The Influence of Forest Structure on Sumatran Orangutan Nesting and Densities in the Lowland Dipterocarp Forests of North Sumatra

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Contents

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Abstract

Prior studies on Bornean orangutans have suggested that orangutans were primarily selecting nest sites that provided more stable and sheltered platforms thereby offering greater comfort rather than selecting for nests which reduced the risk of predation by limiting access to ground predators (Ancrenaz et al. 2004a; Cheyne et al. 2013). The aims of this study were to answer three questions: why are nests built in a particular tree, why was the nest in that position and height within the tree and why build the nest in that part of the forest and not another? Nest and forest structure data were recorded from transects conducted at two sites in North Sumatra; Sikundur (a naturally recovered site) and Sei Betung (reforested site). Selection patterns for tree and forest structure variables showed no significant difference across sites when modelling nest trees against forest trees. Nest trees had properties that both increased both comfort through nest stability and shelter from adverse weather as well as attributes which reduced the threat from predators. However, a preference for trees with narrow trunks was also found, which would limit access to ground predators but also reduce stability, suggesting that predator avoidance may take precedent over comfort. A greater proportion of Position 2 and 3 nests were found in Sei Betung where tree height and connectivity are lower, further suggesting that predator avoidance has a greater influence than comfort or stability on Sumatran orangutan nest placement. The lower connectivity in Sei Betung was associated with increased rarity of tree-tied nests (Position 4) compared to Sikundur which went against our expected results based on those of Prasetyo et al. (2009). Over 60% of nest trees in Sei Betung held multiple nests, suggesting that there is significant pressure upon preferred nest sites in Sei Betung. Nest densities were most closely associated with variables linked with forest recovery such as higher canopy density, fewer gaps, increased rugosity and higher stem density. Nest densities were also associated with reduced distance to the edge of the forest, further research is needed to determine whether this is due to orangutans utilising neighbouring plantations. Our results show the need for protecting habitat not only for preferred food species but also nest trees.

Chapter 1: Literature Review

1.1 Orangutan biology

1.1.1 Distribution and conservation status

Orangutans, species belonging to the genus *Pongo* are the only non-human great apes (*Hominidae*) currently found in Asia (von Koenigswald 1982). though they once were found across South East Asia during the Pleistocene period their range is now restricted to the two islands of Borneo and Sumatra (von Koenigswald 1982; Jablonski et al. 2000; Bacon & Long 2001; Ibrahim et al. 2013). The genus is represented by three species which are split allopatrically with a single species found on Borneo; *P. pygmaeus* that is made up of three subspecies (*P. p. pygmaeus*, *P. p. morio* and *P. p. wurmbii*) (Ancrenaz et al. 2016) and two species on Sumatra*; P. abelii* and *P. tapanuliensis* (Nowak et al. 2017; Singleton et al. 2017; Nater et al. 2017) (see Fig 1 and Fig 2). The two Sumatran species are also split geographically with the Sumatran orangutan being found in the north of the island mostly within the Leuser Ecosystem and peat swamps of the west around Suaq Balimbing and the Tapanuli orangutan being restricted to south of Lake Toba in Batang Toru which is the southernmost range of orangutans on Sumatra, with the exception of the reintroduced individuals around Bukit Tigah Puluh National Park (Wich et al. 2003; Russon 2009; Kelle et al. 2014; Nowak et al. 2017).

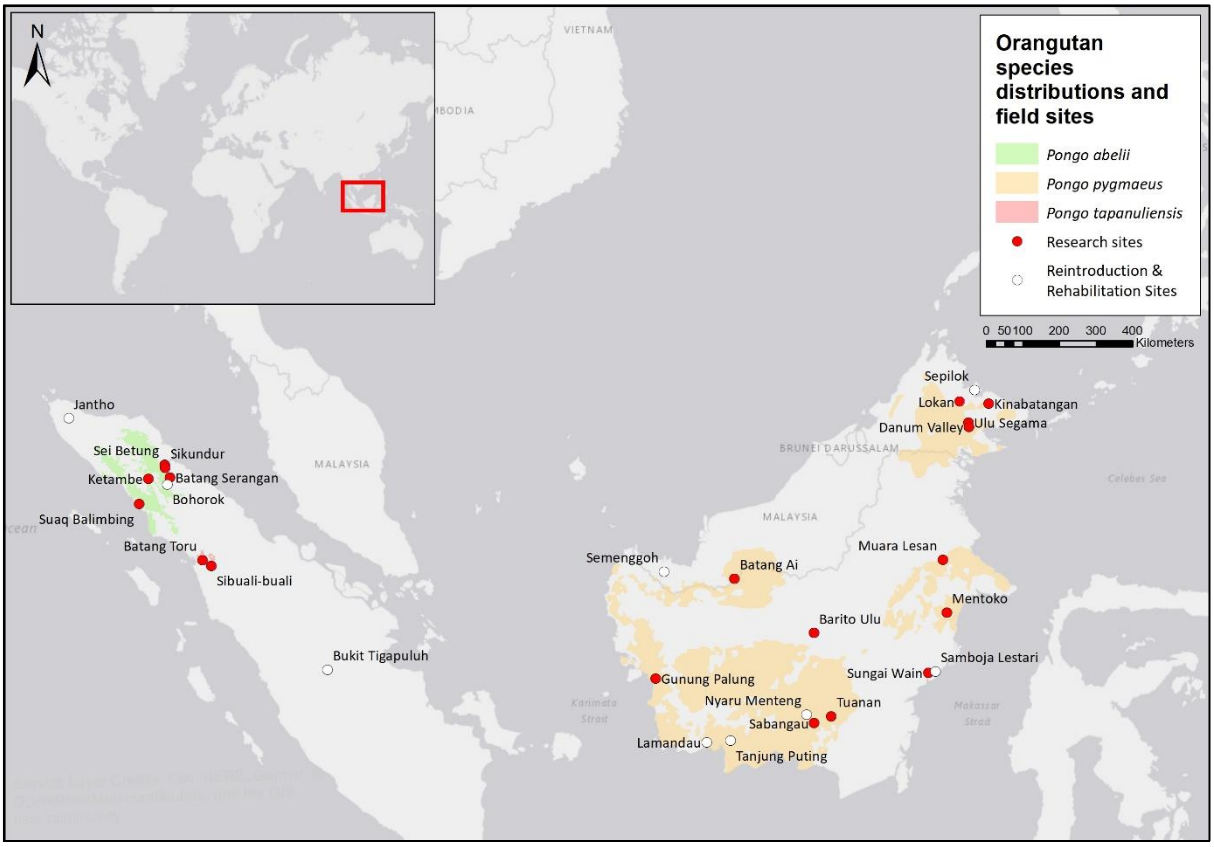

Figure 1-1 Distributions of the three extant species of orangutan; P. abelii, P. tapanuliensis and P. pygmaeus from Wich & IUCN (2016a). *The map also displays the locations of all major orangutan field research sites, reintroduction and rehabilitation sites in Sumatra and Borneo.*

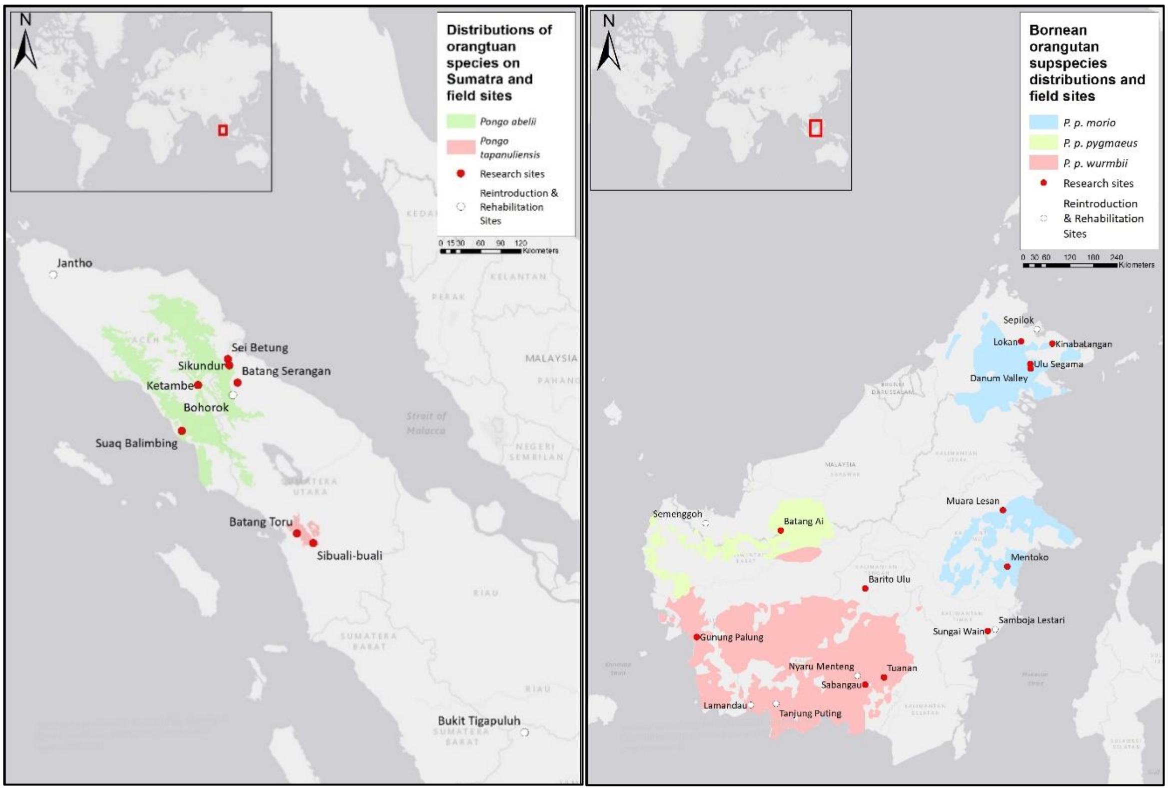

Figure 1-2 Orangutan species distrbutions in Sumatra for P. abelii and P tapanuliensis (left) and distributions of subspecies of P pygmaeus on Borneo (right) and the major field research sites and reintroduction and rehabilitation sites on both islands. Distributions from Wich & IUCN (2016b, 2016c)*.*

At present, all three of the recognised species of orangutan are listed as critically endangered by the IUCN Red List (Ancrenaz et al. 2016; Nowak et al. 2017; Singleton et al. 2017).Orangutans are listed as such due to the multiple threats which they face from habitat loss and fragmentation for agriculture and timber extraction (Ancrenaz et al. 2015, 2016; Singleton et al. 2017), hunting for food and killing in retaliation for crop raiding and during land clearance (Davis et al. 2013; Meijaard et al. 2011; Wich et al. 2012; Abram et al. 2015), and capture of individuals for the illegal pet trade (Shepherd 2010; Freund et al. 2017).

1.1.2 Diet

Orangutans are generally frugivorous though their diet actually quite varied. The diet of orangutans consists primarily of fruit, leaves, flowers, bark and invertebrates (Morrogh-Bernard et al. 2009; Russon et al. 2009a), though there are also instances of meat eating with orangutans being observed consuming slow lorises (*Nycticebus coucang*) (Utami & Van Hooff 1997; Hardus et al. 2012b), gibbon (*Hylobates lar*) (Sugardjito & Nurhuda 1981), grey tree rats (*Lenothrix canus*) and birds eggs (Russon et al. 2009a). Current records have observations of orangutans feeding on a total of 1693 different species, this includes 1666 plant species (including fruit, leaves, bark and pith), 16 invertebrate species, 4 species of vertebrate and 7 foods belonging to the category other; honey, fungi, moss, urine, soil and water (Russon et al. 2009a).

1.1.3 Sexual dimorphism and male bimaturism

Orangutans unusually display both extreme sexual dimorphism in body size and bimaturism amongst males (Utami-Atmoko et al. 2009). Male orangutans grow considerably larger than females and also develop male secondary sexual characters (SSC's) which further differentiate them which consist of flanged cheeks and a throat sack which enable the male to produce long calls (Mackinnon 1974; Rijksen 1978; Galdikas 1983; Galdikas 1985a; Utami-Atmoko, Mitra-Setia, et al. 2009). These long calls can be used to advertise their presence, orient themselves to other orangutans spatially and potentially co-ordinate a network of loose associations between males and females within the area (Galdikas 1983; Galdikas 1985a; Askew & Morrogh-Bernard 2016). Mitra Setia & van Schaik (2007) further suggest that long calls also influence female attraction as adult females were significantly found to approach long calls, in particular those made by dominant males. Unusually, male orangutans exhibit bimaturism in the form of two physically distinctive morphs of fertile, sexually active adult males who differ significantly in appearance: flanged and unflanged, which also employ generally different reproductive strategies: call and wait versus go and search/sneak and rape (Harrison & Chivers 2007; Utami-Atmoko et al. 2009a; Utami et al. 2002).

1.1.4 Social structure

Unlike all other species of great ape, orangutans are considered to be semi-solitary in terms of social structure, living in a fission-fusion system, with loose communities organised around a dominant flanged male (Mackinnon 1974; van Schaik 1999; Mitra-Setia et al. 2009) rather than the large, loosely organised fission-fusion groups of chimpanzees (*Pan troglodytes*) and bonobos (*Pan pansicus*) (Kuroda 1979; Maryanski 1987; de Waal 1995; Surbeck et al. 2011) or the stable, cohesive heterosexual groups that Eastern (*Gorilla beringei*) and Western gorillas (*Gorilla gorilla*) live in (Maryanski 1987; Yamagiwa et al. 2003; Robbins et al. 2004). Individuals live in highly overlapping home ranges with orangutans occasionally aggregating in or near large fruit trees such as strangling figs (14 individuals were observed in one fig tree in Ketambe) (Rijksen 1978; Sugardjito et al. 1987; Mitra-Setia et al. 2009). These feeding aggregations during periods of high fruit abundance such as masting events may develop into travel bands in which the individuals travel together in a coordinated manner (Utami-Atmoko et al. 2009a; Utami et al. 1997; Sugardjito et al. 1987; Mitra-Setia et al. 2009; van Schaik 1999; Singleton & van Schaik 2002).

Female orangutans are more social than males and have been found to form distinct clusters and preferred associations with other females thought to be close relatives (Singleton & van Schaik 2002; Knott et al. 2008; Singleton et al. 2009). Female orangutans will regularly form associations with immature individuals of various age, most often their young but also unrelated, unflanged males and other females from the same cluster (Mitra-Setia et al. 2009). Along with associations with immature individuals, female orangutans will also form associations with preferred flanged males such as in consortships where they will travel together for a period ranging from days to months and will engage in sexual behaviours. The consort pair are not mutually exclusive as other females, unflanged males and adolescents may also associate with the consort pair (Schürmann & van Hooff 1986; Utami-Atmoko et al. 2009).

Compared to female orangutans, males are more solitary in nature. Non-dominant flanged males in particular avoid encounters with dominant flanged males and larger unflanged males in turn are avoided by females and smaller unflanged males alike (Mitra-Setia et al. 2009). Flanged males are highly aggressive to other adult males, in particular they will attack flanged males that are assessed as weaker than themselves (Galdikas 1985b; Mitani 1985; Utami-Atmoko et al. 2009b). Compared to flanged male-flanged male interactions, flanged males are more tolerant of unflanged males but only from a distance and will chase unflanged males away when consorting with a female (Schürmann 1981; Utami & Setia 1995; Utami-Atmoko et al. 2009b). Unflanged males associate with females with no offspring more often than flanged males, in part due to their greater mobility which allows for them to be able to maintain an association for longer compared to a flanged male (Wich et al. 2006; van Schaik et al. 2009; Utami-Atmoko et al. 2009a). Along with associations with females, unflanged males do also succeed in siring offspring, though mainly with females who are not mate-guarded by flanged males or when opportunities arise (Utami-Atmoko et al. 2009a; Banes et al. 2015).

1.2 Nesting ecology

The three species of orangutans are the largest living extant arboreal mammalian species (Cant 1987a, 1987b), spending almost all of their lives in the canopy. The daily building of nests to sleep and rest is a behaviour shared between all great ape species (Hashimoto 1995; Hall et al. 1998; Blom et al. 2001; Mehlman & Doran 2002; Kouakou et al. 2011; Samson & Hunt 2014; Serckx et al. 2016). Nest building is a complex behaviour which takes a number of years for a young orangutan to master through observing their mothers and practice (van Noordwijk & van Schaik 2005; Prasetyo et al. 2009; van Noordwijk et al. 2009).

Nest building is one of the essential skills which young orangutans and other great apes learn from their mothers, as although nest building in great apes does have an innate component it is not completely instinctive and only through exposure to nest building adults and learning from them that immatures are able to craft adequate nests (Videan 2006; Prasetyo et al. 2009; van Casteren et al. 2012). Immature orangutans share a nest with their mothers irrespective of their age for both night and day time rest period. As the mother builds the nest immatures have been observed at all study sites to be attentive and appear to be attempting to help by adding twigs, branches or leaves (van Noordwijk et al. 2009). Orangutan infants begin to practice nest building around 0.5 years of age, with 1-2 year olds frequently observed practicing nest building whilst their mother is stationary such as when feeding or resting (Prasetyo et al. 2009; van Noordwijk et al. 2009). By the age of 3 (and some younger), most young orangutans are able to build nests adequate enough for a brief nest even though they will still spend the night sharing a nest with their mother, this shows that they acquire the sufficient skills for nest building long before independence and provides the young with a significant time to refine and master nest building techniques (van Noordwijk & van Schaik 2005; van Noordwijk et al. 2009).

1.2.1 Nest construction

Once a suitable site has been chosen the orangutan will first being to construct the base or foundation of the nest by bending, pulling and breaking some larger branches inward toward the centre and then weaving and twisting these together to lock them into a basic nest structure which roughly forms a butterfly pattern of branch endings that are concentrated into two roughly opposite corners (Prasetyo et al. 2009; van Casteren et al. 2012). Following this the orangutan will begin to add layers of smaller branches (normally those with many leaves) by bending, breaking and weaving them in place to create the layer known as a mattress or rim (Prasetyo et al. 2009; van Casteren et al. 2012). Only chimpanzees of the other great ape species also add mattresses to their nests (Fruth & Hohmann 1996; Prasetyo et al. 2009). Leafy branches which are detached from the surrounding area are further placed on top of the base structure to form a lining. Finally, to finish building the basic nest, whilst standing on the nest the orangutan will braid branches and fold the tips of these branches to the centre of the nest and intertwine them with the mattress, which they continue until the nest has a strong structure (Prasetyo et al. 2009). Once the basic structure is complete the orangutan may add additional special features such as pillows made from small leafy twigs at one end or blankets made of loose leafy branches or add a roof made of a loose cover of braided branches which are woven together to make a solid, almost waterproof object (MacKinnon 1971; Russon et al. 2007; Prasetyo et al. 2009; van Casteren et al. 2012). Such additional features like pillows and roofs are widespread behaviours but usually restricted to either particular islands or subspecies (Russon et al. 2009b). The nests built by orangutans are considered to be the most complex, sturdiest and long lasting of all ape nests, not only because of the addition of features such as pillows, blankets, roofs or secondary bunk nests (Anderson 1984; Anderson 1998; Prasetyo et al. 2009; Russon et al. 2007; van Casteren et al. 2012; MacKinnon 1971; Groves & Pi 1985; Ancrenaz et al. 2004a)

1.2.2 Nest function

Nest building in primates has been hypothesised to have arisen due to the need for a comfortable sleeping platform as the bodies of apes are too large to comfortably sleep on a bare branch (Fruth & Hohmann 1996; Stewart et al. 2007; Prasetyo et al. 2009; van Casteren et al. 2012), a method for improving thermoregulation (Stewart 2011b; Samson & Hunt 2012; Fruth et al. 2018), avoiding biting insects (Largo et al. 2009; Stewart 2011b; Samson et al. 2013) and offer a safe place to rest, away from potential predators (Anderson 1984, 1998; Pruetz et al. 2008; Stewart & Pruetz 2013).

1.2.2.1. Improving sleep quality through comfort

A comfortable platform to sleep on allows for high-quality rest and sleep by reducing disturbances in the night (Fruth & Hohmann 1996; McGrew 2004; Stewart 2011; van Casteren et al. 2012). By building nests through the careful bending, weaving and braiding of branches and adding leaves to aid in cushioning, apes are able to create strong nests which can support their body weight and provide softer, more cushioned sleep sites (Goodall 1962; Van Lawick-Goodall 1968; Prasetyo et al. 2012; Prasetyo et al. 2010; Stewart et al. 2007). The use of nests has been suggested to allow for longer periods of uninterrupted sleep and promotes longer individual sleep stages which thereby leads to higher quality sleep (Fruth & Hohmann 1993; Stewart 2011b; Samson & Hunt 2014). In captive orangutans the production of more complicated nest designs was found to lead to higher-quality sleep and less gross-motor movements and increased overall sleep time (Samson & Shumaker 2013).

Along with offering a cushioned platform which reduces stress on tissues and pressure points to promote higher-quality sleep, nests also promote improved comfort and sleep quality by offering greater positional stability. Greater positional stability offers greater comfort as by building nests it reduces the chance of falling from branches which would be more likely should an ape with their larger body size in comparison to the surrounding supporting branches choose to rest on a branch rather than building a nest (Baldwin et al. 1981; Samson 2012; Samson & Hunt 2014). By building nests in more stable sites which are less likely to move or experience wind sway, apes are also able to increase both physical comfort as well as mental wellbeing by the reassurance that the nest won’t fail in the night thereby allowing for more relaxed and higher quality sleep (Anderson 1998; Cheyne et al. 2013). Both chimpanzees and orangutans have been observed to build their nests in locations to reduce serious wind-sway (Goodall 1965; Reynolds 1965; Mackinnon 1974; HORR et al. 1977; Anderson 2000; Cheyne et al. 2013). Samson & Hunt (2012) noted that wind sway increased with nest height, therefore the danger of nest collapse increased with nest height. They also noted that at their field site in Toro-Semliki, chimpanzees tended to nest at a height three-quarters (0.74) the elevation of the total tree canopy, leaving a quarter of the canopy empty. Nests were found to be built at similar heights in Fongoli (0.76), but in Assirik nests are built much higher within the canopy (0.94) which Samson & Hunt (2012) suggest could be due to site differences in climate as well as the physical attributes of the different tree species used at each site. This suggests that there is a potentially a “maximum safe height” for nests within a tree that is determined by both a trees structural properties and site-specific conditions such as average wind speeds, rainfall and exposure.

Sleeping platforms or nests also offer improved comfort by providing protection from adverse weather conditions such as rain or strong winds (Goodall 1962; Anderson 1984; Prasetyo et al. 2012; Kano 1982; Cheyne et al. 2013). By using local microhabitat features such as overhead branches, leaves, nest height and the density of forest stands apes can try to minimise the effects of adverse weather conditions. More sheltered positions can offer greater protection from rain which has been observed in bonobos (Kano 1982; Anderson 2000), whereas chimpanzees in Assirik has been observed to build more open nests that were higher within the crown and with less overhead vegetation in the wet season reduce discomfort from dripping vegetation in the event of night-time rain and offer more expose to the morning sun to warm and dry (Baldwin et al. 1981; Anderson 2000). For this research comfort is defined by both the stability of the nest, reduction of wind sway and protection from adverse weather conditions.

