total forest cover loss for Sumatera and Kalimantan 2000–2008 was 5.39 Mha, which represents 5.3% of the land area and 9.2% of the year 2000 forest cover of these two islands."

An area of forest is only able to carry a finite number of individuals of a species. Although no exact numbers have been recorded, at current size the combined Indonesian forests can support "X" number of orangutans. Orangutans are unable to live outside of the

forest and "densities are lower in moderately to heavily logged forest than in unlogged areas of comparable habitat" (Husson et al. 2009:94). As forested lands decline, so too will the *Pongo* population.

Forest Fragmentation. While forest loss is in itself of concern, the orangutan is more affected by forest loss in the form of fragmentation. An orangutan requires a large range; females have home ranges of 850 hectares and males 2500 hectares. The BBSFL was 692,850 hectares of contiguous forest in 1972. However, selective logging broke the land up into 1094 fragments. Although the forest contained three large fragments (17,673 ha, 120,000 ha, 159,000 ha), "approximately 45% of the fragments were <2.7 ha…and some 72% of the fragments were separated by more than 1 km" (Gaveau et al. 2006:5).

Orangutans are incapable of surviving in such tiny patches of forest and cannot cross a one-kilometer (possibly longer) break in forest canopy. An orangutan living in a small and isolated patch of forest is trapped. Starving and desperate, individuals will attempt to cross between patches of forest, which often results in being captured for trade or hunted (by tiger or human). An individual will also, if there is a possibility, resort to the raiding of agricultural crop fields, which again often results in being captured and/or killed (Campbell-Smith et al. 2011b).

Fallback Foods. Although unable to survive in tiny fragments of forest, *Pongo* can, and does, live in patches of forest smaller than desired by feeding on fallback foods, or "foods whose use is negatively correlated with availability of preferred foods" (Marshal & Wrangham 2007). When fruit is unavailable the orangutan feeds on unripe fruits, bark and vegetable matter. These foods are problematic, however, because they are not necessarily abundant or

accessible, and further they do not properly fulfill macro- and micronutrient needs (Hanya and Chapman 2012; Lambert 2011). Orangutans lose weight and are energetically stressed when forced to rely on bark for the majority of their calories (Conklin-Brittain 2006). Knott (1998:1076-77) explains: "disease resistance may be compromised during periods of low fruit availability as more energy is needed to fight infection…[and] prolonged periods of negative energy balance may compromise the ability of orangutans to conceive." A reliance on fallback foods threatens population health and replenishment. The species cannot survive if confined to a small patch of forest in which their dietary needs cannot be properly met.

Securing Land

Highly specialized, *Pongo* is unable to survive outside of a forest environment and selective logging reduces populations by 20% to 30%, and even upwards of 50%, in certain areas (Felton et al. 2002, Hardus et al. 2011). Delgado and van Schaik (2000:212) summarize the orangutan's plight:

> 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.

Orangutan habitat is quickly diminishing. Government corruption has made it challenging to both preserve and secure remaining forest fragments and those sections of forest that have been allocated for protection.

Corruption. Although overseeing impressive economic growth, the Indonesian government is both decentralized and corrupt (Gaveau et al. 2006). Segments of forest have previously been, and continue to be, established as Protected Areas (PAs), but the economic incentives that come with logging and palm-oil production are favored in preference to conservation efforts. PAs have subsequently been cleared both legally and illegally (Gaveau et al. 2006). 29,400 km^2 of PAs were established in West Kalimantan in 1985. Using Geographic Information System and remote sensing analyses, Current et al. (2004) found that by 2001 63% (18,500 km^2) of these PAs had been intensively logged. PAs are expected to be further logged as "decentralization regulations implemented in 2001 now allow local districts to issue small logging parcel leases (1 km^2); this has resulted in the virtually uncontrolled harvest of remaining accessible lowland" (Curran et al. 2000:1002).

Conservation. Extensive, contiguous forests are a nonnegotiable in the conservation of *Pongo*. Van Schaik (2001:34), echoing the mainstream approach to conservation within primatology, states:

> Effective orangutan conservation requires protected areas, simply because the red apes only thrive in unexploited old-growth forests. To stop the destruction and degradation of protected areas, we need a renewed emphasis on park protection. At the same time, once government-level support for parks is secured, we need more external support for the management of these parks, since Indonesia is economically in a difficult position to allocate enough money to conservation.

The Indonesian government supports economic development over conservation, and any conservation efforts are often negated by corruption. To protect land and institute effective

park management will no doubt be an arduous and timely battle. *Pongo* is on the brink of extinction; for the orangutan there is no time left.

An Alternative Approach

If drastic measures are not taken immediately, orangutans are likely to be extinct in the wild by the end of this century. Recent proposals and current conservation efforts focus on the protecting of peat-swamp forest areas (Morrogh-Bernard et al. 2014; OFI 2015). These forests are increasingly rare and PAs are difficult to protect.

In contrast, I propose efforts be placed in the permanent securing of smaller, more obtainable, patches of forest. I argue *Pongo*, although living in solitary, is a socially inclined and behaviorally flexible primate. Orangutans are capable of living in "mono-social" groups and, subsequently, in restricted ranges. However, small patches of forest do not yield the food necessary to sustain the caloric and nutritional needs of one orangutan, let alone a group. Consequently, I argue for the provisioning of wild populations as a radical solution to extensive population and habitat loss.