1.2.2.2. Thermoregulation

The use of nests for rest and sleep has also been theorised to offer improved thermoregulation by providing insulation to reduce heat loss at night or avoiding higher humidity and temperatures (van Casteren et al. 2012; McGrew 2004; Stewart 2011; Prasetyo et al. 2012; Anderson 1984; Anderson 1998; Koops et al. 2012; Fruth & Hohmann 1993). Research by Samson & Hunt (2012) found that arboreal nests as opposed to terrestrial nests in Toro-Semliki in Uganda experienced greater temperatures, wind sway and heat stress but lower humidity levels. The thermoregulatory and insulation properties of the arboreal nests of chimpanzees were empirically tested by Stewart (2011), and found that arboreal nests did indeed offer reduced heat loss which in a savannah habitat with low overnight temperatures could be crucial to the survival of chimpanzees there. Koops et al. (2012) found that in the rainforest habitat of Seringbara, Republic of Guinea where overnight temperatures are higher that humidity avoidance appears to drive much of the nest selection within this site. Chimpanzees within Seringbara were found to nest at higher altitudes with lower humidity during the wet season and avoided lower altitudes when overall humidity was highest and avoided nesting at altitudes below 800m year-round due to the higher humidity. Furthermore, chimpanzees nested higher within the trees during the wet season than during the dry season as higher nests offer higher temperatures and lower humidity (Koops et al. 2012a; Samson & Hunt 2012). Chimpanzees and other apes may be choosing to avoid high humidity as in higher temperatures, high humidity reduces the efficiency of heat loss through evaporation and conversely in colder temperatures high humidity increases heat loss through convection (Bell & Greene 1984). Further to the use of nests for thermoregulation, western lowland gorillas (*G. gorilla gorilla*) have been observed sleeping on dry earth during dry periods and as conditions became wetter and colder were observed to build nests more regularly along with building more complex designs with changing climatic conditions and nests in trees more frequently with increased rainfall (Remis 1993; Tutin et al. 1995; Mehlman & Doran 2002). As both extremes of heat and cold would influence an individual’s comfort and quality of sleep, I decided to include aspects of thermoregulation such as nest height and canopy closure above the nest as part of the overall sleep comfort hypothesis.

1.2.2.3. Vector avoidance

Nest have also been posited as a way of avoiding insect-borne pathogens by acting as physical barriers to insect vectors such as mosquitoes (Prasetyo et al. 2010; Stewart 2011; van Casteren et al. 2012; McGrew 2004; Nunn & Heymann 2005), certain tree species used for nesting could also have chemical properties which act as repellents to mosquitoes and other biting insects as well (Stewart 2011; Samson et al. 2013; Samson & Hunt 2014). By moving and building new nests daily, apes may be able to reduce the possibility of infestation by ectoparasites (Anderson 1998; Mackinnon 1974). Though little studied, there does appear to be some evidence for orangutans selecting nest trees with anti-mosquito properties (Largo et al. 2009) and carrying the leaves from plants with mosquito repellent properties to line their nests (Russon et al. 2007, 2009b; Kuze et al. 2011). Chimpanzees similarly have been found to preferentially build nests within trees belonging to the genus *Cynometra* which has natural mosquito repellent properties (Samson et al. 2013). Empirical testing by Stewart (2011b) found that by sleeping in an arboreal nest they experienced less bites than by sleeping on the ground, suggesting that the nest structure either acted as a physical barrier to the biting insects or dislodged them from the body.

1.2.2.4. Reducing the risk of predation

Great apes are considered to be at low risk of predation to large carnivores due to a combination of large body size (Zuberbühler & Jenny 2002), low densities (Hayward et al. 2006), predominant distribution in closed forest habitats (Lehmann et al. 2009; Stewart & Pruetz 2013) and in the case of African ape species living in groups offers greater protection from predators through increased vigilance and numbers (Schaik 1983). However, there are records of predation (though rare) occurring on all great ape species with leopards (*Panthera pardus*) being the predominant predators of African great apes (Fay et al. 1995; Pruetz et al. 2008; Boesch 1991; Anderson 1984) though lions and hyenas are also potential predators (Tsukahara 1993; Stewart & Pruetz 2013). Orangutans due to their more solitary nature could potentially be at greater risk of predation but only realistically face predation threats from three species: large reticulated pythons (*Python reticulatus*), Sunda clouded leopards (*Neofelis diardi*) and Sumatran tigers (*Panthera tigris sumatrae*) (Mackinnon 1974; Rijksen & Rijksen-Graatsma 1975; Rijksen 1978; Sugardjito 1983; van Schaik & van Hooff 1996).

Such threats from predation though low, could have significant impacts upon apes and their populations due to their long life-histories, in particular their slow maturation to reproductive age and long inter-birth intervals due to the need for extended maternal care (van Noordwijk & van Schaik 2005; Jones 2011; Stewart & Pruetz 2013). The long life history of apes and in particular orangutans makes them especially susceptible to the pressures of excessive mortality through predation and hunting due to the time required to replace lost members (Musick 1999). With predation offering such risks to ape populations it would be expected that apes should also have evolved behavioural counter-strategies which has led to the low currently observed rates of predation (Stewart & Pruetz 2013). Such anti-predatory behaviours have been observed including alarm calls which chimpanzees have been observed vocalizing in response to leopards (Boesch 1991) and both Sumatran and Bornean orangutans in response to tigers and clouded leopards (Rijksen 1978; Lameira et al. 2013). Both chimpanzees and orangutans have also been observed to throw sticks and rocks at perceived threats such as leopards, lions, tigers and clouded leopards (Van Lawick-Goodall 1968; Rijksen 1978; Boesch 1991; Lameira et al. 2013; Stewart & Pruetz 2013). The building of nest is another such behaviour which limits the risk of predation (Stewart & Pruetz 2013).

Whilst nests offer apes improved comfort and more stable sleeping sites, one of the primary functions of animal construction behaviours is to provide defence from predators. This anti-predatory function of nests and other shelters can two forms; concealment and repulsion of attack once detected (Hansell 2005; Stewart & Pruetz 2013). Nests potentially offer apes protection through crypsis, reducing the apes visibility to searching predators by presenting the leafy mass of the nest rather than the silhouette of large-bodied primate on a branch (Sugardjito 1983; Prasetyo et al. 2009; Stewart & Pruetz 2013). The primary anti-predatory function that has been hypothesised for nest building in apes is that by nesting arboreally it makes the nest builder inaccessible to potential nocturnal predators whilst the individual is sleeping and vulnerable (Stewart & Pruetz 2013). The nesting of apes has been well studied and found that in many cases apes are highly selective of nest sites in regards to tree species, areas of landscapes and particular morphological or structural characteristics of trees (Tutin et al. 1995; Brownlow et al. 2001; Ancrenaz et al. 2004a; Prasetyo et al. 2009; Hernandez-Aguilar 2009; Cheyne et al. 2013; Stewart & Pruetz 2013; Hernandez-Aguilar et al. 2013). Given the potential importance of reducing the risk of predation it should be expected that orangutans and other apes should take measures in selecting nest sites which improve the nest sites anti-predatory functions such as by either making access more difficult for a predator or facilitating easier escape for the nesting individual (Anderson 1984, 1998; Pruetz et al. 2008; Stewart & Pruetz 2013).

Such anti-predation adaptations have been observed in the nests of chimpanzees such as nests having escape routes (Baldwin et al. 1981; Anderson et al. 1983), building the nest near to the forest edge or over streams or gulley's to increase the relative height of the nest (Van Lawick-Goodall 1968) and in savannah habitats building higher nests with less overhead vegetation and more clumped together as a group which could be seen as methods of reducing predations by nocturnal predators (Baldwin et al. 1981). Further to this, chimpanzees in Issa have been found to select trees that are both taller and larger and with higher first branch heights than other suitable trees in the vicinity which could be a method of reducing access to ground predators (Stewart & Pruetz 2013; Hernandez-Aguilar et al. 2013).

Pruetz et al. (2008) found that when comparing chimpanzee nest heights between two sites in Senegal, these were lower in Fongoli where most predatory species had been extirpated through hunting compared to Assirik which is part of Niokolo Koba National Park where hunting has been forbidden since the 1950’s and so has a large population of predators. Pruetz et al. (2008) further noted that when comparing their data to earlier nest height data from Assirik in the 1970’s, the nest heights had increased coinciding with the recovery of the populations of predators within the national park. Building upon this, when comparing chimpanzee nesting between Issa and Fongoli; where Issa had high densities of ground predators and were largely absent from Fongoli, Stewart & Pruetz (2013) found that not only were chimpanzees nesting in higher trees in Issa but also nesting in more peripheral positions within the crowns of trees. By nesting higher within trees and in more peripheral positions, the nest builders are able to reduce access to predators through distance but by being closer to the terminal ends of branches they also reduce the potential for predators to be able to reach them due to the branches being unable to support the weight of the predators. Stewart & Pruetz (2013) theorised that nest building could be a method of creating stable sleep sites in more terminal locations on branches that prior to nest construction could not support the weight of the nest building individual. Only by the weaving, folding and breaking of the branches to for the structure of a nest would the nest builder be able to safely rest in such a branch location.

Adaptations to reduce the risk of predation have also been recorded for orangutans, with juveniles and paired mothers with infants having been observed nesting further away from food trees, whilst for adult males and females without young it is more normal for them to sleep in the general vicinity of the last food tree they visited but it is rare for them to nest in the fruiting tree (Sugardjito 1983). Avoiding nesting in active fruiting trees, in particular those which the most recently fed in is one of the most frequently reported aspects of nest tree selection for orangutans (Sugardjito 1983; Anderson 2000; Prasetyo et al. 2009, 2012; van Casteren et al. 2012). This has both anti-predatory (Sugardjito 1983) and comfort driven functions as by avoiding nesting in active fruiting trees orangutan avoid disturbance throughout the night and rest periods by other orangutans as well as other frugivorous species such as macaques, gibbons, fruit bats (Sugardjito 1983; Anderson 1998; Prasetyo et al. 2012) and biting insects such as ants (Whitten 1982b) which are attracted by the fruit. Avoiding nesting in active fruit trees and further from fruiting tress reduces the risk of predation as Sugardjito (1983) hypothesised that nocturnal predators such as clouded leopards, focus their arboreal search near to active fruit trees which are frequently visited by nocturnal frugivores (Sugardjito 1983; Prasetyo et al. 2009).

1.2.2.5. Ground nesting

The rarity of ground nesting in orangutans is likely an anti-predatory response along with being a method of ensuring comfortable, undisturbed, high quality sleep by avoiding high humidity, damp ground and rain dripping from overhead foliage. Ground nesting in orangutans is only known for large flanged males in Borneo (Ashbury et al. 2015) and is completely unknown in Sumatra, this is most likely due to the presence of large ground predators in Sumatra which are absent from Borneo, in particular Sumatran tigers and Sumatran dhole (Mackinnon 1974; Rijksen 1978; Sugardjito 1983; Rijksen & Meijard 1999). The main predators in Borneo are also present in Sumatra, but both species are capable of climbing and are adept at arboreal hunting; the reticulated python and Sunda clouded leopard, therefore there may be less pressure to avoid ground nesting in Borneo as in Sumatra (Mackinnon 1974; Rijksen & Rijksen-Graatsma 1975; Rijksen 1978; Sugardjito 1983; Brodie & Giordano 2013; Ashbury et al. 2015; Hearn et al. 2015).

Though adult orangutans are generally larger than the preferred prey size of clouded leopards which tend to prefer prey no larger than themselves (11-25kg), they are well within the potential prey size of tigers, with research by Hayward et al. (2012) suggesting that the preferred prey size of tigers is 60-250kg, this would place flanged male orangutans at the lower scale of this at 80kg (Markham & Groves 1990). However, much of the data for Hayward et al's (2012) analysis came from tigers in India and Russia and given the smaller body size of Sumatran tigers (Nowell & Jackson 1996) it should be assumed that potentially they could target smaller prey so both male and female orangutans (80kg and 40kg respectively (Markham & Groves 1990)) should be potential prey for tigers in Sumatra. Given this extra and very real threat from a ground predator, it is unsurprising that ground nesting is unheard of in Sumatra compared to Borneo (Prasetyo et al. 2009) and therefore we should not expect to find any instances of ground nesting in this study. Though there are no records of orangutan deaths due to pythons they are potentially the only natural predator in Borneo which could kill an adult orangutan as pythons have been recorded killing and consuming an adult female sun bear in Borneo (Fredriksson 2005) and responsible for a number of fatal attacks on humans in Indonesia, Sarawak and the Philippines (Lang 2010; Headland & Greene 2011). The presence of pythons could potentially be why terrestrial behaviour is still uncommon in Borneo (Loken et al. 2013; Ashbury et al. 2015).

A number of studies have similarly found links between increased rarity in ground nesting and higher predator densities in chimpanzees (Stewart et al. 2011; Stewart & Pruetz 2013). Further to this Stewart & Pruetz (2013) noted that there was a significant increase in the proportion of terrestrial nests built in Fongoli between in their study Stewart et al. (2011) compared to the earlier study by Pruetz et al. (2008). Not only were ground nests more common but average nest heights were also lower between the two studies, these two results suggest that in Fongoli the removal of predators has allowed chimpanzees to feel safer to build nests closer to the ground. Stewart & Pruetz (2013) however did note that the period that their studies had been conducted over had also been a period in which the chimpanzees had been exposed to a sudden increase in human contact, as the researchers were attempting to habituate the group. Furthermore, the detection and decay rates of ground nests versus arboreal nests at different height may also differ leading to variation in numbers found (Stewart &

Pruetz 2013). Other papers have also noted that chimpanzee ground-nesting generally occurs in places where predator numbers are low (Furuichi & Hashimoto 2000; Koops et al. 2007). However, this is not the case for all chimpanzee populations as in Bili in the Democratic Republic of the Congo 10.9% of all chimpanzee nests are ground nests even though there is a good population of leopards present as well (Hicks 2010; Koops et al. 2012b).

In the swamps of La Belgique in South-East Cameroon there is a positive selection for chimpanzees building ground nests to avoid human hunters as well as a lack of nesting trees and high densities of terrestrial herbaceous vegetation used for building ground nests (Tagg et al. 2013). Tagg et al. (2013) found that during the dry season when water levels were low, chimpanzees were moving into the swamp areas in La Belgique which gave them respite from hunting pressure as human hunters rarely entered the swamps and this also allowed the chimpanzees to feed upon preferred *Uapaca spp.* fruits. As the human hunters focused their hunts in the *terra firma* forests using guns to hunt arboreal primates, arboreal nesting would place chimpanzees in higher threat of the hunter's guns so ground nesting would help to make the individuals more inconspicuous and reduce this threat and may counterbalance the risks from predation and encounters with large herbivores like elephants or buffalo (Tutin et al. 1995; Hicks 2010; Tagg et al. 2013). Though in this instance the high rate of poaching led to an increase in ground nesting in two other studies in the Democratic Republic of Congo (Hicks 2010) and Cameroon (Last & Muh 2013) increased hunting, agriculture and human activity was found to lead to fewer ground nests.

Though there is strong evidence for arboreal nesting being a response to predation, there must be further reasons as to why apes build lower nests and more ground nests once the threat of predation is removed. One simple reason is that ground nests are both simpler, quicker and easier to construct and use less energy to produce than arboreal nests (Tagg et al. 2013). Ground nests in Fongoli are less complex and built with fewer steps and are often made of thin malleable materials when compared to arboreal nests, likely due to ground nests not requiring a supportive structure compared to arboreal nests (Stewart 2011a). Along with being less complex in design they are also less energetically demanding to produce, as there is less energy needed to stabilize the body whilst constructing the nest as there is for arboreal nests and there is no added energetic cost of ascending and descending trees to access the nest (Samson & Hunt 2012). Ground nests also offer safer, more stable nests and potentially longer periods of undisturbed sleep in areas with strong winds or during windy weather as arboreal nests experience both significantly greater wind sway, wind speeds and intensities of wind gusts than ground nests and as such there is less chance of nest failure or falling from the nest (Brownlow et al. 2001; Samson & Hunt 2012). As such, gorillas have been observed to abandon arboreal nests in favour of bare ground during dangerous storms as safety outweighed comfort and the threat from ground predators (Tutin et al. 1995). Lastly, ground nests were found to offer more stable temperatures and less thermal stress than arboreal nests so should offer greater comfort and undisturbed sleep than arboreal nests (Samson & Hunt 2012).

Compared to other apes, gorillas appear to be the most flexible in terms of nesting pattern, with the incidence of ground nesting for western lowland gorillas (G. gorilla gorilla) varying greatly between sites from 7.36% of nests in Petit Loango, Gabon (Furuichi et al. 1997) to 96.2% of nests built in La Belgique in Cameroon (Willie et al. 2014). Not only do gorillas more regularly build ground nests than other ape species but sometimes sleep on the bare earth without constructing any form of night nest which is a behaviour not shared with any other ape species (Tutin & Fernandez 1985; Fay 1989; Remis 1993; Yamagiwa 2001; Mehlman & Doran 2002). Two theories as to why gorillas so readily build ground nests compared to other ape species are both due to their larger body size compared to other apes. Firstly; the larger body size of gorillas may reduce the number of potential arboreal nest sites available due to a lack of trees able to support their weight, secondly their larger body size may both reduce the number of predatory species that can prey upon them but also reduce the chance of being predated on by those species which can tackle prey of their size (Yamagiwa 2001). In spite of their large body size, even mature male gorillas have been recorded building arboreal nests, though the majority of arboreal nests are built by juveniles and females (Yamagiwa 2001; Mehlman & Doran 2002).

Variations in rates of ground nesting in gorillas have been purported to be due to factors associated with variations in both habitat and climate. The availability of nesting material such as terrestrial herbaceous vegetation (THV) and shrubs appears to be a good predictor of ground nesting numbers as in the montane forests of Virunga where THV are abundant 97.1% of all nests were ground nests whereas in the tropical forests of Petit Loango THV are very rare and ground nests only account for 7.3% of all gorilla nests in that site. Nest heights and increased rates of arboreal nesting in gorillas have also been found to be linked to the season with significantly more arboreal nests being built in Lopé to potentially avoid nesting on the damp ground (Williamson 1988) and in Bai Hokou similar tendencies were reported by Remis (1993) who suggested that increased feeding on arboreal fruits may be responsible for higher incidences of arboreal nesting during the wet season (Yamagiwa 2001). Though terrestrial nesting is far more common in gorillas and their large body size excludes them from predation by most predators, gorillas are still vulnerable to predation in particular immature individuals in particular leopards with a number of records of leopards predating upon or attacking both mountain and lowland gorillas (Schaller 1963; Tutin 1992; Fay et al. 1995). With such threats, arboreal nesting may be an anti-predatory response by gorillas in particular immature individuals whilst they are vulnerable. Yamagiwa (2001) found that the dominant silverback may also play a part in protecting the troop from both predators and outside males who could kill the immatures. They found that following the death of the lead male, both adults and immatures built significantly fewer ground nests and following the joining of a new silverback to the group the immature individuals still produced few ground nests as they may have not trusted in the new male’s protector ability as with the old males.

There is significant support for ground nesting and nesting lower in trees being a sex linked behaviour with male chimpanzees in Budongo, Uganda (Brownlow et al. 2001) nesting lower than females, along with male chimpanzees being found to produce the majority of ground nests in Nimba (Koops et al. 2007, 2012b). Male orangutans have also been observed to nest in lower more stable positions than females or juveniles in Kutai National Park (Rayadin & Saitoh 2009). As in other ape species, arboreal nests are most frequently built by female and immature gorillas, with mature silverbacks rarely producing arboreal nests and the predominant producers of ground nests (Yamagiwa 2001; Mehlman & Doran 2002). Sexual dimorphism and the significantly larger size of mature males compared to female and immature apes plays a significant part in this as the number of potential arboreal nest sites is lower for males due to the greater support required from the nest trees as with greater body mass the chance of injury through nest failure greatly increases (Yamagiwa 2001; Koops et al. 2012b). However, though both orangutans and gorillas show significant levels of sexual dimorphism in terms of body mass, this is much less pronounced in chimpanzees and bonobos and so may not have as much of an effect upon nest site selection for either species (Richmond & Jungers 1995). Alternatively, the higher incidence of ground nesting in male chimpanzees and bonobos could have arisen due to mate guarding behaviours with males building ground nests beneath the arboreal nests of females in oestrus as has been observed in bonobos (Fruth & Hohmann 1993) and has been suggested for chimpanzees in Nimba (Koops et al. 2007). Later research by Koops et al. (2012b) however found no support for this theory as many of the pairs of elaborate ground nests and arboreal nests were either produced by the same male or maternally related males and suggested that mate guarding still may occur but that ground nesting may be as originally hypothesised a method of reducing risk of injury through nest failure.

1.2.3 Nest site selection

Nest tree selection is not random but highly selective in orangutans and other apes, with certain tree species and tree architecture used preferentially more than others (Ancrenaz et al. 2004a; Stanford & O’Malley 2008; Prasetyo et al. 2009; van Casteren et al. 2012; Cheyne et al. 2013; Samson & Hunt 2014). Nest site selection and nest position can be influenced by both comfort and predator avoidance with certain nest positions and nest sites lending them to provide either greater comfort and stability (Ancrenaz et al. 2004a; Stewart et al. 2007; van Casteren et al. 2012; Cheyne et al. 2013; Samson & Hunt 2014) or camouflage and more difficulty of access to a potential predator and easier escape route for the nest builder (Sugardjito 1983; Anderson 2000; Pruetz et al. 2008; Stewart & Pruetz 2013). Orangutans in highly disturbed areas have been found to prefer nesting in the largest trees available and preferential nest trees have been found to have a high rate of reutilisation which could lead to more frequent interactions and competition for ideal nest sites (Delgado & Van Schaik 2000; Ancrenaz et al. 2004a). Nest positions have been linked to ontogenetic difference with smaller, immature individuals nesting higher in the tree and using more precarious nest sites to reduce the risk of predation whilst larger adults build in lower more stable nest positions (Rayadin & Saitoh 2009; Prasetyo et al. 2012). There are also geographic and possibly cultural differences in the preference for utilising certain nest positions with orangutans in the highly disturbed peat swamps of Borneo highly favouring the tree-tied nest position; where the branches from more than one tree are used to form the nest platform (later referred as Position 4 nests), which are rarely used by other orangutan populations (Prasetyo et al. 2009; Malone & Strier 2011). This has been suggested to be either a product of cultural differences in orangutan nest preferences or a response to the lower density of large trees in the sites of Sabangau and Tuanan compared to other forest sites (Prasetyo et al. 2009).