Behavioral Flexibility

The peat-swamp forests of Indonesia are disappearing. *Pongo* must adapt to these changes in environment or face probable extinction.

Primate Plasticity

Primates, like many mammals, are extremely flexible animals in regard to environmental change. A species' ability to quickly adapt is physiologically, morphologically and behaviorally determined (Box 1991; Lambert 2011). Chivers (1991:5) explains: "the central issue in considering tolerance to environmental change – the secret to survival of both individuals and species – lies in the ability to locate, consume and process adequate food." Behavior is fundamentally flexible, but restrictions in digestive anatomy (physiology) and locomotion (morphology) must also be considered. Most primate genera lack restrictive anatomical specializations and can, therefore, adapt to environmental change.

Pongo. In contrast, *Pongo* is highly inflexible in regard to their physiology and morphology. When discussing flexibility primatologists tend to focus on proximate versus ultimate or evolutionary causes (Lambert 2011), but to best understand the whole picture Jones (2005:xviii) argues we must understand "[flexibility] in relation to evolutionary causes and consequences." In this context the orangutan's plight becomes clear: the Ponginae subfamily experienced an extended period of co-evolution in a stable environment. When faced with environmental fluctuation, *Pongo* retreated south into Indonesia, following the receding peat-swamp forests, and went extinct in the northern areas of Pakistan and Thailand. Choosing to

follow the receding peat-swamp forests and, therefore, avoiding adapting to environmental fluctuations during its evolution, *Pongo* developed specialized anatomy: the orangutan is an arboreal frugivore. Forest degradation is threatening the orangutan's specialized way of life. Specialized taxa, especially those that exhibit high resource use and have a slow life history like the orangutan, are most at risk for extinction (Harcourt et al 2002).

Primatologists recognize three adaptive variables: physiologic, morphologic, and behavior (Lambert 2011). The orangutan is unable to adapt to current habitat degradation physically (physiologically or morphologically), but can adapt behaviorally. It is for this reason I choose to focus on the behavioral flexibility of *Pongo*.

Primate Social Systems

Primate societies display a remarkable breadth of diversity. In a key text, "Evolution of Primate Social System" (2001), Peter M. Kappeler and Carel P. van Schaik break down the primate social system, the definitions observed in this paper.

A social system is defined as a "set of conspecific animals that interact regularly and more so with each other than with members of other such societies" (Kappeler and van Schaik 2001:709). There are three main components. *Social organization* examines the spatiotemporal cohesion of the group, or how members of the species in question prefer to spend their time in regard to others: solitary, pair-bonded, and group living. Group living is the most prevalent form of social organization, while solitary is the least observed. *Mating system* describes the prominent pattern of copulation: monogamy, polyandry, polygyny, and polygynandry. *Social structure* depicts the interactions between conspecifics: male-male, female-female, male-female, and parent-offspring.

Kappeler and van Schaik (2001:707) explain that "social organization and mating system are more closely linked to each other than either one is to social structure." However, they are quick to clarify that mating system can, and does, differ from social organization; a species with a pair-bonded social organization might participate in a polygynandry mating system, as opposed to a perhaps seemingly more logical monogamous mating system. Additionally, social organization and social structure are not necessarily cohesive. The three components of a social system do not always correspond and a single component does not

provide an accurate depiction of a primate society. Social organization, mating system, and social structure interact to form a species' distinctive social system.

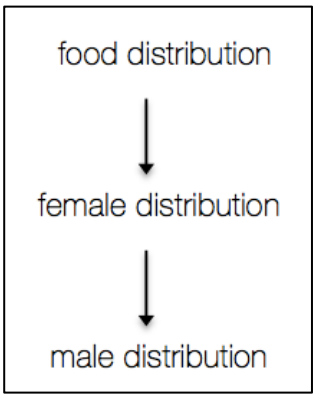
Historically, primatologists believed the three components of a social system to be concordant. The social system as a whole was described in regard to social organization (Kappeler and van Schaik 2001). Further, social organization was indicative of a primate's personality and social capabilities (Fuentes 2011; Parga and Overdorff 2011). Group living species were considered socially gregarious and sexually promiscuous. Pair bonded species, like their group-living cousins, were social gregarious, but differ in being sexually monogamous. Solitary species were antisocial, if not aggressive, toward conspecifics, and sexually promiscuous (Kappeler and van Schaik 2001). However, British primatologist Richard Wrangham challenged this assumption in the late 1970s and early 1980s. He posited that social organization is not reflective of inherent sociality.

Socio-Ecology

Socio-ecology is the study of an organism's behavior in relation to the environment in which the organism lives. Within primatology, as spearheaded by Wrangham, socio-ecology is the "study of how environmental variables (usually food, its seasonality, distribution, and abundance) influence primate group size, composition, and social dynamics" (Parga and Overdorff 2011:12). Primatologists work to identify patterns across primate species and the selective pressures behind them.