Ancrenaz et al. (2004b) found Bornean orangutans were significantly preferring nesting in the largest available trees in Kinabatangan (KOCP) whilst Cheyne et al. (2013) found that though orangutans were preferring smaller trees than KOCP, orangutans were similarly nesting in the upper canopy at their site in Sabangau. Predator avoidance was ruled out as a factor in nest site selection for both studies due to the lack of large ground predators in Borneo (Ancrenaz et al. 2004a; Cheyne et al. 2013). Rather than predator avoidance both studies concluded that comfort and nest stability were responsible for the selection for nests in the upper canopy as larger, more stable trees that were less likely to fall or be susceptible to wind sway were selected (Ancrenaz et al. 2004a; Cheyne et al. 2013). In KOCP which is a degraded habitat tree fall is common due to abiotic factors such as wind so nesting in the tallest, largest trees could be a method of reducing the risk of tree fall and increase the opportunity for high quality, relaxed sleep as there is less need to be alert (Ancrenaz et al. 2004b). Cheyne et al's (2013) study further built on this conclusion of preferring the most stable nest site, though unlike in KOCP the orangutans in Sabangau were preferring to nest in smaller tree they still preferred to nest in the upper canopy but were positively selecting for trees with large trunk diameters and in particular those with features such as buttress or stilted roots and large basal areas which help to reduce sway (Nicoll & Ray 1996; Soethe et al. 2006; Cheyne et al. 2013).

Our field sites in Sikundur and Sei Betung offer a perfect opportunity to test these hypotheses. Both sites are located 10km apart and are classed as lowland dipterocarp forests, with the only difference being that Sikundur was selectively logged over 40 years ago and has been allowed to naturally recover (Knop et al. 2004; Priatna et al. 2006) whereas Sei Betung was previously an illegal oil palm plantation which was clear felled and since been replanted over the last 15 years (Kettle & Koh 2014; Wich et al. 2016b; Hartini et al. 2017). This difference in disturbance levels offers a perfect opportunity to test whether the availability of large trees does influence the proportions of position 4 nests built by controlling for cultural difference as both sites are so close it is possible for individuals to travel between both sites. Furthermore, we are able to test wither disturbance levels or changes to forest structure influence nest site selection and test whether in more disturbed sites orangutans prefer to build nests in the tallest available trees or if they select the most stable trees as suggested by Ancrenaz et al. (2004a) and Cheyne et al. (2013). As tigers are confirmed to be in the area surrounding our field sites (Luskin et al. 2017), this therefore also allows us to test the anti-predator hypothesis as unlike in both studies by Ancrenaz et al. (2004a) and Cheyne et al.(2013) predators which are a threat to adult orangutans are present.

1.2.4 Nest reuse

Nest reuse is relatively common in orangutans when compared to other ape species with published numbers for orangutans ranging between 3% in Danum Valley (Kanamori et al. 2017) to 31.9% in Birawa in East Kalimantan (Rayadin & Saitoh 2009) whereas for chimpanzees figures range between 6% (Stewart et al. 2011) and 13.8% (Plumptre & Reynolds 1997), for gorillas its rarer, between 2.8% (Sunderland-Groves et al. 2009) and 4.1% (Iwata & Ando 2007) and extremely rare in bonobos; 0.2% (Fruth & Hohmann 1996). This higher rate of nest reuse by orangutans has been posited to be due to resource limitations (Rayadin & Saitoh 2009) as orangutans build larger nests than chimpanzees (Groves & Sabater Pi 1985) and build nests higher than gorillas (Fruth & Hohmann 1996), thus the number of potential nest sites must be lower for orangutans, thereby requiring that nests are reused more frequently. The rate of reuse of nests and nest sites in orangutans appears highly variable with field site and in particular disturbance levels as more disturbed sites tend to have fewer potential nest sites. The loss of potential nest sites explains why sites such as Kinabatangan and Birawa have such high rates of reuse (14.6% and 31.9% respectively) (Ancrenaz et al. 2004a; Rayadin & Saitoh 2009) when compared to sites with medium levels of disturbance such as Tanjung Putting and Gunung Palung National Park (9.51% and 12% respectively) (Johnson et al. 2005; Prasetyo et al. 2012) and less disturbed sites like Danum Valley and Ketambe (3% and 6.2% respectively) (Prasetyo et al. 2009; Kanamori et al. 2017).

1.3 Nest position selection

Nest position selection has been less studied in Sumatra, with Sugardjito's (1983) seminal study reporting that Sumatran orangutans prefer nesting higher in the canopy and within larger trees. Because of the presence of Sumatran tigers and dholes this may be an anti-predatory response as well as comfort and stability driven. Nest heights and nest tree heights do appear to be generally higher in Sumatra than Borneo for both day and night nests (Prasetyo et al. 2009). Studies by both Rayadin & Saitoh (2009) and Prasetyo et al. (2012) found that immature Bornean orangutans nest higher within the canopy than adults and tended to build smaller nests nearer to the ends of branches. Immature orangutans are more vulnerable to predation by arboreal predators such as pythons and clouded leopards due to their smaller size (Rijksen 1978; Wilting et al. 2006; Matsuda et al. 2008) therefore nesting higher in a tree and in more peripheral positions reduces the chances of both being seen or attacked by these predators. Large adult orangutans are generally too large for either of these predatory species to normally be able to kill (Rijksen 1978; Wilting et al. 2006; Matsuda et al. 2008) so for adults comfort and stability is more important as the higher and more precarious branches used by the immatures are incapable of supporting the weight of a fully grown adult. Both Rayadin & Saitoh (2009) and Prasetyo et al. (2012) found that adults nested lower in the tree than juveniles, built larger nests and in more stable locations closer to the stem.

Building nests higher in the canopy also provides further benefits beyond predator avoidance, including possible increased comfort through a reduction in airborne parasite numbers (Prasetyo et al. 2009; Stewart 2011b) though Koops et al. (2012b) were unable to find evidence for mosquito densities differing with height or altitude but this may have been due to limited sample sizes and may have been true for one site but not all field sites. Nests may offer mosquito repellent properties through the release of chemicals or aromas which deter mosquitoes via the breaking of branches and the chemical properties of the nest tree (Stewart 2011b), as orangutans have been observed nesting in trees with mosquito repellent properties (Largo et al. 2009) and carrying leaves and branches from such trees to line new nests (Kuze et al. 2011), so the anti-vector hypothesis cannot be discounted but may be less associated with nest position and more with nest site selection. Nesting higher within the tree has also been suggested to improve comfort through reduced humidity, however nesting very high within the canopy or above the level of the surrounding canopy presents a drawback of increased exposure to the wind and rain, with increased wind speeds and strength causing greater branch sway which would increase sleep disturbance and risk of branch failure (Samson & Hunt 2012). Nest height generally seems to be linked to the height of the nest tree and this may differ across sites due to differing forest structures and tree heights (Prasetyo et al. 2009; Badji et al. 2017).

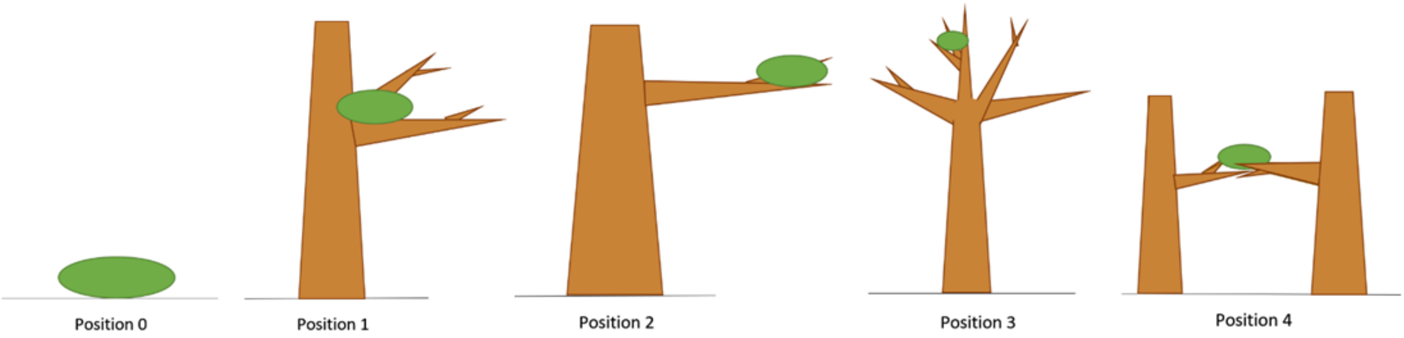

Figure 1-3 Nest positions of orangutans as proposed in the University of Zurich Orangutan Network standardised field methods (University of Zurich 2015)

Generally there are five widely accepted nest positions utilised by orangutans including ground nests (position 0) (Prasetyo et al. 2009; Orangutan Network 2015). These five positions are based upon the nests' height and placement within the crown in relation to the main stem. Position 1 nests are built lower in the crown and close or against the main stem. Position 2 nests are built towards the end of a horizontal branch and use side branches weaved together to form the platform. Position 3 nests are built towards the top of the crown, usually within a fork with no main stem overhead; only smaller branches and leaves. Position 4 nests also known as tree tied nests are those where more than one tree is used to build the nest, this can either from tying together the branches of trees or using the tops of smaller trees and locking these together to form a stable platform (Prasetyo et al. 2009, 2012; Orangutan Network 2015).

The different nest positions may have arisen due to both the extreme sexual dimorphism shown in orangutans and changes in body size with age (Markham & Groves 1990), the tree architecture and its mechanical properties lending it to a certain nest position or the forest structure making certain tree types more or less common and increasing the likelihood of certain nest positions being used. Rayadin & Saitoh (2009) noted that young orangutans nested higher and in more peripheral positions whereas large flanged males nested lower in the canopy and closer to the stem. Flanged males may therefore be limited to only using more stable nest positions such as Position 1 and similar to chimpanzees only being able to utilize more peripheral nest positions in larger trees which possess the biomechanical strength to support their weight (Hernandez-Aguilar et al. 2013). Position 1 nests being the lowest to the ground and closest to the main stem would theoretically be the most stable of all nest positions but are also the most easily accessible to a predator, therefore it could be that large adults, in particular flanged males may prefer to build nests in this position due to their significantly larger body size and reduced susceptibility to predation (Sugardjito 1983; Anderson 2000; Rayadin & Saitoh 2009). As Position 1 nests are built lower within the crown if predator avoidance responses are important, it should be expected that such nests be built in trees with higher first branch heights as this would both effectively increase the potential nest height but also offer a more difficult route to the nest to ground predators (Koops et al. 2012a).

Conversely, Position 2 and 3 nests are built within the periphery of the crown and offer much more difficult access to predators, so therefore are more likely to be built by females and younger individuals. By being at the end of a branch Position 2 nests have more limited access and approach routes (Stewart & Pruetz 2013) but if built within a well-connected tree or one that is close to its neighbours also offers an easier escape route (Anderson et al. 1983; Anderson 2000; Rayadin & Saitoh 2009). Being at the end of a branch though also presents a significant drawback in reduced stability and possible increased branch sway and to support the weight of an adult orangutan very large branches would be needed. Such large branches tend to be on larger trees and are a rare commodity as the production of horizontal branches is expensive due to gravity and needs to be thicker nearer to the trunk (Horn 1971; Rayadin & Saitoh 2009; Hernandez-Aguilar et al. 2013). As significant biomechanical strength is required in the branch to support the weight of an orangutan in more peripheral position such as Position 3 nests, it should be expected to find that such nests are built in significantly larger trees than other nest positions (Hernandez-Aguilar et al. 2013). In more disturbed habitats where large trees have been removed it should be expected that position 3 nests are less common or that the few trees remaining which are large enough to support position 3 nests would experience significant reuse.

By being built within a fork Position 3 nests are significantly more stable than Position 2 nests but do not offer as easy an escape route (Samson & Hunt 2014). In open savannah areas with large numbers of predators chimpanzees have been observed nesting higher within the tree crowns and in many cases open crowns with little to no cover above them to reduce the directions from which a predator may access the nest or attack (Baldwin et al. 1981; Anderson 2000; Pruetz et al. 2008; Stewart & Pruetz 2013; Badji et al. 2017). If this behaviour translates to orangutans then it should be expected to find more Position 3 nests in more open forests and in areas where predators are present, and thereby more frequently in Sumatra than Borneo, also given orangutans preference for nesting in the upper canopy this should be one of the most commonly used nest positions (Ancrenaz et al. 2004a; Prasetyo et al. 2009, 2012; Cheyne et al. 2013).

In most forests Position 4 nests are rarely used by Sumatran orangutans with the other three positions generally being used in similar proportions despite differences in forest structure and habitat type such as in the two Sumatran sites of Ketambe (dryland forest) and Suaq Balimbing (peat swamp) (Prasetyo et al. 2009). However, orangutans at two peat swamp sites in Kalimantan (Sabangau and Tuanan) show significant preferences for building Position 4 nests and build these much more frequently than the other positions, in particular Position 3 nests. It has been theorised that this could be a product of the forest structure and a paucity of larger nest trees due to logging which has occurred at both sites or could be due to geographic and species differences or cultural differences in nest position preference (Prasetyo et al. 2009).

1.4 Nests as tools for informing conservation and management strategies

The nests of orangutans provide a useful tool to gauge orangutan population densities and with the long-term monitoring of these nests assess the health of the population (van Schaik et al. 1995; Hashimoto 1995; Johnson et al. 2005; Cattau et al. 2015). The densities of nests can also provide information on habitat preference and on the impacts of anthropogenic disturbance such as hunting, logging (Hardus et al. 2012b; Marshall et al. 2006; Husson et al. 2009; Wich et al. 2012; Spehar & Rayadin 2017) or abiotic disturbance such as forest fire (Russon et al. 2015). Previous studies have shown that orangutans are able to cope with minor disturbance from humans such as low-intensity selective logging (Knop et al. 2004; Ancrenaz et al. 2004a, 2004b, 2010; Marshall et al. 2006; Husson et al. 2009), but orangutan densities are significantly lower in those habitats experiencing greater levels of disturbance from actions such as more intense logging, land clearance and planting of plantations; with these actions having already had sever impacts upon orangutan populations (Rao & van Schaik 1997; Felton et al. 2003; Husson et al. 2009; Prasetyo & Sugardjito 2011; Cattau et al. 2015; Russon et al. 2015; Voigt et al. 2018). Hunting has been found to have a huge influence upon orangutan numbers in the vicinity of settlements that hunt (Marshall et al. 2006; Wich et al. 2012b). The use of reforestation sites by orangutans is less well understood (Knop et al. 2004; Wich et al. 2016b; Hartini et al. 2017) and understanding how the habitat preferences of orangutans differ across levels of disturbance or forest recovery will give invaluable information regarding the value of human led reforestation vs naturally recovered forests for orangutans populations and conservation.

Habitat loss and habitat change driven by the increasing width of human influence and exacerbated by climate change are major threats currently pushing orangutan populations closer to extinction (Mantyka-Pringle et al. 2015; Ancrenaz et al. 2016; Wich et al. 2016a; Singleton et al. 2017; Voigt et al. 2018). Understanding how habitat change affects orangutans and how they utilise this space is key to developing effective conservation and management plans to ensure their continued survival (Levin 1992). Due to the long period of time that orangutan nests are visible and the fact that orangutans build new nests daily, they are an extremely useful tool for studying orangutan populations and habitat preferences and the effects of anthropogenic disturbance such as hunting and logging (van Schaik et al. 1995; Russon et al. 2001; Buij et al. 2003; Morrogh-Bernard et al. 2003; Felton et al. 2003; Knop et al. 2004; Johnson et al. 2005; van Schaik et al. 2005; Mathewson et al. 2008; Spehar et al. 2010; Prasetyo & Sugardjito 2011; Wich et al. 2012b; Cattau et al. 2015). Given the continuing deforestation and increasing rate of human disturbance across the orangutan's range understanding how orangutans cope and utilise these changing habitats is crucial to their conservation (Wich et al. 2016; Voigt et al. 2018).

As more and more areas of pristine and undisturbed forest disappear from the orangutan's range and gradually their habitat becomes ever more influenced by people it is important to learn and understand more about orangutans and how they use the forest and how changes to the forest affect them. Orangutans have been found to travel through and forage in plantations but still rely upon natural forests for sleeping, resting and feeding as diets in less disturbed forests are likely to have higher nutrients quality compared to what is available in many plantations such as oil palm fruits and the cambium of *Acacia magnium* trees (Meijaard et al. 2010; Campbell-Smith et al. 2011a, 2011b; Wich et al. 2012a; Ancrenaz et al. 2016; Spehar & Rayadin 2017). Understanding how orangutans utilise recovered sites and reforestation site will help to provide further information for conservation managers for determining the value of disturbed lands surrounding protected areas as a potential to expand orangutan habitats to further promote conservation efforts.

1.5 Threats – habitat loss, degradation, conflict and hunting

Though the world may be home to a vast diversity of life, these species are not uniformly distributed across its surface, instead some regions are biodiversity hotspots holding significantly higher than average species densities and rates of endemism than others (Myers et al. 2000; Brooks et al. 2002). Four of the 25 global biodiversity hotspots are found in South East Asia: Sundaland, Wallacea, the Philippines and Indo-Burma, showing the importance and value of this region of the world to global biodiversity and role as a "true reservoir" of biodiversity (Myers et al. 2000; Evans 2016). Though South East Asia may be a reservoir for biodiversity, it is also one of the most threatened regions, currently experiencing the rapid loss of primary forest habitat through human disturbance and conversion for agriculture and timber and mineral extraction. This rapid habitat conversion is likely to result in 75% of forests lost and a 40% reduction in biodiversity in South East Asia by the year 2100 (Sodhi et al. 2010).

The principal causes for this rapid conversion of forest lands is the rapid increase in the human population over the past two centuries', and the ever-increasing global demand for food and products (Meyer & Turner II 1992; Laurance et al. 2014). The population of South East Asia in particular has seen extremely rapid population growth, with the regional population in 1800 totalling around 30 million, 80 million in 1900, 524 million by the year 2000 and currently at 660 million in 2019 (Jones 2013; Worldometers.info 2019). This rapid increase in human population has brought with it an increased pressure upon the environment through populations seeking resources in terms of space for urban areas, the expansion of agriculture for food and cash crops along with the extraction of resources such as coal, precious minerals and ore from the ground and timber from the forests (De Koninck & Dery 1997; Sodhi et al. 2004; Alvarez-Berríos & Mitchell Aide 2015; Drescher et al. 2016). This increase in deforestation, agriculture and resource exploitation is fuelled by the global demand for these products originating from these tropical lands such as the demand for tropical hardwoods in China (Kaplinsky et al. 2011), palm oil in China and India (Hansen et al. 2015), gold and other precious metals and gems driven by the constant annual rate of increase in international gold prices (Swenson et al. 2011; Alvarez-Berríos & Mitchell Aide 2015; Akpalu & Parks 2018) and the increasing global demand for meat and increased meat consumption (Machovina et al. 2015).

Of all the nations within South East Asia, Indonesia stands out both because of its high levels of biodiversity nationally but also because it is currently experiencing the second highest rate of deforestation amongst tropical countries behind Brazil (Hansen et al. 2008; Harris et al. 2012; Stibig et al. 2013; Abood et al. 2015). Since 1950, Indonesia has lost an estimated 68 Mha (million hectares) of its forest land to logging and conversion (Tsujino et al. 2016) with 0.82 Mha of forest lost per year in the decade between the year 2000 and 2010 which accounted for 56% of the total forest loss for South East Asia during this time (Stibig et al. 2013; Abood et al. 2015). The planting of monocultures of cash crops such as oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*), candlenut (*Aleurites moluccanus*) and fast growing tree species such as *Acacia mangium* for pulp production along with mixed agroforestry operations have been principally responsible for the conversion of forest lands within Indonesia (Robertson & van Schaik 2001; Wich et al. 2011a; Voigt et al. 2018). Logging concessions and fibre plantations currently account for the largest forest loss in Indonesia with ~6.6 Mha of forest having been lost to fibre plantations (pulp and paper), logging concessions, oil palm plantations and coal mining in the decade between the year 2000 and 2010 (Abood et al. 2015). Along with the clearance of forests, the structure of the remaining forests is being altered through human actions, in particular by selective logging which presents further threats to the species that call these forests home, in particular arboreal species such as orangutans (Hall et al. 2003).

The loss of forests is particularly evident on the island of Sumatra where 70% of its forestands have already been converted through intensive forest clearance as of 2010 (Laumonier et al. 2010; Margono et al. 2012, 2014; Drescher et al. 2016). Much of the deforestation on Sumatra is associated with prior forest degradation (Margono et al. 2012, 2014) with the principal actions causing this degradation being agricultural incursions, timber extractions (Gaveau et al. 2014a; Linkie et al. 2014) and fires (Gaveau et al. 2014b; Sloan et al. 2017) with much of this being illegal.

The rapid rate of forest clearance and land conversion along with the rapidly growing human population on Sumatra has serious implications for orangutans (Ancrenaz et al. 2016; Singleton et al. 2017; Nowak et al. 2017; Wich et al. 2016). The rampant deforestation, logging and land clearance for industrialised plantations was found to be responsible for a loss of over 100,000 orangutans on Borneo between 1999 and 2015 which accounts for around 50% of the total population (Voigt et al. 2018). The orangutans in Sumatra face a similarly bleak future if current predictions for forest loss continue with 4500 individuals expected to be lost by 2030, a loss of 30% of the total orangutan population on Sumatra (Wich et al. 2016a).

1.5.1 Logging intensity and orang-utan densities

Areas with more recent or more intense logging have significantly lower orangutan densities than those where either the forest has had time to recover, where the logging and disturbance was less intense or that were left intact (Rao & van Schaik 1997; Felton et al. 2003; Knop et al. 2004; Husson et al. 2009; Prasetyo & Sugardjito 2011; Cattau et al. 2015; Russon et al. 2015). A few studies have found that in areas which have experienced low-intensity or selective logging, there is no significant difference in orangutan density from that of unlogged areas (Ancrenaz 2004; Ancrenaz et al. 2005; Marshall et al. 2006; Husson et al. 2009; Ancrenaz et al. 2010) and similarly in areas which have had a significant amount of time to recover since disturbance (>30 years) (Knop et al. 2004).

The reduction in orangutan numbers associated with medium to high intensity has been suggested to be due to a number of factors, the primary reason being due to the changes in forest structure. Those changes in forest structure found to most heavily influence orangutan numbers were the removal of large trees and important food species leading to lower fruit availability in these areas reducing their carrying capacity for orangutans (Rao & van Schaik 1997; Wich et al. 2004a; Husson et al. 2009; Hardus et al. 2012a). Fruit availability, in particular the density of fig trees and soft-pulp fruits is a strong predictor of orangutan densities (van Schaik et al. 1995; Buij et al. 2002; Wich et al. 2004b). If these important food trees are removed through human actions, it could lead to the collapse of the local orangutan population or the movement of orangutans away from these sites, to areas where the fruit are still present which could put excess pressure on the food stocks within that habitat.

Along with the clearance of forests, the structure of what forests remain is being further altered through human actions, in particular by selective logging which presents further threats to the species that call these forests home (Hall et al. 2003). Selective logging has been found to be associated with more homogenous forests with lowered species richness and a more simplified vertical structure (Norris et al. 2010). Though selective logging produces significantly less disruption to forest canopy and vegetation cover compared to conventional logging methods it still does cause some disruption to and small scale-fragmentation of the canopy (Pereira et al. 2002). The removal of larger emergent trees in particular leads to a reduction of continuous canopy and tree density which could possibly affect the availability of good nest sites as taller, larger trees were also preferentially selected for nests in Borneo (Ancrenaz et al. 2004; Prasetyo et al. 2012; Cheyne et al. 2013).

In some cases orangutans have been found to use secondary regrowth forests to a greater extent than any other mammalian species within the area (Gregory et al. 2012; Spehar & Rayadin 2017). Degraded forests such as those which have been selectively logged and those naturally regenerated after forest fires are also utilised by orangutans though their densities are lower in the more degraded areas (Rao & van Schaik 1997; Felton et al. 2003; Husson et al. 2009; Prasetyo & Sugardjito 2011; Cattau et al. 2015; Russon et al. 2015). Orangutans have been reported to utilise reforested areas replanted by humans, though similarly to in heavily logged areas, they show significant clustering of nests in small pockets of the site (Wich et al. 2016; Prasetyo & Sugardjito 2011; Ancrenaz et al. 2004b). Even heavily converted areas such as oil palm plantations, paper and pulp plantations and agroforestry areas have been found to be utilised by orangutans (Meijaard et al. 2010; Campbell-Smith et al. 2011a; Ancrenaz et al. 2015). An assessment by Meijaard et al. in 2010 found unexpectedly high orangutan densities within *Acacia* plantations (planted for paper and pulp) though the authors had concerns as to the long-term viability of these populations due to the lower food availability.

1.5.2 Hunting and the illegal pet trade

As the forest is opened up to logging and roads are cut through these forests, the opportunities for hunters to enter the forest and reach further into the forest also increases (Husson et al. 2009; Wich et al. 2011a). The hunting and capture of orangutans poses a huge threat to the long term survival of orangutan populations as hunting has been found to have a more serious negative impact upon orangutan populations than logging and habitat degradation alone (Marshall et al. 2006; Ancrenaz et al. 2004; Husson et al. 2009). Hunting has been found to be highly influential upon orangutan densities with orangutan numbers being significantly lower near to human settlements known to hunt orangutans than those that do not, likely due to the orangutans being removed from those forests and not actually avoiding them (Marshall et al. 2006; Wich et al. 2012b). Orangutans are hunted for bushmeat, traditional medicine and for the exotic pet trade (Marshall et al. 2006; Wich et al. 2012b; Davis et al. 2013; Nijman 2017). Hunting for food occurs most notably in regions where the population are majority non-Muslim in parts of North Sumatra and Borneo as for Muslims the consumption of the meat of primates is considered "haram" (Rijksen & Meijard 1999; Wich et al. 2011a, 2012b; Davis et al. 2013). The capture of orangutans, mainly infants for the pet trade occurs in two instances; as a by-product of the killing of the mother from conflict-killing when found crop raiding in plantations and from hunting specifically for the pet trade where hunters deliberately target adult females who they kill in order to take the young for the pet trade regardless of whether they were crop-raiding or not (Nijman 2009; Campbell-Smith et al. 2010; Wich et al. 2011a; Freund et al. 2017).

Hunting for trade offers further threats to orangutans due to the number of individuals killed in order to capture one young individual for the pet trade, and then the further amount that die in transit to the customer which may be both within Indonesia or internationally such as Taiwan prior to 1980 and more recently Thailand (Nijman 2009; Nijman et al. 2017). The number of individuals that have died for one single individual to reach a bird market, rescue centre or zoo was termed as the "loss rate" (Nijman 2005, 2009). Conservative models by Nijman (2005), put this at 2 but more realistic models placed this at 4, other sources have suggested loss rates of 2-4 (Rijksen & Meijard 1999) and even up to 8-10 (Galdikas & Briggs 1999). However, it appears that Bornean orangutans are the species predominately traded rather than Sumatran orangutans and Bornean specimens even appear in Sumatran markets (Nijman 2009). Also there appears to be a shift in recent years away from the trade in apes in Indonesia and increase in the trade in lorises and smaller monkey species (Nijman et al. 2017). Therefore, the pet trade may be a more minor threat to orangutans in the wild when compared to the greater pressures of habitat loss and hunting.

1.5.3 Vulnerability to extinction

Orangutans have the longest inter-birth interval and latest weaning age of any great ape and receive the longest period of unshared proximity to their mother among the great apes (van Noordwijk et al. 2009; (van Noordwijk & van Schaik 2005). Their long interbirth interval is one of the primary factors which make orangutans so vulnerable to extinction (van Noordwijk & van Schaik 2005; van Noordwijk et al. 2009; Jones 2011). Orangutans' slow life history mean they are highly susceptible to excessive mortality or harvest due to the time required to replace lost members (Musick 1999). Large mammal species in the tropics such as orangutans are particularly at risk of extinction (Fritz et al. 2009) due to the rapidly increasing human populations in the tropics (Jones 2013; Drescher et al. 2016) and the associated increasing rates of habitat loss within the tropics for agriculture, timber and mineral extraction to supply to ever increasing global demand for palm oil, timber and other resources (Sodhi et al. 2004, 2010; Marlier et al. 2015; Drescher et al. 2016; Hughes 2017). Land cover change is expected to have a huge impact on orangutan numbers with climate change and the expansion of agriculture as well as a number of large-scale infrastructure projects planned in sensitive areas (Struebig et al. 2015; Wich et al. 2016a). Orangutans also face added pressures of hunting (Owens & Bennett 2000; Fa et al. 2002; Isaac & Cowlishaw 2004; Collen et al. 2006; Fritz et al. 2009; Hughes 2017) and fruit shortages due to climate change increasing dry periods and the risk of wildfires (Mantyka-Pringle et al. 2015; Jantz et al. 2015; Loo et al. 2015; Hughes 2017; Sloan et al. 2017).

1.5.4 Orangutans in Sumatra- Leuser Ecosystem and Batang Toru

The majority of the orangutans on Sumatra, ~89% of the remaining population of Sumatran orangutans are to be found within the Leuser Ecosystem in North Sumatra and the remainder in adjacent areas to the south (Wich et al. 2011a, 2016a; Singleton et al. 2017). The separate population of Tapanuli orangutans are found in the Batang Toru region to the south of Lake Toba (Nowak et al. 2017; Nater et al. 2017). The Leuser Ecosystem is a globally significant conservation area, being of particular significance as it is the last remaining ecosystem on Earth where orangutans, tigers, elephants and rhinoceros co-occur naturally (Sloan et al. 2018a). Whilst a large portion of the Leuser Ecosystem falls within the boundaries of Gunung Leuser National Park and established as a National Strategic Area for ecological protection and is therefore protected under Indonesian national law this has still not prevented Leuser from experiencing forest loss, anthropogenic disturbance and exploitation of its resources both legally and illegally (Wich et al. 2011a; Sloan et al. 2018b). The Leuser Ecosystem is currently the subject of infrastructure development plans which are being contested between the regional and central governments (Tata et al. 2014).

Much of Leuser's current and future threats are becoming increasingly centred on infrastructure and the push for infrastructure development within the national park's boundaries. Part of Leuser Ecosystem is classed as a UNESCO World Heritage Site (WHS) as the Tropical Rainforest Heritage of Sumatra, but since 2011 this has been listed as a World Heritage Site in Danger due to "serious and specific" infrastructure threats (GOI 2018; Sloan et al. 2018). These threats include a number road building projects which have already had significant impacts upon Leuser by facilitating smallholder agricultural encroachment along these roads (Gaveau et al. 2009; Linkie et al. 2014) and a larger highway has been planned which would bisect the WHS but it has currently been stayed by the central government but a reapplication is pending by North Sumatra province (Sloan et al. 2018a). There are also currently plans for building a number of electricity generation plants, hydro-electric dams, geothermal power plants and electricity transmission lines within the Leuser Ecosystem (Sloan et al. 2018a). These numerous threats show how precarious the future prospects for Sumatran orangutans may be as they are slowly pushed into smaller fragments of forest as more is lost to agricultural and infrastructural expansion.

Such infrastructure development projects and the associated habitat fragmentation and habitat loss are placing further pressures upon the already Critically Endangered populations of the newly discovered Tapanuli orangutan in Batang Toru (Nowak et al. 2017; Sloan et al. 2018b). A number of road building projects, the zoning of 14% of habitat for agriculture and eligibility for conversion and the proposed building of a hydroelectric dam could flood a further 8% of habitat all threaten to further fragment and reduce the little remaining habitat of the Tapanuli orangutan and draw them closer to extinction (Sloan et al. 2018b)

1.6 Conclusions

Given the number of threats facing Sumatran orangutans in particular the rapid loss and conversion of their forest habitats to plantations and agroforest landscapes, it is vital to gain as much information upon the species ecology as possible. Reforestation projects offer the opportunity to regain what was lost but the value of these projects to orangutans and how orangutans utilise such environments is little studied (Wich et al. 2016b), as such this project offers the potential to fill this significant gap in the literature by offering the first in-depth study of nest site selection and assessment of population densities linked to the recovery of the forest structure. The nests built by orangutans offer an invaluable method of assessing population densities and habitat use for a species that otherwise is relatively difficult to find (Prasetyo et al. 2009; Tagg et al. 2013). As orangutans build nests daily and spend significant proportions of their time resting within nests resting (Nowak & Singleton 2016), it is important to understand how changes to the forest structure and availability of nest trees influences nest site selection and nest reuse. Such information is vital to provide more targeted and informed conservation management strategies and developing land management strategies for national parks and conservation areas as to better promote the conservation of this species. As much of the previous research into orangutan nesting has been focused in Borneo, gaining further information upon Sumatran orangutan nesting and the potential differences in nesting habits could also provide further information to the evolution and development of the two species. Prior studies on orangutan nest site selection have discounted the predation avoidance hypothesis when those previous studies were conducted in Borneo where predation pressures are almost non-existent for adult orangutans besides from humans, whereas in Sumatra adult orangutans are potential prey for tigers (Sugardjito 1983; Ancrenaz et al. 2004a; Cheyne et al. 2013). This study offers the potential to truly test whether predation or comfort through improved quality of sleep has greater influence upon orangutan nesting in Sumatra. Furthermore, both studies by Ancrenaz et al. (2004a) or Cheyne et al. (2013) failed to consider nest positions which as Stewart & Pruetz (2013) noted that by comparing nest positions within trees is it possible to control for other cross-site differences in other variables with may influence nest characteristics such as nest height. By investigating nest position as well as nest site selection we are able to truly test whether orangutans are building their nests as an anti-predatory response and not just knowing which trees are preferred.

1.7 Thesis Aims and overview

The overall aim of this study is to examine how forest structure influences Sumatran orangutan nest ecology by investigating nest site selection, nest position and orangutan densities in a naturally recovered forest and reforestation site. These different aspects were chosen to understand how forest structure influences nesting across three scales; the tree the nest is built in (nest tree), nest height and position within the nest tree and lastly the nest trees' position within the larger habitat, which will allow us to answer three basic questions: Why is the nest in this area? Why did the orangutan choose this particular tree? Why did the orangutan build the nest in that position and height?

Chapter 1 provides a review of the relevant literature beginning with a brief overview of orangutan biology, nesting ecology, nest site selection and nest positions and then cover the threats orangutans currently from habitat loss, degradation, conflict with humans and hunting. Through this literature review I will provide relevant background to ensure a contextual setting for each of the data chapters.

Chapter 2 focuses on nest tree selection and understanding why particular trees are chosen based on tree architecture. Aspects of tree architecture are then compared to those within a 5m radius of the nest tree and control trees to determine which properties are most important when selecting a nest tree.

Chapter 3 focuses on nest positions and how the architecture of the nest tree and surrounding trees influence the positioning of the nest within the crown. By sampling in a relatively intact site and highly disturbed site this allowed us to test whether a preference for building nests that utilise multiple trees for the frame (Position 4) is due to a paucity of large trees in the area or if it is a geographical/cultural difference between orangutan populations and species as was hypothesised by (Prasetyo et al. 2009). The confirmed presence of Sumatran tigers in our study area provided our study with the opportunity to test whether nest positions were driven by comfort or predator avoidance unlike the previous studies from Borneo by Ancrenaz et al. (2004a) and Cheyne et al. (2013).

Chapter 4's focus is upon the influence of forest structure on orangutan nests on a broader scale by investigating how forest structure influenced the distribution of nests throughout the sites. We examine which variables most influence orangutan densities in these lowland dipterocarp forests of Sumatra and whether these important variables were the same regardless of disturbance levels or not.

Chapter 5 summarises and integrates the information from each chapter to give an overview of orangutan nest ecology and the influence forest structure has on this. Lastly this study is placed in the context of management, conservation and conflict implications in terms of the orangutan populations in the lowland forests of North Sumatra. Information gaps and areas which demand further research attention are also highlighted.

Chapter 2: Nest site selection in Sumatran orangutans (*Pongo abelii)* in the disturbed lowland dipterocarp forests of North Sumatra

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2.1 Introduction

Nest building is a behaviour shared by all great apes (Goodall 1962; Mackinnon 1974; Sugardjito 1983; Fruth & Hohmann 1993, 1996; Tutin et al. 1995; Prasetyo et al. 2009) with adults building new nests almost daily (van Casteren et al. 2012). A number functions for nest building have been hypothesised including; improving sleep quality through comfort, improved thermoregulation, biting insect avoidance and reducing the risk of predation (Anderson 1984, 1998).

One of the most important functions a nest offers is improved physical comfort whilst sleeping through the provision of a comfortable platform to sleep on and cushioning through the weaving of small branches and addition of soft leaves (Goodall 1962; Van Lawick-Goodall 1968; Stewart et al. 2007; Prasetyo et al. 2009, 2012). Secondly nests offer protection from adverse weather conditions such as rain and strong winds (Goodall 1962; Kano 1982; Anderson 1984; Prasetyo et al. 2009; Cheyne et al. 2013) as well as avoiding the wet and damp ground in wetter habitats or during rainy seasons (Remis 1993). Improving quality of sleep through comfort could be considered one of the primary functions of nest building as the provision of a comfortable platform to sleep on allows for higher quality rest and sleep by reducing disturbances in the night and reducing strain on the musculature (Fruth & Hohmann 1996; McGrew 2004; Stewart 2011b; van Casteren et al. 2012). Nests produced by orangutans are considered to be the most complicated in design of all ape nests, and related to comfort can include features such as pillows, blankets, roofs or a second bunk nest which improve comfort and protection in the case of bunk nests for young individuals (MacKinnon 1971; Anderson 1984, 1998; Russon et al. 2007; Prasetyo et al. 2009; van Casteren et al. 2012). Those nests with more complicated designs have been found to lead to better, more high quality sleep in orangutans (Samson & Shumaker 2013).

Sleeping in arboreal nests also potentially offer improved thermoregulation by aiding in the reduction of heat loss at night and avoiding higher day time temperatures and humidity (Anderson 1984, 1998; Fruth & Hohmann 1993; McGrew 2004; Stewart 2011b; Prasetyo et al. 2012; van Casteren et al. 2012; Koops et al. 2012a). However, research by Samson & Hunt (2012) found that compared to ground nests, arboreal nests actually experienced greater temperatures, wind sway and heat stress but experienced much lower humidity levels. Koops et al. (2012) found that nest site selection of chimpanzees in the rainforest habitat of Seringbara appeared to be primarily driven by humidity avoidance, with nests being built higher in the trees during the wet season as higher nests allowed for higher temperatures but lower humidity, reducing the threat of heat loss due to the rain. Avoiding higher humidity in rainforest environments would be more beneficial to an individuals comfort and health as high humidity reduces the efficiency of heat loss through evaporation and conversely in colder temperatures high humidity increases heat loss through convection (Bell & Greene 1984). As both extremes of heat and cold would influence an individual's comfort and quality of sleep, I decided to include aspects of thermoregulation such as nest height and canopy closure above the nest as part of the overall sleep comfort hypothesis.

Nests also offer protection from biting insects and disease vectors such as mosquitoes by acting as physical barriers to such vectors (McGrew 2004; Nunn & Heymann 2005; Prasetyo et al. 2009; Stewart 2011b; van Casteren et al. 2012). Furthermore, certain tree species used for nesting could also have chemical properties which act as repellents to mosquitoes and other biting insects as well (Stewart 2011b; Samson et al. 2013; Samson & Hunt 2014). Both chimpanzees and orangutans have been observed to preferentially nest in trees known to have mosquito repellent properties (Largo et al. 2009; Samson et al. 2013). At some field sites orangutans have also been observed carrying leaves and branches from previous nests to line new nests, some of these may be branches from tree species which have mosquito repellent properties (Russon et al. 2007, 2009b; Kuze et al. 2011). Empirical testing by Stewart (2011) found that the researcher was bitten significantly less by mosquitoes and other biting insects when sleeping in an arboreal nest as opposed to sleeping on the ground. Koops et al. (2012) however in their research into the nesting habits of chimpanzees in Seringbara found no evidence to support the anti-vector hypothesis, however this is a single study and site differences in climate, predation pressures and human pressures have all been found at different sites to be significant predictors of nest site selection (Pruetz et al. 2008; Koops et al. 2012a; Last & Muh 2013; Tagg et al. 2013). However, such doubts and the difficulties that Koops et al. (2012) experienced in trapping mosquitoes as well as the lack of botanical knowledge to know whether any of the plant species at our field sites had mosquito repellent properties meant that I did not further investigate this hypothesis but I did not discount it's potential importance in nest site selection.

The other and probably most important function of nests along with improving comfort is reducing the threat of predation whilst the nest builder rests or sleeps, this works by both camouflaging the animal as it rests by shielding it from view and breaking up its silhouette with the leafy structure of a nest, secondly and most importantly, arboreal nesting reduces access for predators to approach the sleeping nest builder (Sugardjito 1983; Pruetz et al. 2008; Stewart & Pruetz 2013). Nests produced by chimpanzees have been observed to have such anti-predatory adaptations such as having escape routes (Baldwin et al. 1981; Anderson et al. 1983), building the nest near to the forest edge or over streams or gulley’s to increase the relative height of the nest (Van Lawick-Goodall 1968) and in savannah habitats building higher nests with less overhead vegetation and more clumped together as a group which could be seen as methods of reducing the ability for nocturnal predators to approach or kill an individual unseen (Baldwin et al. 1981). Further to this, chimpanzees in Issa have been found to select trees that are both taller and larger and with higher first branch heights than other suitable trees in the vicinity thereby reducing access to ground predators (Stewart & Pruetz 2013; Hernandez-Aguilar et al. 2013).

Adult orangutans and other great apes have very few natural predators due to their large body size, but they are still at risk of predation from a small number of species including large pythons (*Python reticulatus*), Sunda clouded leopards (*Neofelis diardi*), Sumatran tigers (*Panthera tigris sumatrae*) (Mackinnon 1974; Sugardjito 1983; van Schaik & van Hooff 1996; Rijksen 1978) and for the African ape species leopards (*Panthera pardus*) (Boesch 1991; Fay et al. 1995; Stewart & Pruetz 2013) and lions (*Panthera leo*) (Tsukahara 1993) are the main potential predators. However low the potential risk of predation, the potential impact predation can have upon apes and their populations would warrant taking such precautions. Orangutans along with all other apes have long life-histories, in particular they are slow to mature and reach reproductive age and have long inter-birth intervals due to the need for extended maternal care (van Noordwijk & van Schaik 2005; Jones 2011; Stewart & Pruetz 2013). This long life history of apes makes them particularly susceptible to the pressures of excessive mortality through predation and hunting due to the time required to replace lost members (Musick 1999). Therefore though the risk may be low, and building arboreal nests may expend more energy than building ground nests the effort may be worth reducing such a risk which could threaten a populations health.

Ground nesting is extremely rare in orangutans and is predominantly observed in large male orangutans and only for Bornean orangutans and is completely unheard of in Sumatra (Ashbury et al. 2015). This likely due to the greater number of ground predators in Sumatra where Sumatran tigers, dhole (*Cuon alpinus sumatrensis*) and clouded leopards are all still present, whereas clouded leopards are the only one of these three species found on Borneo (Brodie & Giordano 2013). Large adult orangutans are generally too large to be predated on by clouded leopards but juveniles are within the size category of their preferred prey. Clouded leopards have been recorded preying on proboscis monkeys (*Nasalis larvatus*) which are comparable in size to juvenile orangutans (Wilting et al. 2006; Matsuda et al. 2008). Adult orangutans however do fall into the preferred prey sizes for tigers (Hayward et al. 2012b), as such there is greater potential for predation in Sumatra with body size not offering protection as in Borneo which may explain why ground nesting is so rare in Sumatra.

The presence of large herbivores, in particular elephants may also contribute to the rarity of ground nests in Sumatra as well as Borneo. Western gorillas (*Gorilla gorilla*) in Gabon have been observed to select nest sites which minimise disturbance by elephants (*Loxodonta cyclotis*) (Tutin et al. 1995; Anderson 1998). It could be posited that avoiding disturbance by elephants which are present in both Sabah (*Elephas maximus borneensis*) and Sumatra (*E. maximus sumatrensis*) could also play a part in nest site selection as the majority of reports of ground nesting in orangutans come from Kalimantan where Bornean elephants are absent as are the ground predators found in Sumatra (Choudhury et al. 2008; Ashbury et al. 2015).

Though the how (Goodall 1962; Fruth & Hohmann 1996; van Casteren et al. 2012) and why apes build nests (Anderson 1998; Stewart et al. 2007, 2011) is relatively well studied, the factors influencing the selection of nest sites is still relatively understudied especially when comparing previous research on orangutans against the African great apes (Prasetyo et al. 2009; van Casteren et al. 2012). Orangutan nest site selection is known to be selective as certain tree species have been observed to be more preferred than others with the most common tree species not always being the one used most often for nesting (Ancrenaz et al. 2004; Prasetyo et al. 2010; van Casteren et al. 2012; Cheyne et al. 2013). One of the most widely reported aspects of orangutan nest site selection is the avoidance of nesting in fruiting trees (Sugardjito 1983; Anderson 2000; Prasetyo et al. 2009, 2012; van Casteren et al. 2012). This has been linked to both predator avoidance (Sugardjito 1983) as well as avoiding disturbance from other orangutans as well as other frugivorous species such as macaques, binturong and fruit bats (Sugardjito 1983; Anderson 1998; Prasetyo et al. 2012; Colon & Campos-Arceiz 2013) as well as biting insects such as ants (Whitten 1982).