Working within the fundamental framework that all organisms need energy and must eat in order to survive, food is considered *the* selective pressure (Lambert 2011). The socio-ecological cascade models the distribution of primates across an environment. Only able to

reproduce under optimal dietary circumstances, socio-ecologists understand females to be a fragile resource: female density and distribution is dependent upon the density and distribution of food. Males, able to mate under any circumstance, are not a limited resource: male density and distribution results from access to receptive females (Fuentes 2011; Husson et al. 2009).



When food is plentiful and concentrated in one area, primates are able to live in large in groups. When food is scarce and scattered across the environment, primates benefit from living in smaller numbers, whether that is in small groups, in pairs or in solitary (Hanya et al. 2011; Hanya and Chapman 2012). Fruit is a particularly unevenly distributed food source and "thus fruit-eating primates are seen to have greater limitations on group size than primates that are not so reliant on fruit. Indeed, although there are exceptions, it has been demonstrated that frugivorous primates in larger groups travel farther than those in smaller groups" (Lambert 2011:519). Individuals respond to the distribution of food across their environment. A species' social system is a product of environmental constraints.

Orangutan Sociality

In 1942, (136) Earnest Hooton, author of the first primate textbook published in the United States, *Mans Poor Relations*, described the orangutan, based largely on captive observations, "as stolid, depressed, melancholic, apathetic, phlegmatic, sad, grave, brooding, reflective, etc." His description stuck. It has long been presumed that orangutans live in solitary because they are antisocial. However, employing the socio-ecological model, solitary species are not inherently antisocial, but rather have adapted a solitary lifestyle in response to ecological pressures. The orangutan, despite previous assumptions, is socially inclined.

Personality. A psychological study entitled "Personality and Subjective Well-Being in Orangutans" (2006) conducted by Weiss, King, and Perkins resulted in striking findings regarding the orangutan personality. As discussed here, personality is a measure of general demeanor representative of well-being. A total of 182 orangutans were tested. Subjects spanned 41 zoological parks located in Australia, Canada, and the Untied States. The Five-Factor Model (FFM), previously used in human testing, was used to examine orangutan personality. The model measures the five domains considered to be indicative of personality: neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness. Utilizing a modified FFM, it was determined that orangutans show low neuroticism, high agreeableness, and high extraversion: they are relaxed, sympathetic, and "social" beings. *Pongo* exhibits a high tolerance for conspecifics and enjoys interaction/stimulation.

Pro-social Behavior. In a similar study, Liebal et al. (2014) found orangutans to be pro-social great apes. Pro-social behaviors include helping, comforting, and sharing. These

actions are motivated by feelings of empathy and sympathy. Empathy is to feel *with*, while sympathy is to feel *for*. Liebal et al. (2014:2) asked "whether great apes show greater pro-social behavior towards a conspecific who has been harmed than towards a conspecific who has not been harmed," as would be expected of a pro-socially inclined creature. This was measured through the offering, or non-offering, of a stick. Among chimpanzees and gorillas, 21 orangutans from the Wolfgang Köhler Primate Research Center (Germany) and Orangutan Care Center and Quarantine (Borneo) were included in the study. Zoologists recognize altruistic behaviors to be motivated by the possibility of reciprocation and, thus, are actually not selfless in nature. The study mitigated this problem by combining the apes with multiple partners and only conducting the test once for each pair; there was no chance for reciprocation. In contrast to both chimpanzees and gorillas, Orangutans were observed to help conspecifics regardless of the circumstance. Additionally, it was found that "orangutans mostly actively offered the sticks to the victims, while the few stick transfers in chimpanzees were mostly tolerated takings" (Liebal 2014:6).

Pongo displays key personality markers evident among group living apes, like *Pan* or *Gorilla*, and displays pro-social behaviors; orangutans are not antisocial. Fruit is an unpredictable resource and the orangutan has, consequently, benefited from living in solitary. Observing orangutans in Cabang Panti, Knott (1998:1077) found that "when fruit was abundant and occurred in large patches, orangutans readily formed groups." Although not the most gregarious of primate species, when provided with the opportunity to be social, orangutans do congregate in groups and individuals opt to interact with conspecifics.

Orangutan Social System

Traditionally, the orangutan is considered *the* solitary ape. I am proposing *Pongo* be relocated into small patches of permanently protected forest and live in groups. To suggest a solitary species is capable of peaceful group living might seem radical. However, research conducted in the last 30 years has revealed the orangutan, as evident by their social system, to be more and more social than was previously assumed. Here I will discuss the *Pongo* social system: social organization, mating system, and social structure.

Social Organization

Social organization examines the spatiotemporal cohesion of a population: how do members of a species prefer to spend their time in regard to conspecifics? There are three primary categories of social organization in which primates participate: solitary, pair bonded, and group living. Solitary individuals forage alone and "the movements of different individuals about their habitat are not synchronized" (Charles-Dominique 1978:139). Kappeler and van Schaik (2001:713) define a pair bonded social organization as the "permanent association of one adult male and female" in which there is "synchronized spatial association between the pair." Lastly, although the composition of a group can differ dramatically between species – one male multi-female, one female multi-male, multi-male multi-female, – the majority of primates live in groups of three or more individuals (Kappeler and van Schaik 2001). Again, and this of key importance, group living primates experience synchronized spatial association.