In recent years there have been a number of studies which focused more upon nest site selection and how the structural properties of the tree may influence this. For example, van Casteren et al. (2012) investigated the mechanical design and architecture of nests and found that there was a certain amount of engineering ingenuity, technical knowledge and choice in the construction of nests as more compliant branches were used in the centre and stronger ones used in the edges which may help improve both comfort and safety. Cheyne et al (2015) investigated nest site selection in Sabangau and found that there was a selectivity for trees belonging to the *Anacardiaceae* and *Elaeocarpaceae* families. Their study also found that comfort and stability seemed to drive nest site selection more than predator avoidance with trees exhibiting properties that would provide greater stability being preferred. A significant preference for nesting in trees with buttress or stilted roots, larger than average DBH and large basal areas were found by Cheyne et al (2013). Orangutans in Sabangau were found to avoid nesting in extremely tall trees, but the height at which they built their nests was within the upper canopy (Cheyne et al. 2013). These properties help to reduce sway in the wind and provide greater nest stability (Nicoll & Ray 1996; Soethe et al. 2006). Another paper which examined nest site selection of orangutans was that by Ancrenaz et al. (2004) who studied nesting behaviours in a disturbed forest in Sabah, Malaysia. Ancrenaz et al. (2004) found that nest site selection was influenced by the forest structure and composition with nests being built in the tallest trees available. Further to this, in the most disturbed areas, nest tree reuse or trees with multiple nests were found in greater frequencies than in less disturbed sites, nest tree reuse is highly variable between study sites though there does appear to be link between disturbance levels and increased nest site reuse (Rayadin & Saitoh 2009; Kanamori et al. 2017). Similar to these studies, in this study our aim is to understand what the principal drivers of nest site selection are for Sumatran orangutans and how these may be influenced by the structural properties of the trees within the site and how changes to forest structure may then alter nest site preferences.

Understanding how human disturbance influences forest and tree structure and nest site selection is crucial as currently Indonesia is experiencing the second highest rate of deforestation amongst tropical countries. Of all the regions within Indonesia, Sumatra in particular stands out as 70% of its forested area having now been converted into plantations and agricultural lands through intensive forest clearance as of 2010 and with some Sumatran provinces having lost nearly 50% of their forest cover between 2000 and 2012 (Margono et al. 2012; Supriatna et al. 2017). Forests are being cleared for conversion to agriculture and oil palm plantations as well as being affected by the extraction of valuable timbers through both clear felling and selective logging (Hall et al. 2003; Abood et al. 2015). Selective logging has been found to be associated with more homogenous forests with lowered species richness and a more simplified vertical structure (Norris et al. 2010). The removal of larger trees in particular leads to a reduction of continuous canopy and tree density which could possibly affect the availability of good nest sites as these taller, larger trees were found to be preferentially selected as nest sites in Borneo (Ancrenaz et al. 2004a; Prasetyo et al. 2012; Cheyne et al. 2013).

Ancrenaz et al. (2004) found that an increase in disturbance and the removal of preferred nest trees increases selection pressure on the remaining potential nest trees and increases the probability that orangutans will need to reuse nest trees or build in trees which already contain nests. This in turn could lead to a change in the shape or structure of the crown through the bending, breaking and healing of branches, creation of forks and other deformities which could lead to an even greater rate of reutilisation due to the increase in these useful properties (Stewart et al. 2011). Ancrenaz et al. (2004) observed this in a highly disturbed forest in Sabah and noted an increase in the reutilisation of these altered trees by the same or different individuals which led to creation of “villages”. The increased reuse of nest sites due to these changes in crown structure which allow for easier nest creation is a form of “niche construction” and has similarly been observed in chimpanzees (Stewart et al. 2011). This increase reutilisation of nest sites and formation of villages could lead to what is normally a semi-solitary species being forced to come into contact more frequently with other individuals (Delgado & Van Schaik 2000). Furthermore, in disturbed habitats these modified trees may be highly utilised by the orangutans there and the removal of these trees may have a much more significant impact upon the orangutans through the reduction of potential nest sites when compared to selective logging in less disturbed sites. With the close proximity of our field sites but differing levels of disturbance we are able to test whether nest site reuse is influenced by disturbance levels and control for cultural and species differences in preference patterns.

As forests in Sumatra become increasingly degraded through logging the importance and need for understanding how orangutans cope with this habitat change becomes greater. Understanding and being able to quantify how changes to forest structure and composition can affect nest site selection can provide vital information for developing informed conservation strategies for orangutans. Currently much of the focus of habitat protection for great apes is focused upon the protection of important food species and generally disregards the importance of understanding the value of “quality” nest trees (Morgan & Sanz 2007). Therefore, being able to understand and quantify which trees are most important for nesting can provide information which can be implemented into conservation management plans and by land managers to protect these potentially useful nesting trees which will in turn further aid the conservation of these critically endangered apes.

A limitation of the previous papers which have investigated nest site selection is that nest trees have been compared to trees from random plots or transects across the forest which in many cases can include trees from parts of the forest where orangutans may not visit at all or are completely unlikely to use (Ancrenaz et al. 2004a; Prasetyo et al. 2012; Cheyne et al. 2013). Our aims are to investigate and determine what variables are most important in nest site selection by comparing the parameters for the nest tree against both the average forest trees as other papers have done, along with those trees within 5m of the nest tree which are of equal opportunity to be used as a nest tree, therefore providing a more appropriate comparison to understand nest site selection. As well as understanding general nest site selection our study investigated whether or how this differs with levels of human disturbance. Our field sites are a recovered forest and a recently reforested site on Sumatra (Indonesia) which will provide a comparison between both high and low levels of disturbance and allow us to better understand how orangutans cope with increased habitat fragmentation and forest loss in relation to nesting. As much of the previous studies into orangutan nesting have been conducted on Borneo, they have tended to conclude that comfort is what drives orangutan nest site selection as opposed to anti-predation, in this study we will also consider the properties of the nest trees and how these may link to both drivers.

2.1.1 Hypotheses:

- Given the different histories of each site, we expect to find significantly different forest structure with Sikundur having a higher proportion of tall trees with large DBH and large crowns.

- As the sites are expected to have significantly different forest structures, we expect the nest site selection patterns and nest trees to differ significantly between sites, with the reduced availability of potential nest sites influencing orangutan selection patterns.
- As tigers are known to be in the vicinity of our field sites (Luskin et al. 2017) we expect to find few if any ground nests at either field site.
- Furthermore, we expect to find nest sites selected that have properties that support the anti-predator hypothesis, in particular a greater preference for nesting in taller trees and trees with higher first branch heights than what is otherwise available at each site.
- Following form this point, the expected outcome from the model averaging is to find that FBH and tree height are the most influential variables in the models for predicting nest site selection.
- As Sei Betung has been reforested rather than naturally recovered we expect there to be lower diversity of tree species and thereby orangutans utilising fewer nest tree species than in Sikundur. However, we expect orangutan to be less selective of nest tree species in Sei Betung due to the reduced availability of potential nest sites.
- Finally, as the number of potential nest sites in Sei Betung should be lower than in Sikundur, we expect to find a higher incidence of nest site reuse or multiple nests built in single trees in Sei Betung than Sikundur.

2.2 Methodology

2.2.1 Study Sites

This study was conducted at two field sites; Sikundur also known as Sekundur (3°1’N, 98°02’E) and Resort Sei Betung (4°3’N, 98°07’E). Both sites lie in the east of Gunung Leuser National Park and the Leuser Ecosystem in the Langkat district of North Sumatra (Knop et al. 2004; Wich et al. 2008; Marshall et al. 2010; Hartini et al. 2017; Szantoi et al. 2017). Sikundur is an area of diverse mixed dipterocarp lowland forest that also possesses rich alluvial forest along the rivers, with part of it having been subjected to selective logging over 40 years ago (de Wilde & Duyfjes 1996; Knop et al. 2004; Priatna et al. 2006; Wich et al. 2008b). The research station in Sikundur is currently managed by the NGO SOCP (Sumatran Orangutan Conservation Programme) with field assistants conducting daily follows of orangutans for behavioural research. Sei Betung is a former illegal oil palm plantation that has been actively restored and reforested through the planting of 500,000 seedlings of 97 indigenous tree species across an area of 250 ha (Kettle et al. 2014). Sei Betung is managed by the NGO OIC (Orangutan Information Centre) who are leading the reforestation work at the site and are beginning to study the orangutans there. The two sites are approximately 9km apart but differ considerably with Sikundur still having stands of primary forest and selectively logged areas which have had over 30 years to recover

(Knop et al. 2004; Priatna et al. 2006; Marshall et al. 2009) whilst Sei Betung is nearer to the start of its recovery with replanting first began in 2007 and the complete removal of oil palms from the site in 2012 (Kettle et al. 2014). Data collection was undertaken February-August 2015 and March-September 2016.

2.2.2 Data collection

Transects were used for sampling nests and vegetation in both Sikundur and Sei Betung, 30 500m transects were conducted in Sikundur and 9 1000m transects were used in Sei Betung. Transects in Sikundur were set out using a stratified random grid with the first point being placed randomly with transects being laid on a north-south bearing using the initial point as the southern end of the first transect. The transects were then arranged around this first one being spaced at 300m intervals to the east and west and separated by 150m to the north and south. Transects were placed to ensure that none were split by the Besitang river. The transects were also placed equally according to underlying land units identified by Laumonier, 1997 which were hills, plains and alluvial, with 10 transects being placed in each land unit (see Fig 3.1). These were characterised by slope, elevation and soil profile with the plains and alluvial areas having experienced greater levels of exploitation in the past due to their greater accessibility (Laumonier 1997; Consiglio 2015; Slater 2015). Due to the disturbance that cutting new transects would bring to the Sei Betung study site nine existing transects of 1km length were used, these were 150m apart to the east and west and ran parallel to each other on a north west-south east bearing. The distances set between each parallel transect and the length of the transects was designed to prevent an overlap of observations and with the intention of optimizing the trade-off between having a large number of independent samples and ensuring that transects were long enough to minimise the potential biases due to spatial heterogeneity from such things as the clumping of orangutan nests or variation in habitat and structure along the transect (Johnson et al. 2005). Transects were cut along these lines irrespective of topography or vegetation to ensure that they adhered to the line-transect method assumption that all transects be placed randomly in respect to terrain and were able to cover a representative sample of both field sites (Buckland et al. 2001; Mathewson et al. 2008).

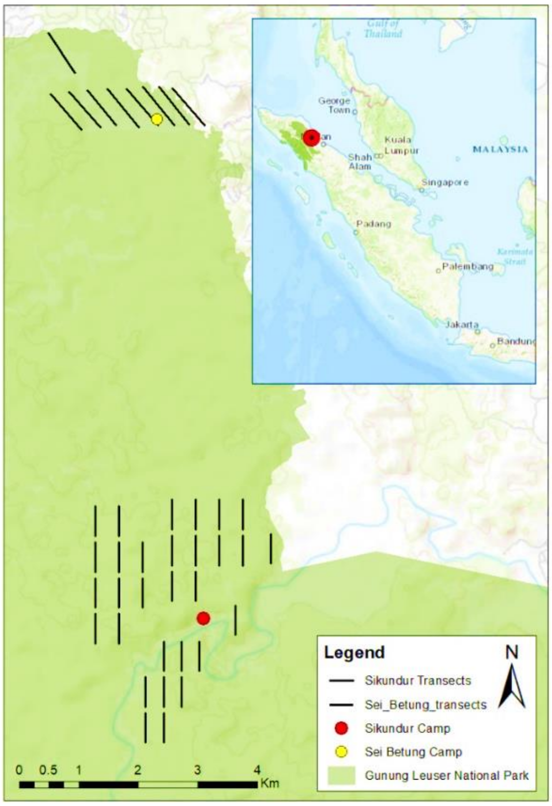

Figure 2-1. Locations of Sikundur and Sei Betung in North Sumatra. Both sites lie within the boundaries of Gunung Leuser National Park

2.2.3 Vegetation survey

Forest structure data were collected by the first author (John Abernethy), Rosanna Consiglio and Helen Slater together with field assistants from the partner NGO's (SOCP in Sikundur and OIC in Sei Betung). Data was collected across 30, 500m long transects in Sikundur and 9, 1000m long transects in Sei Betung. Forest structure transects were conducted once at each field site. Data were collected at 50m intervals along each transect using the point centre quarter method (PCQM) (Cannon & Leighton 1994; Ganzhorn et al. 1997; Ganzhorn 2002; Manduell et al. 2012). Each sampling point was split into four quadrants set at 90˚ to each other and perpendicular to the transect. For each point the nearest tree with a diameter at breast height (DBH) >10cm (measured at 1.3m above the ground) was sampled with the distance to the centre point being recorded for each quadrant. GPS points were collected at each sampling point with a Garmin GPSmap 60Cx to ensure that transects were following the correct predetermined paths and that nest transects followed this pathway accurately.

For each of the sampled trees the height of the crown was measured to the nearest 0.1m using a Nikon Forestry Pro rangefinder by aiming the laser at the highest possible leaf of the tree. Along with tree height, first branch height was also recorded by measuring to the base of where the first branch attached to the trunk using the rangefinder. These two measurements are used to obtain crown size and are also used to calculate the crown volume. Crown size was calculated using the formula:

$$Crown\ size\ (cs) = Tree\ height(TH) - First\ branch\ height(FBH)$$

The radius of the crown was measured in meters from the trunk of the tree to the edge of the crown to the North, East, South and West of the tree using a tape measure. These variables were recorded as the crown radius can be quite variable, therefore by recording from four sides this reduced any potential over or under estimation of crown area. Crown areas was then calculated using:

$$Crown\ area = \sum \frac{\pi N r^2}{4} + \frac{\pi S r^2}{4} + \frac{\pi W r^2}{4} + \frac{\pi E r^2}{4}$$

In this formula*, Nr= North radius, Sr= South radius, Wr= West radius, Er= East radius*

DBH was recorded for each tree using a tape measure and measured to the nearest centimetre. Crown shapes were classified as either spheroid, elongated spheroid, cone, upside-down cone, umbrella, bent over, broken or palms (Table 2.1)

Table 2-1 Definitions of crown shapes used in surveys adapted from Coder (2000) and Manduell et al. (2012)

CROWN SHAPE	DEFINITION
SPHEROID	Sphere shaped/ lollipop shape
ELONGATED SPHEROID	Crown with a height greater than its width and rounded ends
CONE	Cone shaped crown with a wide base that tapers to the top
UPSIDE-DOWN CONE	Crown which dove tails from the first branches, inverse of the cone (also known as inverse tripod)
UMBRELLA	Similar to spheroid or cone but lowest branches tips hang further down than the base of the branch
BENT-OVER	Tree with trunk or crown growing significantly in one direction, typified by lack of crown in one direction
BROKEN	Tree where the crown has broken off leaving either a splintered top or new growth if still alive
PALM	If the tree is a palm species there is no crown but series of large palm leaves

We were able to calculate the crown volumes more accurately than many previous studies by using the crown shapes and radii measurements. These were calculated using the following formulae:

Crown volume radii standardisation:

$$NS\,r\ (North - South\,radius) = \frac{Nr+Sr}{2}$$

$$EW\,r\ (East - West\,radius) = \frac{Er+Wr}{2}$$

$$Hr\ (Height\,radius) = \frac{h}{2}$$

Cone and upside-down cone crown volume:

$$V = \sum \frac{\pi NSr^{2}\frac{h}{3}}{2} + \frac{\pi EWr^{2}\frac{h}{3}}{2}$$

Spheroid, elongated spheroid and bent over crowns:

$$V = \frac{4}{3}\pi NSrEWrHr$$

Umbrella shape crowns:

$$V = \frac{\frac{4}{3}\pi NSrEWrHr}{2}$$

Crown connectivity was measured visually by estimating the proportion of the crown in contact or enclosed by neighbouring crowns using a four point scale; 0-25%, 26-50%, 51-75% and 76-100%, the inverse of this gave the exposure of the crown (Whitten 1982; Manduell et al. 2011; Cheyne et al. 2013). In Sei Betung all tree species were identified to the lowest identifiable taxonomic level (genus and species) by an Indonesian botanist.

2.2.4 Nest transects

Nest transects were conducted on the same transects as the vegetation transects by the first author with a team of 1-2 well trained local field assistants from the partner NGO's. Nest transects were conducted in June 2015, April 2016 and August 2016 in Sikundur and late August/September 2016 in Sei Betung, transects were walked only once per sample period. The transects were walked at a pace of no more than 1km/h. When a nest was visually located, the perpendicular distance from the transect to the centre of the nest was measured using a tape measure as this is utilised along with age of nest and decay rate to estimate nest densities which was used in Chapter 5. Along with these distances the DBH, first bole height (FBH), height of tree, crown shape, connectivity, crown radius from the trunk to the edge of the crown for the north, south, east and west of the tree were recorded along with support availability using the same methodology as vegetation data. Nest height was recorded using the Nikon Forestry Pro laser rangefinder to the nearest 0.2m with measurements taken from the base of the nest.

Nests were placed into age classes through consensus between the lead research and trained observers when uncertain, these classes were reflective of the decay rate. The classes were: 1- fresh leaves, still green; 2- mix of green and brown leaves; 3- all leaves turned brown and some holes forming; and 4- all leaves gone and nest falling apart (van Schaik et al. 1995; Hashimoto 1995; Russon et al. 2001; Felton et al. 2003; Johnson et al. 2005; Spehar et al. 2010). On subsequent transects any old nests which had been previously recorded were omitted, these were identified by the age of the nest and proximity to a GPS point for a prior nest. Nest position was also recorded following the standard methodology set out by the University of Zurich's Department of Anthropology (Orangutan Network 2015) and used in Prasetyo et al. 2012; Rayadin & Saitoh 2009. Position 1- at the base of the branch and close to the main stem; Position 2- at the end of a branch; Position 3- top of the tree crown; Position 4- using the branches of two different trees weaved together (there were no Position 0 which are nests that are found on the ground) (see Fig 1.3).

All nest tree species were identified by trained field assistants. As well as nest trees, all trees within a 5m radius of the nest tree were recorded. These were used to provide a control against the nest tree and to understand if the difference is just for the nest tree and the average forest or whether the nest tree also differed from the trees that were its direct neighbours. For each of these trees the distance to the nest tree, direction with a compass, DBH, first bole height, tree height, crown shape, connectivity and in 2016 field season the species was also recorded. Separate analysis was conducted to compare between nest trees that help single nests or multiple nests to determine why those trees may have contained more than one nest.

2.2.5 Data analysis

Unequal variance *t*-tests also known as Welch's t test, Satterwaite or Welch-Satterwaite tests were used to determine whether there was a significant statistical difference between the continuous structural variables for nest and non-nest trees for each site along with support availability. This test was used due to the non-normal distributions and unequal variances of the data and was recommended by Moser et al. (1989) and Ruxton (2006) as it performs similarly well to the Student's *t*-test, and the power of the unequal variance *t*-test is similar to the Student's even when variances are equal (Moser et al. 1989; Moser & Stevens 1992; Coombs et al. 1996; Ruxton 2006) but is much better at controlling for both Type I and Type II errors and when variances are unequal it outperforms the Mann-Whitney U test (in terms of controlling Type I errors) (Zimmerman & Zumbo 1993; Ruxton 2006).

Generalised linear models and generalised linear mixed effects models were run in R using the lme4 (Bates et al. 2015), car (Fox & Weisberg 2011), lattice (Deepayan 2008) and Matrix (Bates & Maechler 2017) packages. These models were run to understand the relationships between nest and non-nest trees, nest trees and trees within 5 metres of nest trees and between single and multiple nest trees. Generalised linear mixed effects models with binomial error structures were initially used to determine whether field site had any significant effect upon the overall model as a random effect by comparing against a simpler binomial generalised linear model and using the AIC (Akaike Information Criterion) scores and Likelihood-ratio ANOVA chi square tests to determine whether there was a significant difference between the two models and if the random effect had any significant effect upon the model as suggested by Bolker et al. (2009) and Kain et al. (2015).

All model iterations were run including an intercept only model using the dredge function of the MuMIn (Barton 2018) package in R, this package was also used for all model averaging calculations. The models were ranked by their AICc (corrected Akaike Information Criterion) scores which compensate for small sample sizes. A subset of these models was then extracted using the maximum delta ∆AICc values (which is the difference between the AICc of each model from the best performing model) that are <2. This threshold was used as models with AICc values <2 all have substantial support and perform equally well (Burnham et al. 2002; Burnham & Anderson 2004). From this subset of best performing models' parameter estimates were averaged and parameters were weighted by the proportion of models that the parameter was present in. These weights allow for the relative importance of each parameter to be assessed. Plots from the model averaging were produced using the following packages in R; ggplot2 (Wickham 2009), snakecase (Grosser 2018), plyr (Wickham 2011), sjlabelled (Lüdecke 2018a), sjPlot (Lüdecke 2018b) and sjmisc (Lüdecke 2018c).

Selectivity index

For tree height and DBH in categories, support availability, tree species and food tree, Jacobs D value was used as an index to determine if any of the categories were used preferentially or avoided. This index has been used in a number of previous studies to determine nest tree selection in Borneo (Cheyne et al. 2013), canopy selection (Cannon & Leighton 1994) and support use (Hunt et al. 1996; Warren 1997; Manduell et al. 2012). This index standardises the relationship between resource use and availability to numbers between 1 and -1. In this instance +1 is indicative of complete preference and -1 is a complete avoidance of it, 0 is neutral and suggests that the resource is used in direct relation to its relative abundance.

Jacobs D was calculated using:

$$Jacobs\ D = \frac{r - p}{(r + p - 2rp)}$$

$r =$ relative use of a resource (number of nest trees in each data class) as a proportion

$p =$ relative availability of a resource (number of trees for each class available in the habitat) as a proportion

2.3 Results

A total of 199 nests were recorded across both sites with 153 found in Sikundur and 45 in Sei Betung. In total 1200 trees were measured on vegetation transects in Sikundur and 720 in Sei Betung, 62 trees were recorded within 5m of nest trees in Sei Betung and 598 were recorded and measured in Sikundur. However, trees with broken crowns and palms were removed from the analysis as they were significant outliers due to both their rarity and unusual crown shapes which heavily skewed the results in regards to crown volumes and crown size.

2.3.1 Site differences in forest trees versus nest trees

When comparing between Sikundur and Sei Betung all forest structure variables were found to differ significantly with all variables except of crown area being found to be significantly larger in Sikundur than Sei Betung (Table 2.2). However, when comparing nest trees between sites significant differences were only found for tree height and FBH which were both again found to be larger in Sikundur than what was found in Sei Betung (Table 2.2). Comparisons between nest trees and average forest trees for each site showed significant differences for all variables except for first branch height (FBH) (Table 2.3). In all canopy structure variables except FBH nest trees were found to be significantly larger than non-nest trees, with FBH showing no significant difference but were higher for non-nest trees than nest trees (Table 2.3). See Figures S1-6 in Appendix I for boxplots further showing the differences between nest and non-nest trees at each site for each variable.