Pongo. Most primatologists now recognize *Pongo* to be a semi-solitary primate. A recent shift in understanding, Fleagle traces the transition from solitary to semi-solitary in his scholarly text *Primate Adaptation & Evolution*. The first edition, published in 1988, reads: "adult orangutans are usually solitary" (213). Ten years later, in the 1999 second edition, he again writes that "adult orangutans are usually solitary," but adds that while "orangutans appear to live solitary lives, it seems likely that they maintain extensive social networks of individual relationships" (245). Fleagle (2013:159) again alters his initial description in the third edition stating: "adult orangutans are usually solitary, but may come together in travel bands, temporary feeding aggregations, and consortships."

Orangutan social interaction is dependent upon fruit production. Individuals are seen to gather during periods of high fruit production (Knott 1998; Singleton and van Schaik 2001). During a period of fruit abundance, Mitra Setia et al. (2009) observed upwards of 14 adult orangutans concurrently occupying a large strangling fig tree in peace. Realizing that it can be difficult to secure enough calories daily, researchers, like Knott (1998) or Mitra Setia et al. (2009), argue *Pongo* tolerates conspecifics in exchange for access to fruit: orangutans congregate *for* the fruit. In contrast, socio-ecologists argue the orangutan is able to act on inherent social tendencies when food pressures are relieved: orangutans congregate *because* of the fruit. This notion is supported by observations of allogrooming among adults and play between young females and unflanged males.

While brought together in temporary feeding aggregations, an adult orangutan does, still, spend the majority his or her time alone (Mittermeier et al. 2013; OFI 2015). However, orangutans have highly overlapping ranges, suggesting individuals are both aware of the

location of and move in regard to conspecifics, a distinguishing characteristic of group living primates.

Range Overlap. The initial goal of field research in the study of any primate is to locate the primates within their habitat – far more challenging than it might sound. In a study looking at the determinates of home-range size in the Kluet region of the Leuser Ecosystem, Singleton and van Schaik (2001) were surprised to find orangutan home ranges to extensively overlap and individuals to move in regard to conspecifics.

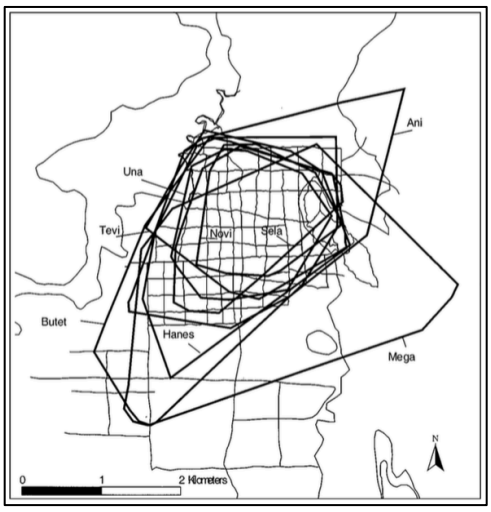


Figure 2: Polygon grid depicting the overlapping home ranges of female orangutans in Suaq Balimbing Park, Sumatra.

(Image taken from Singleton and van Schaik 2001, Figure #10)

Range overlap was observed among females, males, and between female and males. Highly unexpected for a species still deemed, at the time of research, to be intolerant of conspecifics, core ranges overlapped. Within their core ranges, 16 females, nine flanged males, and over 15 unflanged males all regularly visited one four-hectare square patch of forest. There was nothing special about that particular patch of forest – no rare fruit trees, no masting trees, no river, etc. There was, however, a high probability of coming across and interacting with another orangutan. Individuals continued to return, suggesting their choices were, at least in part, socially motivated.

Range overlap is not exclusive to the Kluet region and has since been observed and measured at several research sites across Sumatra. Van Noordwijk (2012:827) examined range overlap in the Tuanan Orangutan Research Area and found "major home range overlap among the many adult males sighted in the area." Among females, the extent of overlap observed was dependent on if the females were related versus non-related. Related female dyads had home and core range overlap of 52.32% and 15.79% respectively, while non-related female dyads displayed 36.90% and 6.85% in overlap.

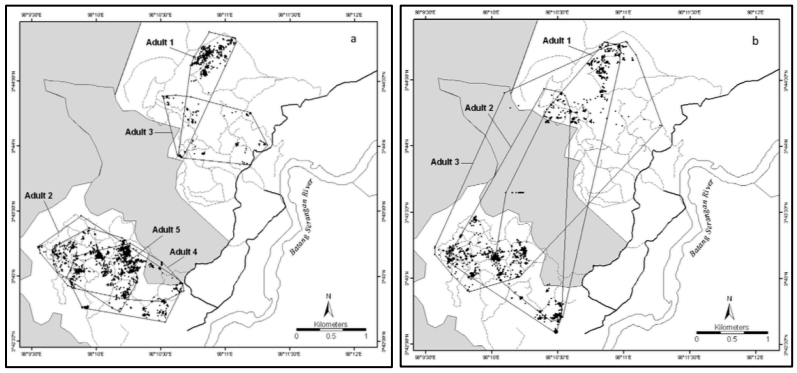


Figure 3: Overlapping home ranges in the Batang Serangan region of Sumatra. Map "a" depicts the ranges of five females. Map "b" depicts the ranges of thee males.