Table 2-2 Comparison between sites of tree structure characteristics for nest and average forest trees (non-nest trees) using Welch's t test

DBH= Diameter at Breast Height, FBH= First Branch Height

Tree type	*Variables*	*Mean*		*Variance*		*Welch's t*		
		Sei Betung	**Sikundur**	**Sei Betung**	**Sikundur**	**t***	**df**	**P**
Nest		*n= 45*	*n=153*	*n= 45*	*n=153*			
	DBH (cm)	21.57±1.63	25.22±0.98	119.32	138.38	1.93	77	0.057
	FBH (m)	4.33±0.28	9.8±0.33	3.52	15.29	12.96	155	**<0.001**
	Tree height (m)	11.26±0.5	17.76±0.46	11.09	31.6	9.67	124	**<0.001**
	Crown size (m)	6.93±0.42	7.96±0.38	7.58	21.37	1.86	123	0.065
	Crown area (m^2)	62.53±7.39	53.61±2.98	2511.24	1351.86	-1.11	59	0.272
	Crown volume (m^3)	219.21±51.03	263±25.14	68772.84	105557.1	0.93	88	0.355
Non-nest trees		*n=720*	*n=1200*	*n=720*	*n=1200*			
	DBH (cm)	16.98±0.31	21.55±0.44	67.49	236.67	8.471	1896	**<0.0001**
	FBH (m)	4.1±0.12	9.48±0.15	10.45	26.65	28.058	1915	**<0.0001***
	Tree height (m)	9.21±0.16	14.9±0.19	18.24	41.31	22.966	1907	**<0.0001**
	Crown size (m)	5.11±0.1	5.42±0.11	6.72	14.4	2.163	1887	**0.0306**
	Crown area (m^2)	36.35±1.22	36.7±1.47	1072.7	2607.37	0.180	1910	0.8568
	Crown volume (m^3)	94.81±7.54	152.76±14	40716.03	235283.19	3.628	1749	**0.0003**

Table 2-3 Within site comparisons of tree structure characteristics of nest and non-nest trees for Sikundur and Sei Betung using Welch's t test (Satterwaite's t test)

DBH= Diameter at Breast Height, FBH= First Branch Height

Field site	*Variables*	*Mean*		*Variance*		*Welch's t*		
		Nest	**Non-nest**	**Nest**	**Non-nest**	**t Stat**	**df**	**P**
Sei Betung		*n= 45*	*n=720*	*n= 45*	*n=720*			
	DBH (cm)	21.57±1.63	16.98±0.31	119.32	67.49	2.77	47	**0.008**
	FBH (m)	4.33±0.28	4.1±0.12	3.52	10.45	0.75	62	0.458
	Tree height (m)	11.26±0.5	9.21±0.16	11.09	18.24	3.93	53	**<0.001**
	Crown size (m)	6.93±0.42	5.11±0.1	7.57	6.72	4.32	49	**<0.001**
	Crown area (m^2)	62.53±7.39	36.35±1.22	2511.24	1072.7	3.46	46	**0.001**
	Crown volume (m^3)	219.21±51.03	94.81±7.54	68772.84	40716.03	3.13	47	**0.003**
Sikundur		*n= 153*	*n=1200*	*n= 153*	*n=1200*			
	DBH (cm)	25.21±0.98	21.55±0.44	138.38	236.67	3.49	224	**<0.001**
	FBH (m)	9.8±0.33	9.48±0.15	15.29	26.65	0.92	226	0.357
	Tree height (m)	17.77±0.46	14.9±0.19	31.6	41.31	5.82	209	**<0.001**
	Crown size (m)	7.96±0.38	5.42±0.11	21.37	14.4	6.53	179	**<0.001**
	Crown area (m^2)	53.61±2.98	36.7±1.47	1351.86	2607.37	5.1	234	**<0.001**
	Crown volume (m^3)	263±25.14	152.76±14	105557.1	235283.19	3.7	248	**<0.001**

The random effect of field site was tested by using a generalised linear mixed effects model and a generalised linear model and then using a Likelihood-ratio ANOVA chi squared test to test whether the random effect of field site had a significant effect or not. Field site had no statistical significant impact upon the model; X^2_{df1}=2.803, P=0.075. Furthermore, the differences in $R^2_{GLMM(m)}$ (marginal R^2) and $R^2_{GLMM(c)}$ (condition R^2) as described by Nakagawa & Schielzeth (2013) for the mixed effects model showed little difference suggesting that the majority of the variance was explained by the fixed effects in the model ($R^2_{GLMM(m)}$= 0.133, $R^2_{GLMM(c)}$= 0.15). Due to this lack of significance the random effect of field site was discarded and a simpler generalised linear model with a binomial distribution was used (Table 4.). FBH and crown volume were removed from the models due to multicollinearity with both having VIF scores >5. Using the dredge function of the MuMIn package all combinations of the remaining variables were tested as candida to determine which variables were most influential in differentiating nest trees from non-nest trees. None of the other 63 candidate models were found to be within 2 AIC units (ΔAICc <2) of the top performing model which was also the full model containing all of the fixed effects (AICc= 1233.1, ΔAICc=0, w=0.406) (Table 2.5.). This result lends further evidence to what was found in the initial analysis that nest and non-nest trees differ significantly in both sites for most tree architecture variables. The null model performed significantly worse than the full model and was the second worst performing model overall with a ΔAICc score of 83.27 (Table 3.5.).

Table 2-4 Anova chi square test of full models to test the effect of field site as a random effect

Model	*Df*	*AIC*	*BIC*	*logLik*	*deviance*	*Adj R^2*	*Chi sq*	*Chi df*	*Pr (>Chisq)*
Tree~Tree.height+DBH+Crown.size+Crown.area+Crown.shape +Connectivity	13	1233.1	1306.5	-603.48	1207	0.0790	-	-	-
Tree~Tree.height+DBH+Crown.size+Crown.area+Crown.shape +Connectivity+(1|Field.site)	14	1231.8	1311	-601.89	1203.8	0.1023	3.180	1	0.075

Table 2-5 Top candidate models with ΔAICc <2 and null model for the comparison between nest trees and average forest trees

Model	*Adj R^2*	*df*	*logLik*	*AICc*	*ΔAICc*	*weight*
Tree~Tree.height+DBH+Crown.size+Crown.area+Crown.shape+Connectivity (Full model)	0.107	13	-603.485	1233.1	0	0.406
Null model	0	1	-657.203	1316.4	83.27	0

As only one candidate model was found to have an ΔAICc score <2 model-averaging was unnecessary. Parameter estimates from the top performing model (Table 2.6.) lend further weight to the initial findings and show that of all the parameters, crown size has the greatest influence on the interaction and is the most important factor in nest site selection for Sumatran orangutans when comparing against average forest trees (β= 0.127, SE= 0.024, P=<0.001). Crown shape and DBH (β= -0.025, SE= 0.009, P=0.009) were also highly important having P values <0.01. Cone and upside-down cone shaped crowns were found to be the most significantly crown shapes in the model (C shaped crown: β=1.659, SE=0.557, P= 0.003, UC shaped crown: β=1.445, SE=0.55, P=0.009) whereas umbrella and elongated spheroid crowns were non-significant (P >0.05). These results also show that tree height and crown area may be less important in nest site selection in comparison to the other variables, in particular crown size though both tree height and crown area were still significant variables (P <0.05). Log likelihood and distributed chi square statistics suggest that the full model is reliable; chi= 107.44, 12df, P=<0.001. Trees with higher connectivity were also found to be more significant with trees in the connectivity categories >50% both having P values <0.05 whilst connectivity 25-50% had P of 0.092 showing that these less connected trees are less significantly used.

Table 2-6 Parameter estimate and standard errors for the variables from the top performing model for comparing between nest and average forest trees.

Crown shape classes: C= cone shaped, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM=Umbrella

Parameters	*Estimate*	*Std Error*	*Z value*	*Pr(>|z|)*	*2.5% CI*	*97.5% CI*
Intercept	-5.462	0.679	-8.044	**<0.001**	-6.94	-4.246
DBH	-0.025	0.009	-2.632	**0.009**	-0.044	-0.007
Tree height	0.039	0.019	2.102	**0.036**	0.003	0.075
Crown area	0.005	0.002	2.502	**0.012**	0.001	0.009
Crown size	0.127	0.024	5.293	**<0.001**	0.08	0.175
Connectivity 25-50	0.777	0.461	1.686	0.092	-0.066	1.766
Connectivity 50-75	0.906	0.436	2.445	**0.014**	0.123	1.858
Connectivity 75-100	1.06	0.433	2.502	**0.012**	0.284	2.008
Crown shape C	1.659	0.557	2.979	**0.003**	0.673	2.911
Crown shape ES	1.044	0.581	1.798	0.072	-0.006	2.329
Crown shape S	1.272	0.53	2.398	**0.016**	0.354	2.485
Crown shape UC	1.445	0.55	2.627	**0.009**	0.477	2.688
Crown shape UM	0.846	0.65	1.302	0.193	-0.396	2.226

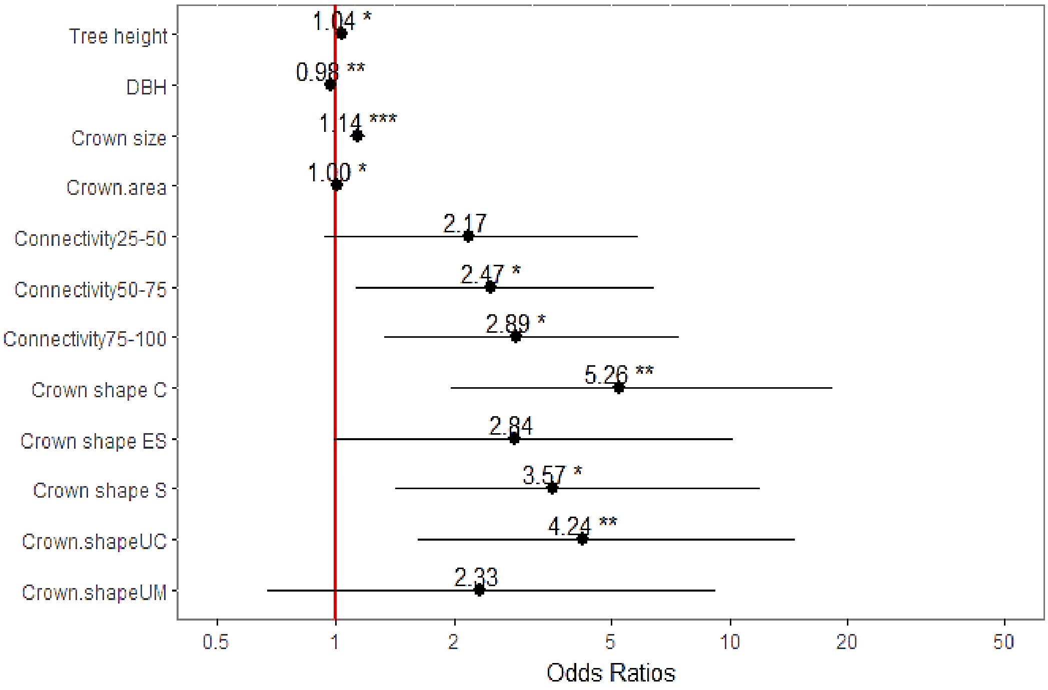

Figure 2-2 Forest plot of the log odds ratios for the parameter estimate of the top performing GLM indicating the difference between nest and non-nest trees. The red vertical line at 1 is the vertical intercept denoting no effect.

*Significance levels: * = <0.05, **= <0.01, ***= <0.001*

Crown shape categories: C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

The forest plot of the estimates in Figure 2.2 shows that crown size is again the most significant variable, however it also reveals that DBH, cone shaped and upside-down cone shaped crowns are also highly significant predictors for predicting between nest and average forest trees with P values <0.01. Crown area, tree height, spheroid crowns and connectivity >50% were all found to also have significant effects on the log odds of whether a tree is a nest tree or average forest tree (P= <0.05) whilst connectivity scores <50%, elongated spheroid and umbrella shaped crowns all showed no significant effect.

The marginal effects in Figures 2.3B, 2.3C and 2.3D show that there is a positive relationship between size and the probability of being a nest tree for tree height, crown size and crown area. A positive relationship can also be seen in connectivity (Fig 2.3F.), with increasing connectivity there is a greater probability of it being a nest tree, though the increase between 50-75% connectivity and 75-100% connectivity is less significant suggesting that increasing connectivity over 75% has less effect than it does when connectivity is >50%. Figure 2.3E displays the increased likelihood of cone, spheroid and upside-down cone shaped crowns being nest trees and that bent-over trees have a significantly lower probability of being a nest tree than any other crown shape suggesting these may be avoided. DBH however in Fig 2.3A shows that there is a negative relationship between DBH and the probability of being a nest tree with smaller trees having a greater probability of being a nest tree than larger ones.

Increases in crown size and crown area have the greatest influence upon the probability of being a nest tree whilst the scale of influence of DBH is relatively small in comparison.

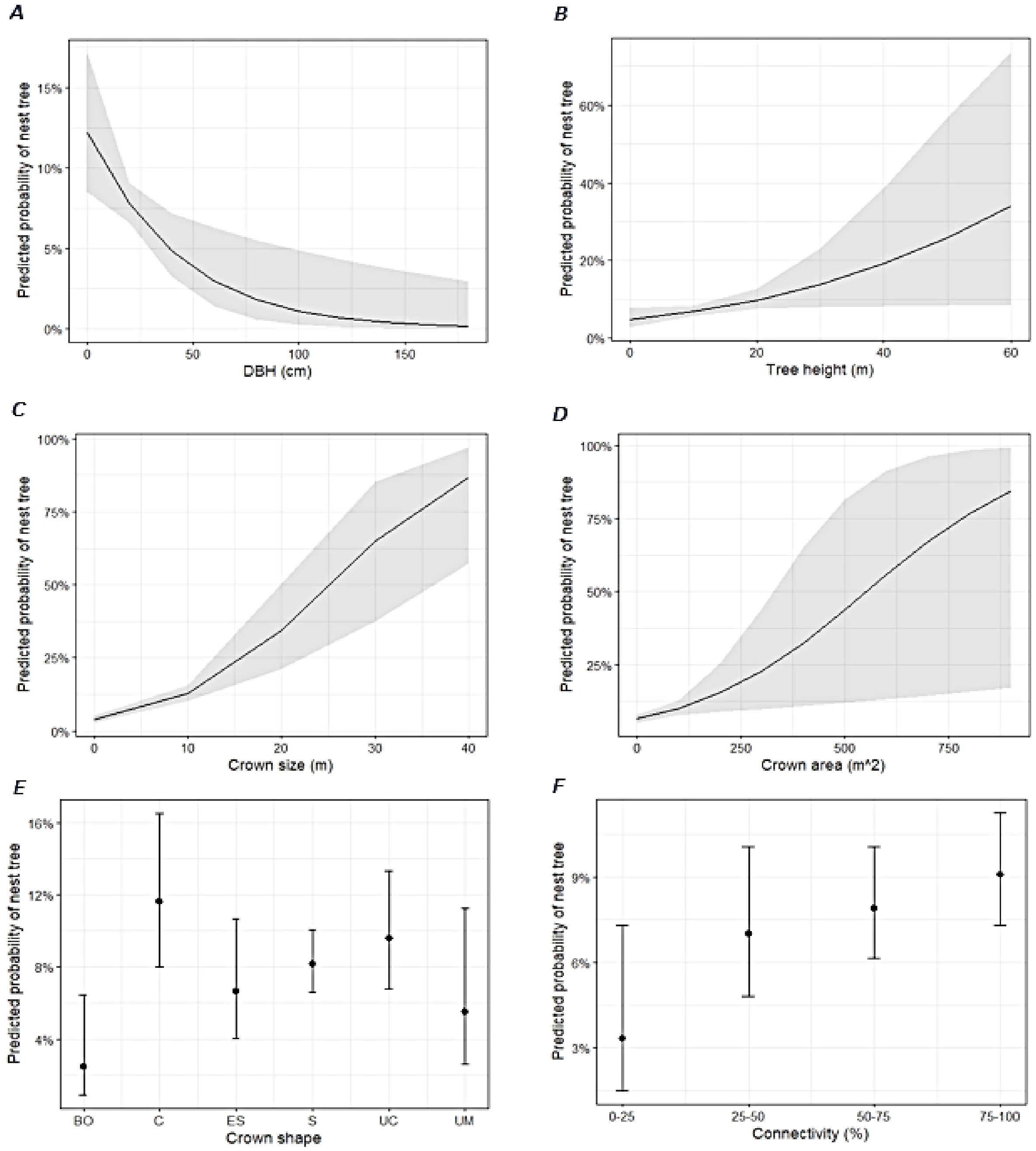

Figure 2-3 Predicted probabilities for DBH (A), Tree height (B), Crown size (C), Crown area (D), Crown shape (E) and Connectivity (F) for the best fitting model of nest tree against average forest tree with the lines denoting the predicted probability of a tree holding an orangutan nest/ The closer a line or point is to 100% the greater the probability of being a nest tree, the closer to 0% a greater probability of being a non-nest tree

Crown shape categories: BO= Bent-Over, C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

Using Jacob's D value of selectivity, the use of a resource relative to its abundance can be measured and visualised. In Figure 2.4 the results of this are presented for Sikundur and Sei Betung. As predicted by the models an increasing rate of preference is observed for DBH, tree height, crown size and crown area. However, the Jacob's D values show that there is actually an avoidance of the extreme values i.e. saplings and emergent trees. Crown shape also follows the predictions of the model with cone and upside-down cone shaped crowns being most preferred and spheroid crowns being used in equal amounts to their availability as both are relatively abundant at each field site whilst bent-over crowns are highly avoided within Sei Betung (Jacob's D -0.65) and Sikundur (Jacob's D -0.55). Connectivity reflects the models for nests in Sikundur however in Sei Betung there is a greater preference for trees in the 25-50% category and a strong avoidance of those >75%. Nests in Sikundur follow the expected pattern with trees with connectivity <50% highly avoided and those with connectivity >50% preferred.

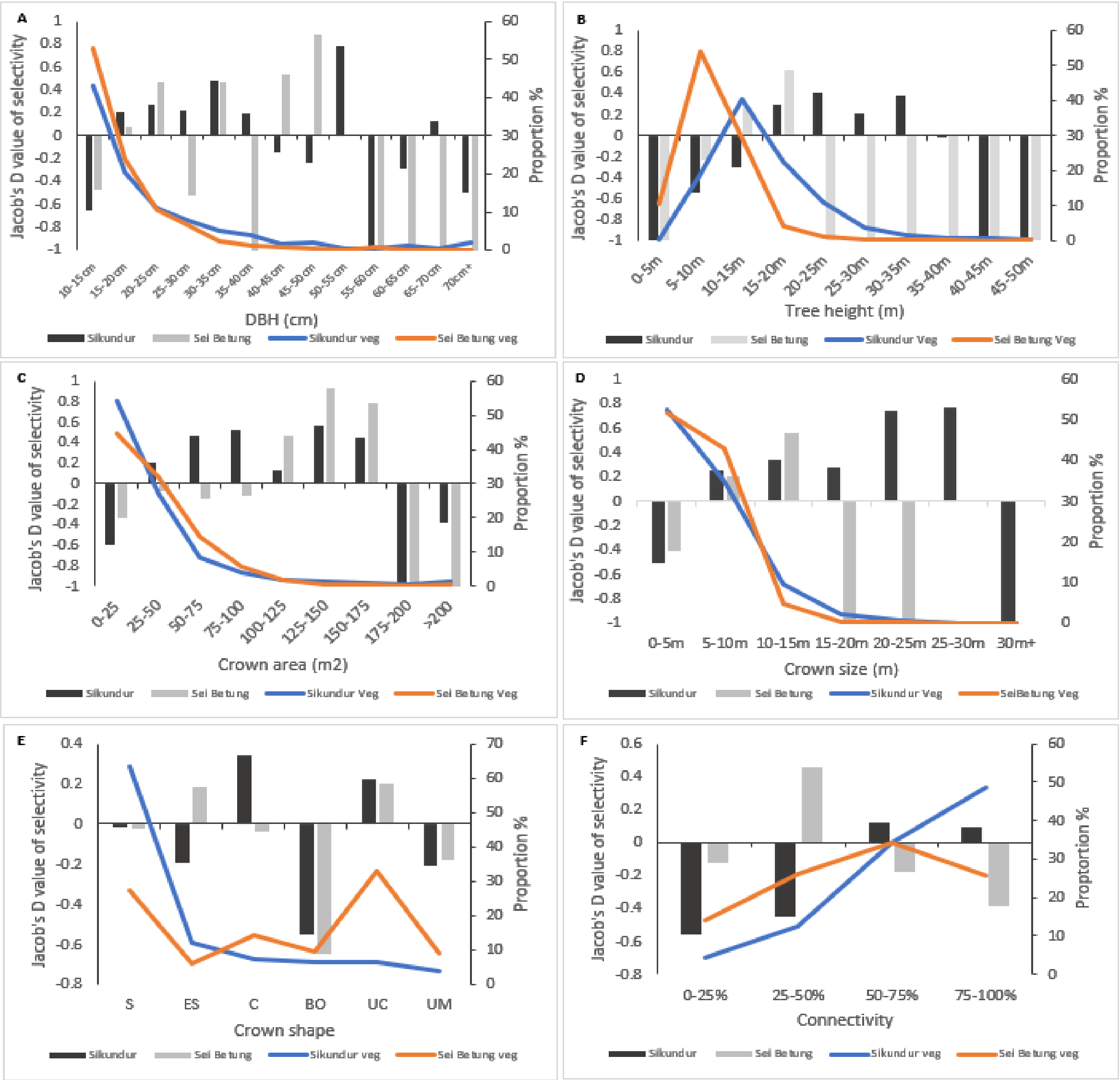

Figure 2-4 Jacob's D values of selectivity for DBH (A), Tree height (B), Crown size (C), Crown area (D), Crown shape (E), Connectivity (F) and the proportions of each size class for average forest trees in Sikundur and Sei Betung shown through the line graphs

Crown shape categories: BO= Bent-Over, C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

2.3.2 Trees in the close vicinity of the nest (<5m)

As with the comparison of nest trees and average forest trees, nest trees were found to be significantly larger than those within 5m radius for all variables except for DBH in Sei Betung and FBH in both sites (Table 2.7). When comparing between sites as was noted in the previous section, nest trees in Sikundur have significantly higher FBH (first branch height) and tree heights than those in Sei Betung, whilst DBH and crown size were found to show no significant difference (Table 2.8). For trees within 5m radius of nest trees trees all variables except crown size were significantly larger in Sikundur than Sei Betung (Welch's t=-1.9, df=87, P=0.061).