(Image taken from Campbell et al. 2011a, Figure #1)

Campbell-Smith et al. (2011a:4) measured range overlap among a population of orangutans in the Batang Serangan region. Range overlap for the three females in the south-east of the study area was 90%. Males, with 89%, shared a similar degree of high overlap. Looking at map "a" and "b" (see Figure 3) it is clear that female and male ranges also overlapped extensively, particularly in regard to the south-eastern area of the study site.

The overlap of home ranges observed in Kluet, Tuanan, and Batang Serangan was so substantial that it was almost as if a "group" of orangutans was occupying one communal home range, not multiple individual ranges. Profuse range overlap strongly corresponds with group living and synchronized spatial association (Kappeler and van Schaik 2001). Despite ample hours of observation proving the orangutan to spend the majority of its time in solitary,

as opposed to groups, several researchers argue *Pongo* does, nevertheless, show signs of synchronous movement.

Synchronized Association. Speaking of solitary primate species in general, understanding that adult males and females must unite to reproduce, Allison Richard (1985) argues that solitary species are not solitary in a classic interpretation of the word, but "live as representative of neighborhoods, in which despite foraging alone, each individual is keenly aware of his or her social surroundings" (quote by Nystrom and Ashmore 2008:239). Speaking of *Pongo* in particular, MacKinnon presents the Community Model. He concludes that "orangutans form social units in which one or two adult males and several sub-adult males are associated with a number of adult females and their young" (van Schaik and van Hooff 2002:10-11). This social unit, which we can call a group, moves in synchrony. Conducted by te Boekhorst et al. (1990), the results of a study in the Ketambe region supported MacKinnon's claim. Several males and females were observed to consistently move in synchrony when traveling in and out of the floodplain (van Schaik and van Hooff 2002). Movement was proved to be socially inclined and not for practical reasons. When the two males left the floodplain, the associated females followed them regardless of food abundance in or out of the floodplain.

Mating System

Copulatory patterns are defined by mating system. Four basic mating systems have been identified in the primate order: monogamy, polyandry, polygyny, and polygynandry. Among monogamous species, males and females mate exclusively with one member of the opposite sex. Monogamy is rare and most species display a form of polyandry, polygyny, or

polygynandry. In polyandry a single female mates with multiple males who, in turn, only mate with her. The opposite, polygyny finds one dominant male mating with multiple females who only mate with him. The most commonly observed mating system, polygynandry is when both the male and the female have multiple mating partners.

Pongo. Orangutans participate in a polygynandrous mating system, in which a male mates with as many females as possible, and a female, too, mates with multiple males per receptive period. Male orangutans mate extensively. Evolutionarily, a male's goal is pass his genes on to the next generation. In order to secure his chances of passing on his genes, the male must, logically, copulate with many females. This notion is heightened for orangutan males because of female hidden estrous. When a female does not externally show her receptivity, the male is at a disadvantage and must act even more "frantically" (Utami Atmoko et al. 2009b). Unlike most solitary species, flanged males do not defend their mating access, but females do show a clear preference for flanged or dominant males.

Despite this imbalance in preference, paternity tests have revealed flanged and unflanged males to be of equal success in reproduction (Utami Atmoko 2009b). How is this the case? Females, and this is particularly of observation in highly sexual-dimorphic genera like *Pongo*, can be subject to forced copulations, in which the larger unflanged male sexually engages with the female against her will. Traditionally, it was assumed forced copulations were common. However, it is becoming unclear as to how "forced" female-unflanged male encounters actually are. Recent findings suggest females, although preferring flanged males, are receptive toward the advances of an unflanged male. The *Pongo* mating system is highly promiscuous.

Social Structure

Conspecific relationships and interactions are described by social structure. There are four fundamental relationships of discussion: male-male, female-female, male-female, and mother-offspring. Male-male interaction is centered on female distribution and characterized by "competition, intolerance and clear dominance relations," while female-female interaction is focused on resource competition and characterized by "philopatry, nepotism, tolerance and despotism" (Kappeler and van Schaik 2001:719-720). The male-female relationship is deeply dependent on the mating system – aspects of female choice, male force, and protection are observed. Finally, the interactions between a mother and her offspring are defined primarily by the offspring's rate of maturation.

Pongo. A predominately solitary existence is argued to have resulted in a "narrow social behavioral repertoire" (Edwards and Snowdon 1980:40) prohibiting orangutans from engaging in frequent and/or complex social interactions. Birutė Galdikas (1999:47) responds:

> Because they lead semi-solitary lives, wild orangutans do not need, or do not display the social skills evident in developing chimpanzees and gorillas, who live in groups. Observations at Camp Leakey showed that when orangutans encounter other individuals, these social skills emerge quickly and relatively effortlessly.

In line with Galdikas, Trevor Poole (1987:327) argues orangutans "display a repertoire of social behavior comparable to that of group-living great apes." Although not mimicking the social behaviors and patterns more readily observed among group living primates, *Pongo* does exhibit social behaviors, as is evident in conspecific interactions.

Male-Male. In contrast to conventional views of avoidance, intolerance, and aggression, male-male relationships are largely marked by tolerance. When speaking of male-male interaction among orangutans, due to the phenomenon of bimaturism, there are three relationships for discussion: flanged-flanged, flanged-unflanged, and unflanged-unflanged.

There is a lack of aggressive behavior observed among orangutans, but what aggression there is occurs between flanged males. Encounters are rare, aggressive encounters are more rare, and serious fighting is extremely rare. Normally a male will simply bare his teeth and "glare" when threatened (Setia et al. 2009). Among primates, male aggression is thought to stem from competition for female access; however, in contrast to this pattern Utami Atmoko et al. (2009a:227) finds "aggression among flanged males is not strongly dependent on the presence of females" and Mitra Setia (1995) recorded almost all aggressive interactions to stem from competition over access to fruit (64% directly at the site of fruiting tree and 36% within close proximity of that tree).

Flanged—unflanged interactions are defined by "imposed" tolerance. An unflanged male tends to be within 40-50 meters of a flanged male – it is not obvious if this is for access to females or for possible protection. While flanged males can be aggressive toward other flanged males, there have been no observed or reported attacks of a flanged male on an unflanged male (van Schaik and van Hooff 1996).

Unflanged-unflanged interactions are friendly. An unflanged male roams independently in search of mating opportunities, but when he does cross an unflanged male(s), will travel, feed, play, participate in allogrooming, and occasionally engage in homosexual interactions (Setia et al. 2009; Utami Atmoko 2009a).

Male-Female. The male-female relationship is almost entirely restricted to mating based interactions. Adult males and females do occasionally interact in a non-sexual manner when bought together by fruit, as has previously been touched upon. Individuals will feed in peace and participate in allogrooming. Young females, usually without offspring, will even engage in play with unflanged males. Although direct interactions are limited to times of copulation and periods of fruit abundance, males and females do appear to have some form of permanent relationship with one another.

Orangutans have at least 32 different sounds in their vocal repertoire (Hardus et al. 2009). The most definitive of these is the male long call emitted by a flanged male. Lasting anywhere from 15 seconds to four minutes, a long call has a "'bubbly' introduction leading to a long sequence of bark-like units or pulses, and ends generally with a series of sighs that may sometimes resemble the opening series" (Delgado et al. 2009:216). A flanged male gives off multiple long calls a day. Although an occasional call will be made in reaction to another flanged male, the majority of calls are given spontaneously. It was initially assumed that long calls were emitted to scare off un-flanged males; however, un-flanged males do not react to the calls. Motivation behind the calls is unknown (there is emerging evidence suggesting males are actually communicating their travel plans through long calls, see van Schaik et al. 2013), but females do react to the long calls. Upon hearing a long call, a female will either move toward the location of the long call/male or quickly move away (Delgado et al. 2009; Mitra Setia et al. 2009). There is clear selectivity in the female's actions.

A female associates herself with a dominant male, and this dominant male, who likely has multiple females with whom he is "allied," will protect her and her offspring against

unwanted interactions with an unflanged or flanged male (Mitra Setia et al. 2009; Utami Atmoko et al. 2009b). While this can be interpreted as an act of aggression against the intruding male and thus the guarding of a possible mate, the flanged male engages in this protective behavior regardless of the female's receptivity; in fact, the flanged male does not try to copulate with the female following the standoff. Utami Atmoko et al. (2009a:240) argue this provides the female with reproductive choice: she "can travel in the direction of a recent long call by [a dominant male] and thus orchestrate a male-male [competition], allowing her to flee."

Female-Female. Once assumed to live in separate, non-overlapping ranges, females interact with other females regularly. Females living in close proximity form clusters. Previous studies have revealed that "female relatives show greater home range over-lap than non-relatives and encounter each other preferentially" (Singleton et al. 2009:210-11). Using polymorphic microsatellite markers and mitochondrial DNA haplotypes, Arora et al. (2012) confirmed that female clusters are in fact matrilineal clusters.

Cluster members experience reproductive synchrony – indicative of group living, – associate preferentially, and are often observed in proximity (within one arms length) of conspecifics (Singleton et al. 2009). Mothers, in particular, are found in proximity, allowing their offspring to play together. A mother will share food with both her offspring and the visiting offspring (Jaeggi et al. 2008), and mothers will help one another collect food, sticks for sleeping nests, etc. Females show almost no signs of aggression. They appear to be exceptionally tolerant of other females and operate under an age based hierarchy (van Schaik and van Hooff 1996). There is little evidence to suggest this configuration is for safety, and this action can therefore be interpreted as a means to facilitate social interaction and bonding.

Mother-Offspring. Birutė Galdikas claims that "wild orangutan infancy is probably the least stressful and most idyllic of any childhood in the tropical rainforest" (1999:38). An orangutan leaves his or her mother around age eight or nine, and a female has only one offspring in her care at a time; she is not reproductively viable until her offspring has left (Galdikas 1999; van Noordwijk et al. 2009). Orangutans stay with their mothers for an extended period unseen in the rest of primate order, excluding humans. Researchers thought offspring stayed with their mothers due to a slow rate of development (van Noordwijk et al. 2009), but this theory falls through upon observing that young juveniles, age three or four, are more than capable of foraging, building a sleeping nest, etc. (Galdikas 1999). Why, then, do juveniles stay with their mothers for so long?