Table 2-7 Comparison of nest trees and trees found within 5m radius of the nest tree using Welch's t test

Field site	*Variables*	*Means*		*Variance*		*Welch's t*		
		Nest	**Within 5m**	**Nest**	**Within 5m**	**t Stat**	**df**	**P**
Sei Betung		*n= 45*	*n=61*	*n= 45*	*n=61*			
	DBH (cm)	21.57±1.63	17.64±1.19	119.32	86.40	-1.95	89	0.055
	FBH (m)	4.33±0.28	5.02±0.38	3.52	8.84	1.46	102	0.147
	Tree height (m)	11.26±0.5	9.76±0.41	11.42	10.33	2.326	93	**0.022**
	Crown size (m)	6.93±0.42	4.74±0.32	7.82	6.28	4.21	90	**<0.001**
Sikundur		*n= 153*	*n=598*	*n= 153*	*n=598*			
	DBH (cm)	25.65±0.98	21.84±0.63	138.38	233.34	2.96	297	**0.003**
	FBH (m)	9.8±0.33	9.82±0.2	15.29	23.63	-0.06	285	0.955
	Tree height (m)	17.77±0.46	15.23±0.26	31.6	39.81	4.85	259	**<0.001**
	Crown size (m)	7.96±0.38	5.41±0.15	21.37	12.71	6.37	201	**<0.001**

Table 2-8 Comparison between sites for nest and non-nest trees found within a 5m radius of the nest trees (within 5m) using Welch's t test

Tree type	*Variables*	*Means*		*Variance*		*Welch's t*		
		Sei Betung	**Sikundur**	**Sei Betung**	**Sikundur**	**t***	**df**	**P**
Nest		*n= 45*	*n=153*	*n= 45*	*n=153*			
	DBH (cm)	21.57±1.63	25.22±0.98	119.32	138.38	1.93	77	0.057
	FBH (m)	4.33±0.28	9.8±0.33	3.52	15.29	12.96	155	**<0.001**
	Tree height (m)	11.26±0.5	17.77±0.46	11.09	31.6	9.67	124	**<0.001**
	Crown size (m)	6.93±0.42	7.96±0.38	7.58	21.37	1.87	123	0.065
Within 5m		*n=61*	*n=598*	*n=61*	*n=598*			
	DBH (cm)	17.64±1.19	21.84±0.63	86.4	233.34	3.13	97	**0.002**
	FBH (m)	5.02±0.38	9.82±0.2	8.84	23.63	11.18	96	**<0.001**
	Tree height (m)	9.76±0.41	15.23±0.26	10.33	39.81	11.26	115	**<0.001**
	Crown size (m)	4.74±0.32	5.41±0.15	6.28	12.71	-1.9	87	0.061

As with average forest trees the random effect of field site was assessed for trees within 5m of nest trees. Unlike with average forest trees, field site was found to be a significant factor using an ANOVA chi square test finding a result of; X^2_{df1}= 118.52, P=<0.001 (Table 2.9.). These results support the initial analysis of the variables separately using Welch's t test which suggested that the sites differed highly. Due to its significance, field site was kept within the model and the following results are from the generalised linear mixed effects model using this random effect. FBH and crown volume were again removed from the models due to multicollinearity and vif scores >5. Two candidate models were identified based on ∆AICc scores <2 (Table 2.10.). The best candidate model contained three fixed effects; crown shape, crown size and DBH and had a much greater weight than the other models; 0.503 compared to 0.195 which suggests that this model is likely to be the best at explaining the interaction as it accounts for 50.3% of the variance. The null model and full model were significantly outperformed by these candidate models and highlight the importance of the parameters within the best candidate models. Connectivity was not a part of any of the candidate models suggesting that this has little importance in nest site selection when comparing against trees within the immediate vicinity of the nest tree.

Table 2-9 Assessment of the importance of field site as a random effect in the modelling of the interaction between nest trees and trees within 5m of nest trees

Model	*Df*	*AIC*	*BIC*	*logLik*	*deviance*	*Adj R^2*	*Chi sq*	*Chi df*	*Pr (>Chisq)*
Tree~Tree.height+DBH+Crown.size+Connectivity +Crown.shape	12	839.71	896.68	-407.85	815.71	0.1801	-	-	-
Tree~Tree.height+DBH+Crown.size+Connectivity+ Crown.shape+(1|Field.site)	13	723.19	784.9	-348.59	679.19	0.3529	118.52	1	<0.001

Table 2-10 Top candidate models based on ⍰AICc scores <2 for nest trees vs trees within 5m of the nest tree

Model	*Adj R^2*	*df*	*logLik*	*AICc*	*delta*	*weight*
Tree~Crown.shape+Crown.size+DBH	0.3517	9	-349.036	716.3	0	0.503
Tree~Crown.shape+Crown.size+DBH+Tree.height	0.3519	10	-348.961	718.2	1.9	0.195
Full model	0.3529	13	-348.593	723.6	7.33	0.013
Null model	0.2452	2	-386.47	777	60.67	0

The model-averaged parameter estimates for the candidate models show that the parameters which have the greatest influence upon nest site selection are crown size (β=0.191, SE= 0.03, z value= 6.36 P= <0.001) and upside-down cone shaped crowns (β=1.843, SE= 0.69, z value= 2.67, P=0.008) (Table 2.11.). This suggests that there may be a selection for upside-down cone shaped trees and for those with larger crown sizes. DBH was also highly significant as a variable (β=-0.017, SE= 0.01, z value= 1.98, P= 0.048) the β estimate for DBH suggests that the DBH for nest trees are smaller than those of the trees within 5m of them. When relative importance is considered, crown size, crown shape and DBH are the most important variables in differentiating between nest trees and those within 5m of them, whereas tree height is relatively unimportant with a value of 0.28 as it only appeared in the second-best performing model.

Table 2-11 Model averaged parameter estimates and relative importance for the top candidate models for nest tree vs tree within 5m

Crown shape classes: C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

Parameters	*Estimate*	*Std Error*	*Adj SE*	*Z value*	*Pr(>|z|)*	*RI*	*2.5% CI*	*97.5% CI*
Intercept	-2.712	4.822	4.829	0.562	0.574	-	-12.176	6.751
Crown size	0.191	0.030	0.030	6.363	**<0.001**	1	0.132	0.249
Tree height	0.003	0.014	0.014	0.195	0.845	0.28	-0.040	0.060
DBH	-0.017	0.008	0.008	1.978	**0.048**	1	-0.033	0.000
Crown shape C	1.241	0.653	0.653	1.899	0.058	1	-0.040	2.522
Crown shape ES	0.180	0.681	0.682	0.264	0.792	""	-1.156	1.517
Crown shape S	1.081	0.614	0.615	1.759	0.079	""	-0.124	2.287
Crown shape UC	1.842	0.689	0.690	2.669	**0.008**	""	0.489	3.194
Crown shape UM	0.482	0.812	0.813	0.593	0.553	""	-1.112	2.077

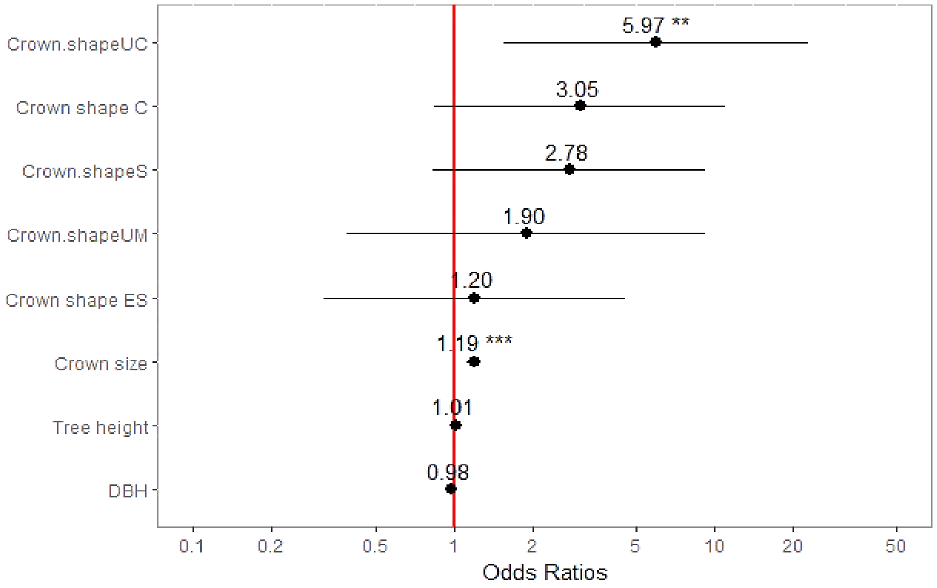

Figure 2-5 Forest plot of the odds ratios of parameters from the top 3 candidate models of the multi-model inference for the interaction between nest trees and non-nest trees found within 5m radius of the nest tree

*Significance levels: * = <0.05, **= <0.01, ***= <0.001*

Crown shape categories: C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down cone, UM= Umbrella

The forest plot of the odds ratios for the parameter estimates of the top candidate models (Fig 2.5.) further supports the previous results showing that crown size and upside-down cone shaped crowns have the greatest impact upon the models. Figures 2.6a, 2.6b and 2.6c show that similar to what was observed with average forest trees, increases in size of DBH, tree height and crown size led to increased probability of it being a nest tree. The marginal effects of crown shape in Figure 2.6d further display the significant preference for building nests within upside-down cone and cone shaped crowns and further shows how rarely bent-over crowns are used for nest sites.

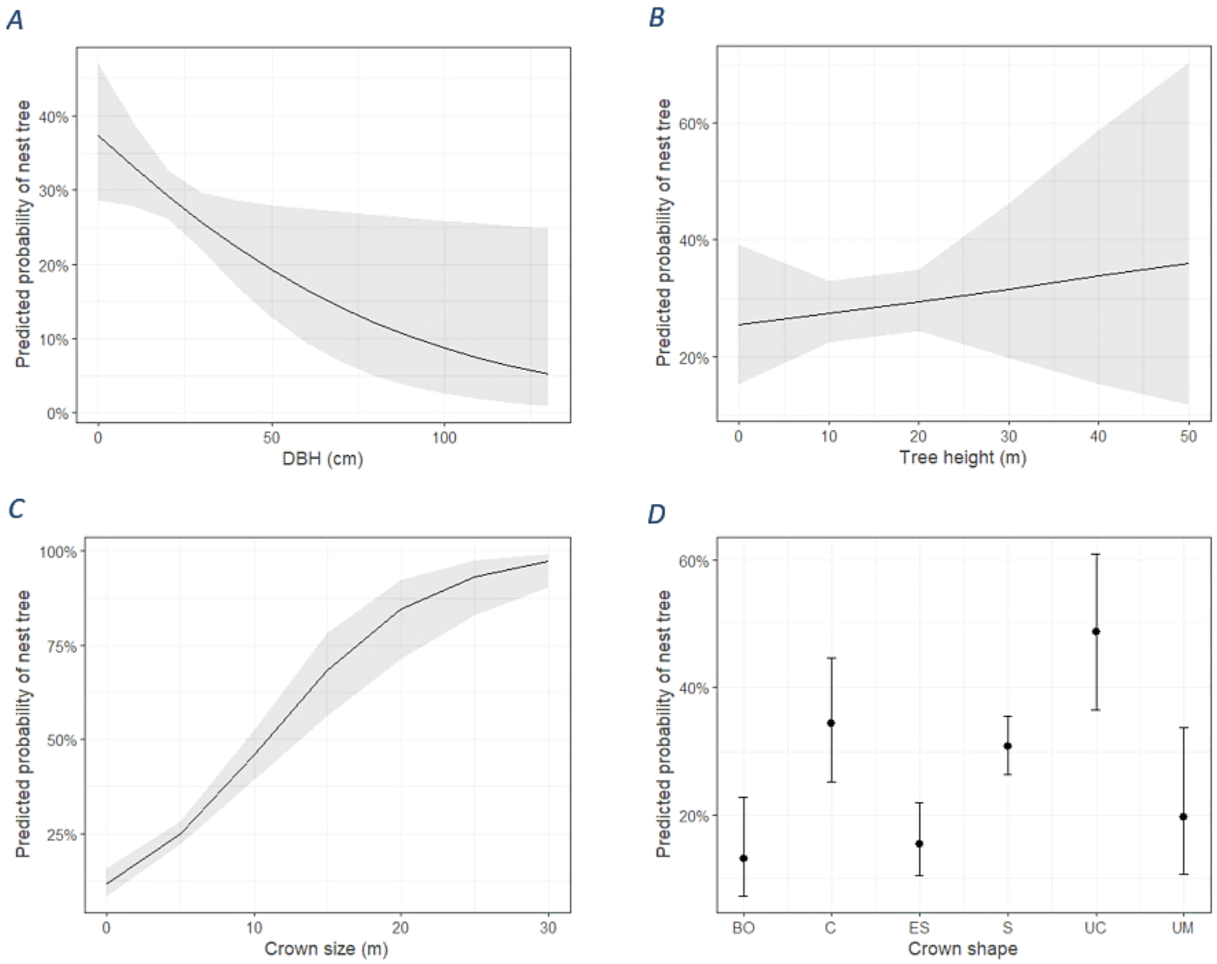

Figure 2-6 Marginal effects plots of DBH (A), Tree height (B), Crown size (C) and Crown shape (D) for the model averaged parameters of the best candidate models determined through model averaging and ΔAICc scores <2 for the interaction of nest trees and those within 5m radius of the nest tree. The plots show the predicted probability of a tree holding an orangutan nest based upon each variable.

Crown shape categories: BO= Bent-over, C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

The Jacob's D values of selectivity for nests compared to the trees within 5m (Fig 2.7.) show similar patterns of selectivity as was observed with average forest trees however, a greater level of selectivity can be observed. Tree height shows a normal bell curve shape in Sikundur with the highest preference still being above the mean whilst in Sei Betung preference is highly selective with only one size class showing a preference rather than avoidance which was trees in the 15-20m height range and showed a highly significant preference value of 0.83. Crown size displays a positive trend of increased preference associated with an increase in crown size and suggests that this is a particularly important variable for nest site selection. Bent-over and broken crowns as well as palms have all been found to be highly avoided as nest sites by orangutans. Upside-down cone shaped crowns were found to be significantly preferred as nest sites in Sikundur and showed a lower rate of preference in Sei Betung which is likely due to their greater availability at that site. Spheroid crowns were more highly preferred in Sei Betung and similar to upside-down cones in Sei Betung show a lower rate of preference in Sikundur likely due to their greater availability at that site. Cone shaped crowns showed no significant levels of preference or avoidance in each site.

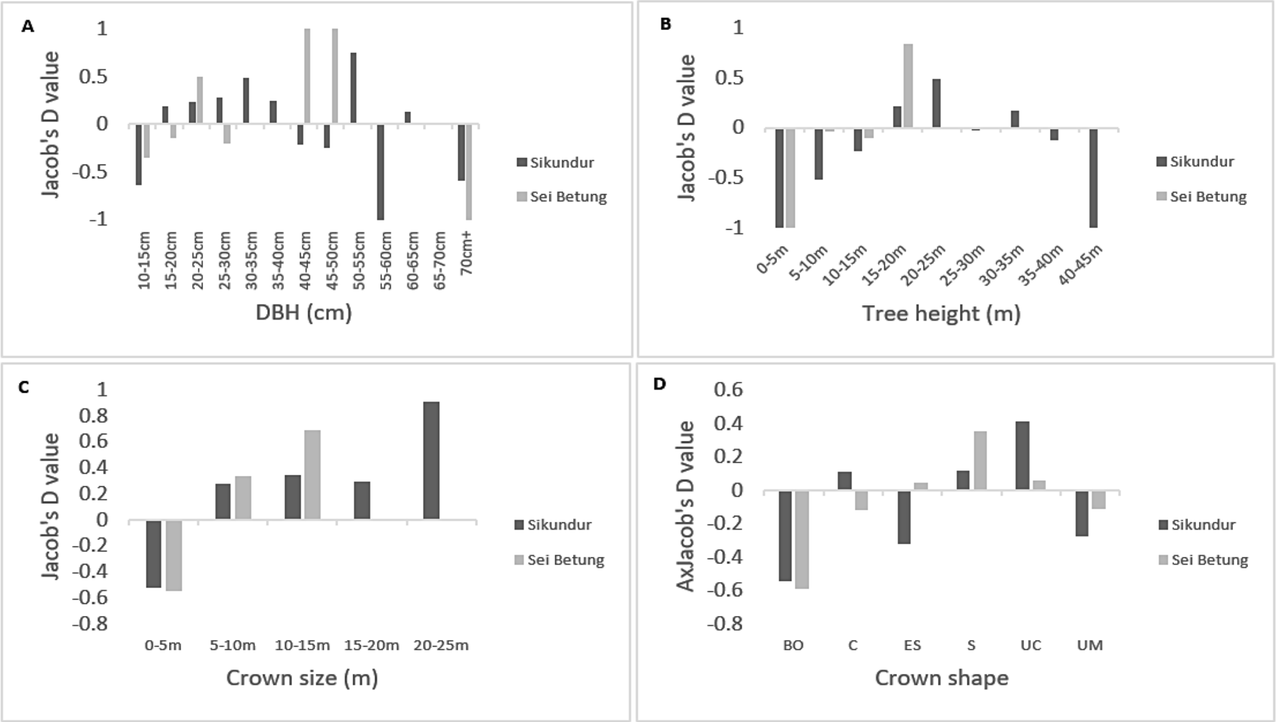

Figure 2-7 Jacob's D values for selectivity for the variables; DBH (A), Tree height (B), Crown size (C) and Crown shape (D) for nest trees in Sei Betung and Sikundur when compared against trees within 5m of the nest tree.

Crown shape categories: BO= Bent-over, C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down Cone, UM= Umbrella

2.3.3 Tree species

When comparing tree species within 5m radius of the nest tree between sites, 43 species were recorded in Sikundur and 21 species were found in Sei Betung. Orangutans were found to build nests in 44 tree species, all 44 of these species were found to house nests in Sikundur and a smaller subset of 14 species held nests in Sei Betung. Utilising the tree species information from the trees within 5m radius of each nest dataset, a high degree of selectivity was observed with certain species being both highly preferred and highly avoided in each site. Of greatest significance were the preferences for trees belonging to the genus *Nephelium*, the genus *Polyalthia* and *Shorea sp.* as they were some of the most frequently used for nest building and had significant positive Jacob's D scores (Fig 2.8). There are also a number of genera/species which were more common around nests but found to be highly avoided for nests building such as *Bridelia tomentosa, Callerya atropurpurea, Elaeocarpus sp., Eleais guinensis, Phyllanthus sp* and *Vitex pinnata* (Fig 2.8.).

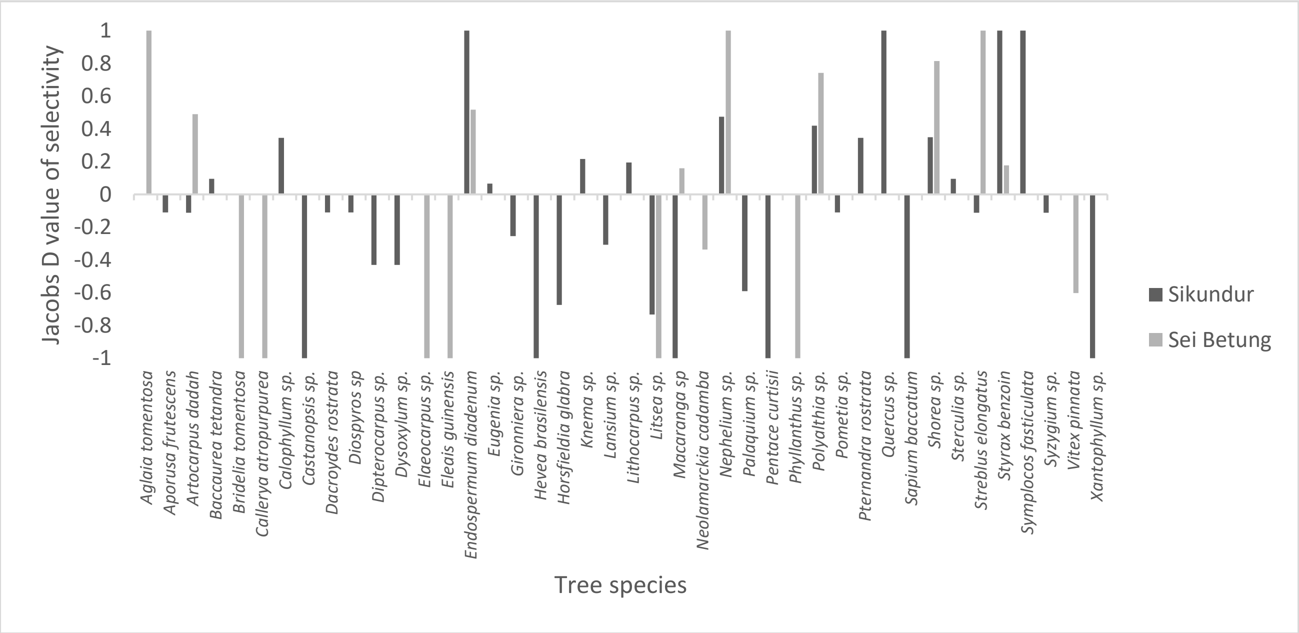

Figure 2-8 Jacobs D values of selectivity for nest trees compared to trees found within 5m of nest trees for Sei Betung and Sikundur

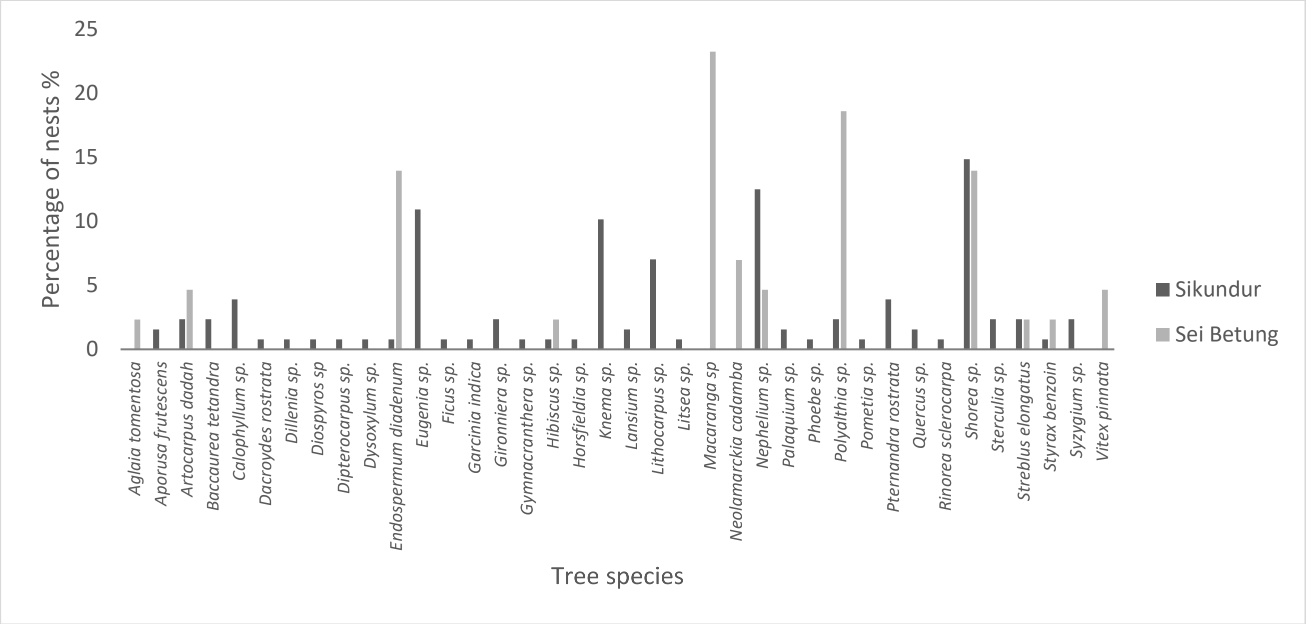

Figure 2-9 Histogram of proportions of tree species used for nest trees in Sikundur and Sei Betung

When looking at the transect data for Sei Betung, the forest composition in Sei Betung was dominated by trees belonging to the *Euphorbiaceae* and *Phyllanthacieae* families which accounted for 38.8% and 20.2% of all trees recorded at the site. Across the 720 trees recorded across the vegetation transects in Sei Betung only 53 species belonging to 26 families were identified whereas 184 species were found in Sikundur from the 873 trees sampled through phenology plots conducted by SOCP field staff (Table 2.12.). The five most abundant species in Sei Betung accounted for 50.9% of all of the trees measured at the site though they only represented 9.4% of the tree diversity of the site. In comparison, the five most abundant in Sikundur accounted for 16.3% of the 874 trees recorded on the phenology plots, with these five species representing only 2.7% of the tree diversity of the site. (Fig 2.9.) This suggests that Sikundur is both a much more diverse forest in terms of species and a more heterogenous forest also in terms of tree diversity when compared to Sei Betung.