It is believed that the orangutan's need for social interaction has prompted an extended period of "infancy." A female orangutan is guaranteed socialization both with her offspring and with other females through her offspring. A female will not fully distance herself from her mother until she herself is ready to reproduce and begin her own social network (Arora et al. 2012). A male compensates for leaving his mother by interacting with other unflanged males as often as he can while in search for mates (Galdikas 1999). Like humans (and some other primates), though, orangutans never fully stop associating with their mothers, visiting up to three or four times a week. The mother-offspring relationship provides permanent social contact.

"Mono-Social" Group Living

There are many ways in which a species, primate or non-primate, can adapt to a difficult environment like the peat-swamp forest of Indonesia. In response to environmental constraints, *Pongo* has adopted a solitary lifestyle. Primates, as an order, exhibit great degrees of plasticity. Having co-evolved in a stable environment, the orangutan is a specialist unable to quickly adapt physiologically or morphologically to a new environment. Despite this, the orangutan is still highly behaviorally flexible. While most primate taxa, when faced with habitat changes, can chose from a variety of possible physiological, morphological, and/or behavioral adaptations, the orangutan is restricted to behavioral adaptation. *Pongo* has been forced, by both external and internal constraints, into a solitary social system. Consequently, orangutans are not inherently antisocial. They are tolerant of, if not "welcoming" toward, conspecifics and display many group-living tendencies. It is for this reason I argue *Pongo* is capable, if provisioned, of "mono-social" group living.

Group Living

In the wild, if they did desire to, due to the uneven distribution and scarcity of fruit, orangutans are not able to live in groups as we classically think of them – a large number of individuals in a small area. Additionally, with no arboreal predators (the orangutan is threatened, when on the ground, by the Sumatran Tiger [*Panthera tigris sumatrae*] and by large snakes), the orangutan has no incentive to live in protective groups. Orangutans are, however, behaviorally flexible animals and are capable of adapting to group living when required.

Vilas Park Zoo. Edwards and Snowdon (1980) wanted to know if orangutans were at all capable of displaying even the slightest hint of social behavior – it was assumed that the orangutan, being solitary, was antisocial and unable to engage in social interaction. They were among the first wave of primatologists to acknowledge that observed social behavior in the wild is not necessarily representative of social potential and argue "that orangutans, at least when group-living in capacity, exhibit the potential to display social behavior" (Edwards and Snowdon 1980:39).

The study was conducted at the Vilas Park Zoo in Madison, Wisconsin. Two orangutan groups were studied. The adult group included a flanged male, three females, and two infants. With the exception of the infants, all member of the group were wild-born, had been in living in captivity for over 10 years and had been a group for three years. The juvenile exhibit held an un-flanged male and two adolescent females. All three were captive-born and again had been living as a group for three years. Both groups lived in extremely small enclosures (adult 43.5 m^2, juvenile 106.2 m^2), putting individuals in constant proximity with conspecifics. Edwards and Snowdon tested the inherent sociality or demeanor of an orangutan when forced to interact with conspecifics.

Edwards and Snowdon measured the degree to which social versus solitary behaviors were displayed. Nine behaviors were classified at social: allogrooming, social contact, parallel, monitoring, play, approach, agnostic-no contact, agnostic-contact, and terminations. Seven behaviors were considered indicative of solitary inclinations: object manipulation, body manipulation, on ground, locomotion, suspension, maintenance, and autogrooming. Further distinctions between positive and negative behaviors were also made.

Both adults and juveniles spent roughly 50% (adult 50.8%, juvenile 50.6%) of their time engaging in social behaviors and "positive-interaction frequencies were higher than total negative-interaction frequencies" (Edwards and Snowdon 1980:50). Adults spent over 61% of their day in close proximity to conspecifics. The most observed social behaviors were monitoring (23.5%) and allogrooming (10%). Agnostic behaviors were only recorded 2.7% of the time. While a select few of these interactions resulted in rough contact (slapping, hitting, biting, hair pulling), the majority of these interactions ended in avoidance. Juveniles spent over 20% of their time in direct contact and 23.9% in "play-contact." Agnostic behavior was rarely recorded (1.1%). In both groups frequent food sharing was observed.

If not friendly, orangutans were certainly tolerant of conspecifics. Edwards and Snowdon comment that "the low levels of aggression found are in contrast to the increased levels of aggression often found in captive primates," suggesting the orangutan is extremely behaviorally flexible and able to live in groups.

Singapore Zoological Gardens. Seven years after the results of work completed at Vilas Park Zoo were published, Trevor Poole (1987) observed the interactions of a group of wild born Bornean orangutans on an artificial island in the Singapore Zoological Gardens. The key to Poole's study was that the orangutans were not living in captivity, as thought of in a classic sense, but within a confined area representative of their natural peat-swamp habitat. While the island, at 450 square meters, is not particularly large, it provides more than enough space for each orangutan to be reclusive and avoid interaction. Poole (1987:316) asks "whether orangutans in [small ranges] will seek out or avoid conspecifics if there are free opportunities for socialization."

The group consisted of three flanged males, two un-flanged males, two females, three adolescent males, and two infants. Behaviors were divided into eleven categories: alone, solitary play, proximity, contact, allogrooming, social play, patrolling, sexual behavior, displaces, material behavior, and aggression.

Poole (1987:319) found that "[flanged] males spend more time alone and have fewer social interactions than [subadult] males, but spend more time in proximity to other individuals." The two sub-adult males, Friday and Letchu, fed in proximity (within in one arm's length) to one another and participated in allogrooming. Adolescent males spent >20% of their day engaged in social play with other adolescent or sub-adult males. Finally, females spent a high percentage (when compared to adult and sub-adult males) of time in contact (direct touching, excludes allogrooming and play) with other females or sub-adult males. Mothers especially were in frequent proximity or contact; the two infants in the study were observed spending 8 – 12% percent of their day in play, a result of their mothers' association.

Throughout the study period, Poole (1987:324) found "no serious, as opposed to playful, attacks were observed," suggesting *Pongo* is capable of peacefully cohabiting with conspecifics. Additionally it was found that, although not gregarious, "females and adolescent males spent somewhat more than one third of their active period in close social contact" and "actively sought one another's company," implying orangutans are not simply adapting to, but actually enjoy living in groups (1987:319).

"Mono-Social" Group Living

In arguing *Pongo* be relocated to small patches of forest and live in "mono-social" groups, I am redefining group living. Although they have a highly multifaceted social system, and of

particular interest social structure, in the wild orangutans spend the majority of their day in solitary. I have argued, employing the socio-ecological model, the orangutan's solitary behavior results from the uneven distribution and scarcity of fruit. Yet in captivity, while much more likely to participate in direct interactions, individuals still spent roughly half of their time engaging in solitary behaviors. I am not proposing the orangutan is going to suddenly become a gregariously social primate, like the chimpanzee. Nonetheless, orangutans quite happily tolerate being in constant confined areas with conspecifics. Edwards and Snowdon (1980) found adults to spend 61% of their day engaged in social activities (allogrooming, social contact, play, etc.) or in *proximity* to one another.

It is this ability to sit peacefully in proximity to conspecifics that is key to the suggestion of *Pongo* successfully living in conservation-constructed groups. The orangutan is habituated to solitude in the wild. This is not an option if placed in a group within a small patch of forest. We know that in captivity, however, an orangutan often acts as if alone, when they are anything but. Not antisocial or social in a gregarious sense, the orangutan can best be described as being predominately asocial when in groups. Orangutans act as if alone (mono), while actually surrounded by conspecifics (social), a concept I term "mono-social." Within primatology the term "group" is more often than not synonymous with gregarious. The orangutan challenges current conceptions, living in "mono-social," as opposed to gregarious, groups. There is no reason, considering the behavioral flexibility and social inclinations of the species, wild-born orangutans will not adapt to closer-confines in a similar fashion.

My Hope for the Future

I do not know if we can secure and protect small patches of forest; in theory it should be easier than attempting to protect a large tract of land, but I am basing that assumption on logic and little evidence. I do not know how we relocate 1000s of orangutans from across the Bornean and Sumatran forests – how do we find them or efficiently transport them? I do not know how we obtain the food needed to provision a large number of orangutans. I have realized in writing this paper that my argument is highly theoretical and based on a limited amount of hard scientific evidence, although not for lack of trying to find more information. There are many unanswered questions, but the orangutan does not have time for us to answer all of them before we act.

Researchers observe wild orangutans to live in solitary. Traditionally, it has been assumed that orangutans live in solitary because they are inherently antisocial. Both wild and, captive studies, however, observe orangutans opting to interact with conspecifics and engaging peacefully, challenging antisocial assumptions. Although perhaps not social, the orangutan is also not antisocial. They can be descried as asocial and are capable of group living. The principles of socio-ecology explain that when food is scarce and/or scattered across the environment primates benefit from living in smaller numbers or in solitary. Fruit, which the orangutan requires for survival, is highly unevenly distributed across the peat swamp forests in which the orangutan resides. Orangutans, forced by their ecology, live in solitary and require extensive home ranges.

The peat swamp forests of Sumatra and Kalimantan, Borneo are diminishing, and diminishing at an unprecedented pace. *Pongo* is in dire need of help. If action is not taken immediately, the orangutan will likely become extinct in the wild before I die. Conservation "requires identifying and addressing the myriad of problems generated when humans exploit natural resources" (Pullin et al. 2013:3). When these problems cannot be addressed straight on, conservationists must consider alternative, sometimes radical, solutions. In conserving the orangutan it has been identified that peat-swamp forest need to be saved from and protected against agricultural clearing and selective logging. The Indonesian government supports economic growth over conservation and, as such, our efforts are struggling.

While we should not abandon current conservation efforts, I propose an alternative approach in which we relocate orangutans into smaller patches of forest and provision them. I believe, if provisioned, *Pongo* is capable of living in "mono-social" groups within politically sustainable, smaller patches of protected forest. If my analysis and prognosis are correct, or even partially correct, the future of the orangutan begins to looks just a little bit more optimistic.

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