*Table 2-12 Numbers of tree species recorded for each field site for overall forest diversity, trees within 5m diameter of a nest tree and nest trees. *Data from phenology plots conducted by SOCP staff*

Field Site	*Number of species*		
	Overall forest	**Around nest**	**Nest tree**
Sei Betung	53	21	14
Sikundur	184*	43	44

2.3.4 Multiple nest trees

A significantly larger proportion of nest trees held multiple nests in Sei Betung compared to Sikundur, with only 11.1% of trees having multiple nests in Sikundur compared to 40% of trees in Sei Betung holding multiple nests. No significant structural differences were found between single nest trees and those that held multiple nests in Sikundur except for tree height which showed that trees holding multiple nests were significantly taller than single nest trees (Welch's t= -2.37, df=34, P=0.024). In Sei Betung multiple nest trees weren't significantly taller (Welch's t= -1.41, df=42, P=0.167) and showed no significance regarding DBH either (Welch's t= -1.63, df= 38, P= 0.112), however, all other variables were found to be significantly larger in multiple nest trees than single nest trees in Sei Betung (Table 2.13.) This lends further evidence for a selection preference for trees with larger crowns as was suggested in the previous models and also suggests that this may differ between sites.

Table 2-13 Descriptive statistics and Welch's t test for trees which held single nests and multiple nests in Sei Betung and Sikundur

Field Site	**Variables**	**Means**		**Variance**		**Welch's t**		
		Single nest	**Multiple nest**	**Single nest**	**Multiple nest**	**t Stat**	**df**	**P**
Sei Betung		*n= 27*	*n=18*	*n= 27*	*n=18*			
	DBH (cm)	18.87	23.93	57.52	165.8	-1.63	38	0.112
	FBH (m)	4.9	3.83	3.83	2.87	1.93	40	0.060
	Tree height (m)	10.53	11.89	7.60	13.72	-1.41	42	0.167
	Crown size (m)	5.64	8.06	6.49	6.01	-3.24	42	**0.002**
	Crown area (m^2)	39.79	82.43	841.28	3187.48	-3.24	35	**0.003**
	Crown volume (m^3)	86.205	335.59	7646.95	94631.77	-3.80	27	**<0.001**
Sikundur		*n= 136*	*n=17*	*n= 136*	*n=17*			
	DBH (cm)	25.04	25.98	137.3	147.72	-0.38	39	0.710
	FBH (m)	9.57	10.84	12.1	29.14	-1.20	32	0.241
	Tree height (m)	17.17	20.44	26.39	47.60	-2.37	34	**0.024**
	Crown size (m)	7.60	9.6	16.08	43.09	-1.55	32	0.131
	Crown area (m^2)	54.53	49.55	1431.14	1016.83	0.72	46	0.475
	Crown volume (m^3)	263.59	260.36	119418.2	45799.19	0.06	63	0.950

The relationship between single and multiple use trees was tested using logistic linear regression. The effect of field site was first modelled and checked using a Likelihood-ratio ANOVA chi square test to test between a generalised linear mixed effects model with field site as a random effect against a simpler generalised linear model. No significant difference was found between these two models; X^2_{df1}=1.44, P=0.2296, therefore the simper generalised linear model with a binomial error structure was used for the further analysis (Table 2.14). FBH and crown volume were removed from the models due to multicollinearity and VIF scores >5. Two candidate models were identified with ΔAICc scores <2. None of these models contained tree height or crown shape as variables which suggests that these are not important in determining why certain trees have multiple nests. Connectivity and crown size were found in all of the candidate models which suggests that the level of connectivity of the tree and size of its crown have significant influences upon nest tree reuse (Table 2.15).

Table 2-14 Results of anova chi square test to determine the importance of field site as a random effect on the linear regression of single nest trees vs multiple nest trees

Model	*Df*	*AIC*	*BIC*	*logLik*	*deviance*	*Adj R^2*	*Chi sq*	*Chi df*	*Pr (>Chisq)*
Multiple~Tree.height+DBH+Crown.size+Connectivity+Crown.shape +Crown.area	13	204.66	247.41	-89.332	178.66	0.3226	-	-	-
Multiple~Tree.height+DBH+Crown.size+Connectivity+Crown.shape +Crown.area+(1|Field.site)	14	205.22	251.26	-88.611	177.22	0.3309	1.4435	1	0.2296

Table 2-15 Best candidate models for explaining the difference between single nest trees and multiple nest trees by ∆AICc scores <2

Model	*Adj R^2*	*df*	*logLik*	*AICc*	*delta*	*weight*
Multiple~Connectivity+Crown size	0.253	5	-95.201	200.7	0	0.165
Multiple~Connecitivity+Crown size+DBH	0.2596	6	-94.656	201.8	1.04	0.098
Multiple~Connecitivity+Crown area+Crown size+DBH	0.2685	7	93.924	202.4	1.72	0.07
Multiple~Connectivity+Crown area+Crown size	0.2545	6	-95.08	202.6	1.88	0.064
Full model	0.3226	13	-89.332	206.6	5.93	0.009
Null model	0	0	-114.006	230	29.32	0

Model averaging found that yet again crown size was the most important variable, it was also the only parameter estimate to have a highly significant value (β=0.088, SE= 0.043, P=0.04, RI= 1). Connectivity was also found to be highly influential with an RI of 1, though did not have a significant P value. DBH had a RI of 0.42 which suggests it may play a relatively important role in determining whether a tree had multiple nests whilst crown area was 0.34 which suggests it plays only a lesser part in explaining why certain trees have multiple nests. The parameter estimates show that multiple nest trees tend to be those with larger crown size and area but lower DBH and most frequently in trees with connectivity of 25-50% (Table 2.16).

Table 2-16 Model averaged parameters from the top candidate models of the interaction of single nest trees and multiple nest trees

Parameters	*Estimate*	*Std Error*	*Adj SE*	*Z value*	*Pr(>|z|)*	*RI*	*2.5% CI*	*97.5% CI*
Intercept	-1.288	0.908	0.913	1.410	0.159	-	-3.078	0.502
Crown area	0.002	0.004	0.004	0.396	0.692	0.34	-0.006	0.015
Crown size	0.088	0.043	0.044	2.021	***0.043***	1	0.003	0.174
DBH	-0.010	0.018	0.018	0.566	0.572	0.42	-0.064	0.016
Connectivity 25-50%	1.456	0.930	0.936	1.557	0.1196	1	-0.377	3.290
Connectivity 50-75%	-0.318	0.894	0.899	0.354	0.723	""	-2.081	1.444
Connectivity 75-100%	-1.288	0.911	0.917	1.405	0.160	""	-3.085	0.508

The forest plot in Figure 2.10 shows that crown area, tree height and crown size have minimal effect on the odds ratio for the models whilst connectivity <25% best predicts trees holding multiple nests whilst connectivity levels of 25-50% and >75% are better at predicting that a tree is a single nest tree. The marginal effects plots in Figure 3.11 show that increases in crown area and crown size are positively associated with an increase in the probability of that tree holding multiple nests. Increases in DBH however are negatively correlated with the probability of holding multiple nests but are more positively associated with greater probability of having a single nest. Crowns with connectivity 25-50% are almost three times more likely to hold multiple nests than those with a connectivity of 50-75% and six times more likely than those with connectivity >75%. The marginal effects agree with the predicted probabilities and show a negative association between tree height and probability of holding multiple nests whilst crown size and crown area display the opposite.

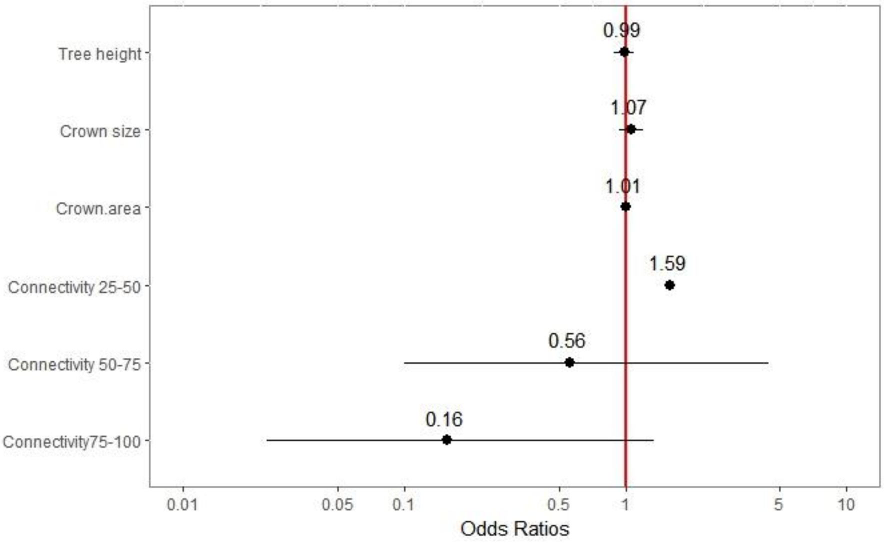

Figure 2-10 Forest plot for the parameters of the best candidate models for testing single nest vs multiple nest trees

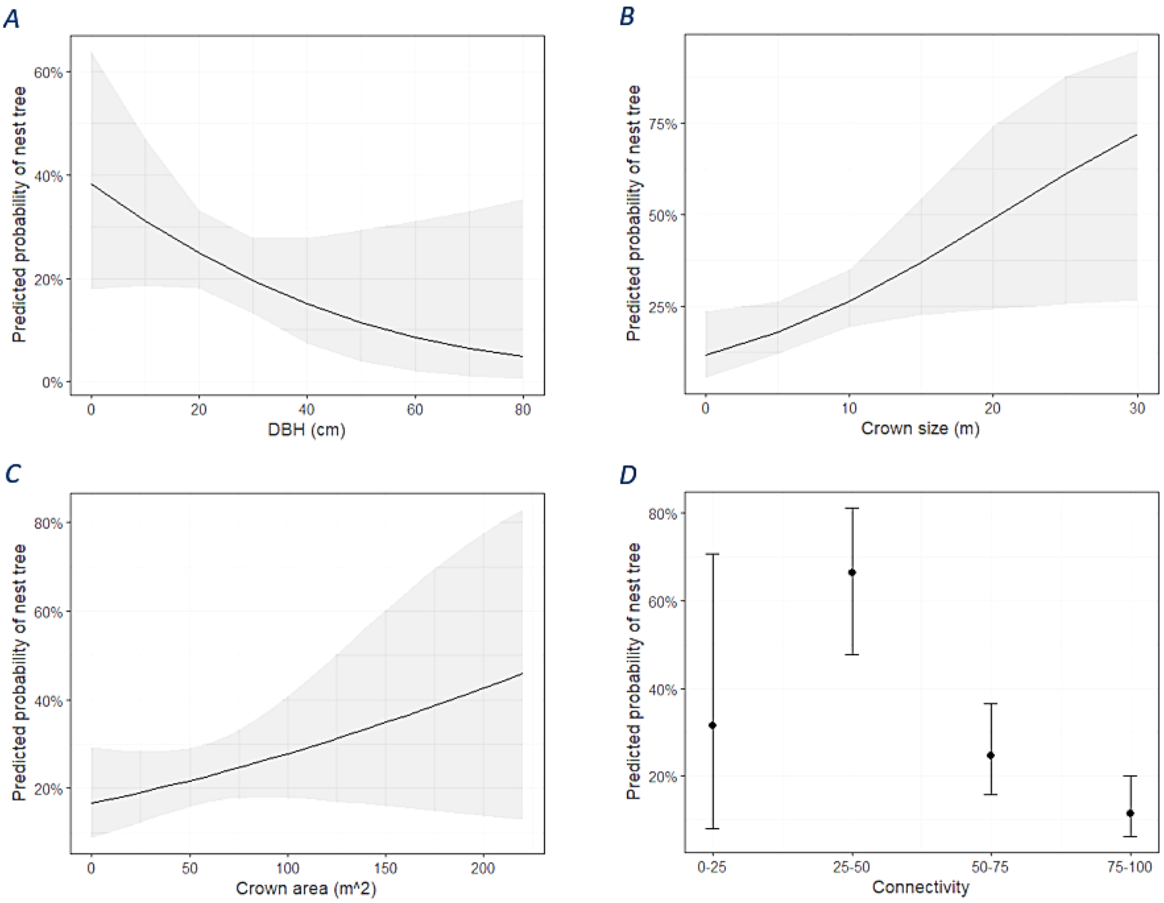

Figure 2-11 Marginal effects plots for the parameters of the best candidate models for the interaction between single nest trees and tree that hold multiple nests. The plots show the predicted probability of a tree holding an orangutan nest for each of the important variables; Tree height (A), Crown size (B), Crown area (C) and Connectivity (D)

2.4 Discussion

In this study we aimed to investigate whether tree structure had an influence upon nest site selection, and which structural variables had the greatest influence on this. To test this we compared nest trees against “average” forest trees which were measured on vegetation transect, similar to the studies by Ancrenaz et al. (2004) and Cheyne et al. (2013). However, we considered that the study of nest selection could be further strengthened by comparing nest trees directly to those within the immediate vicinity of the nest tree (<5m radius) as Mackinnon 1974 noted that orangutans frequently nested near to the last food tree visited. This enabled us to test nest site selection in relation to the other trees immediately available to the animal at the point of nest building and then determine if these differ and whether there are particular tree architecture factors that could explain how nest sites are selected.

2.4.1 Site differences in forest structure

We quantified the structural features of the arboreal environment that were likely to impact upon nest site selection in Sumatran orangutans. As expected the forest structure and composition of Sikundur and Sei Betung differed greatly given the amounts of disturbance each site has experienced and the recovery periods each has had (Rijksen & Meijard 1999; Knop et al. 2004; Kettle et al. 2014; Nowak & Singleton 2016; Wich et al. 2016b). Trees in Sikundur were found to be significantly larger than those in Sei Betung for all parameters except for crown area (Table 2.2). This similarity in crown area for trees which otherwise would be considered significantly smaller in Sei Betung is likely a product of the lower stem density in Sei Betung compared to that in Sikundur. The lower stem density would allow for greater space for the trees to spread out horizontally and reduce the need to compete for light vertically as is required in more dense forests such as Sikundur and allows for the trees in Sei Betung to more quickly shade out their competitors (Yoda 1974; Hartshorn 1978; Clark & Clark 1992; Alvarez-Buylla & Martinez-Ramos 1992; Ackerly 1996; Clark et al. 1996; Sterck & Bongers 2001). This is further evidenced by the significantly greater proportion of upside-down cone shaped trees found in Sei Betung compared to Sikundur as this crown shape with its wide and flat top is better adapted to capturing light at when the sun is at a greater solar elevation angle (>85˚). Whereas, the higher proportions of elongated spheroid and spheroid crowns which predominate Sikundur are best adapted to capture light throughout the day and light when the sun is at its nadir (<45˚) as is the case for elongated spheroid crowns and is indicative of a denser forest structure (Oker-Blom & Kellomäki 1982; Iwasa et al. 1984; Kuuluvainen & Pukkala 1987, 1989; Li & Strahler 1992). The greater crown sizes and higher proportions of crown shapes which have greater volumes is why although crown area is higher in Sei Betung, crown volume is still higher in Sikundur.

2.4.2 Site differences in nest trees

Counter to our second hypothesis, nest trees across both sites were found to be quite similar in terms of structural characteristics. Significant differences between were only found in relation to the height of nest trees and their FBH which is likely a product of the differing average tree heights in each site as was similarly found by Ghiglieri (1984) and Badji et al. (2017). This suggests that orangutans across both sites have similar selection criteria for nest trees and this is further supported by the lack of significant influence of the random effect of field site within the generalised mixed effects model when compared against the simpler generalised linear model. Analysis of nest trees versus those within 5m radius of the nest tree suggested that at this smaller scale there may be a difference in selection criteria between sites as the random effect of site was significant in this instance, however the results from the model were still found to be extremely similar to those from the average forest trees where field site was not significant. Selectivity indices further showed similarities in the preferences across sites and a similar preference across both the average forest trees and those within 5m datasets.

2.4.3 Nest site selection

As expected no ground nests were recorded at either site, further supporting the theory that ground nesting is a behaviour exclusive to Borneo due to the absence of predators capable of predating upon adult orangutans; tigers (Hayward et al. 2012a; Ashbury et al. 2015). Preferred nest site characteristics and selection patterns however don't fully support either hypothesis of improved sleep quality and nest stability or predator avoidance being the principal driver for nest site selection. Six variables were identified by model averaging to be of importance for determining nest site selection for orangutans across both sites; tree height, crown size, crown area, crown shape, DBH and connectivity. Preferences for tree height lend weight to both arguments as orangutans in both sites were found to prefer building nests in larger than average trees, avoiding both small trees and extremely tall trees such as emergent trees. Smaller trees would be avoided as they would provide less support and stability in adverse weather but also offer less distance from the ground and thereby ground predators. Extremely tall trees alternatively, tend to be emergent trees and therefore above the level of the surrounding canopy. It is likely that nests built within these trees would be too exposed to the weather and would provide little comfort or protection from the elements. By being above the level of the surrounding canopy these tall trees would also offer less easy escape routes from the nest and also increases the number of barriers between the nest and ground predators helping to obscure the nest from view (Goodall 1962; Kano 1982; Sugardjito 1983; Anderson 1984; Prasetyo et al. 2009; Cheyne et al. 2013). These results support the conclusions of Ancrenaz et al. (2004) and Cheyne et al. (2013) that orangutans prefer nesting within larger trees and within the upper canopy but do suggest that there may be alternative interpretations for their results than what either study presented as nesting within the upper canopy. Nesting in tall trees also lends support to the thermoregulation hypothesis as Koops et al. (2012) found that chimpanzees during the wet season nested higher in the tree as lower humidity levels were found higher in the tree which may help both with improved heat regulation as well as comfort whilst sleeping.

Future research could look to determine whether nest heights in these taller trees are also within the upper canopy which would improve movement to and from the nest but also potential shelter from the elements which is one of the aspects tested in Chapter 3. What could also be tested is the amount of rain, wind and directly sunlight experienced when nesting above the height of the surrounding canopy, within the canopy and below to determine whether these factors could be of concern when determining nest placement. Chimpanzees are known to nest higher within trees to avoid high humidity in rainforest environments (Koops et al. 2012a) and in more open habitats they prefer to nest at the tops of trees which both limits the amount of dripping from overhead vegetation following night time rain but also allows for greater exposure to the morning sun to warm themselves (Baldwin et al. 1981).

Against what was expected, first branch height was found to have no significant difference between nest and non-nest trees. As the height of the first branch is one of the primary determinants of how easy a tree is to access form the ground this does detract from the predator avoidance hypothesis, though it also doesn't offer any further support to the sleep quality and stability hypothesis (Goodall 1962; Koops et al. 2012a; Hernandez-Aguilar et al. 2013). Of all variables, crown size was found to have the greatest influence upon nest site selection in the models. Orangutans at both sites were found to show a strong preference for nest sites in the largest found crown sizes at each site and strong avoidance of small crown sizes. These larger crowns offer a greater amount of potential nest material and potential nest sites due to their size and increased number of branches. The greater number of branches also offer potentially greater stability through a lower impact of wind sway and reduced chance of tree collapse due to dangerous harmonic sway as the dynamic sway of the branches help to dampen energy transfer from the wind down to the trunk and roots, thereby reducing the chances of the tree falling or breaking (James et al. 2006). This lends significant support to the nest stability and sleep quality hypothesis as Ancrenaz et al. (2004) concluded that one of the primary reasons that orangutans were selecting extremely tall trees in Kinabatangan was to reduce the chance of tree failure due to the frequent windiness of their field site. Future research could look into the weather patterns at both Sikundur and Sei Betung with particular focus on wind speeds and storms and look to see if nest site selection changes with such weather. Female and juvenile gorillas have been observed to abandon arboreal nests in favour of ground nests during storms and heavy winds as safety outweighed the desire for comfort or threat from ground predators (Tutin et al. 1995). Orangutans, similarly may change their nesting patterns as the threat of nest failure increases and potentially outweighs the threat from ground predators.

Further results from the models and preference index on crown area and crown shape further lent support to both the predator avoidance and nest stability and sleep quality hypotheses. The results for crown area were very similar to those of tree height with orangutans preferring trees with crown areas larger than the mean but heavily avoiding the largest trees which would most likely be the emergent trees. Larger crown areas are suggestive of wider crowns which as with crown size would potentially have a larger number of branches which would both offer more nesting material and greater stability due to the dynamic sway of the branches (James et al. 2006; Cheyne et al. 2013). However, wider crowns also offer the potential for a greater diversity of nest positions to be built, in particular more peripheral nest positions such as Position 2 nests (see Fig 1.3) which are used as a predatory avoidance method. To have wider crowns, trees would also need stronger branches to support the weight of these branches and it is these stronger, thicker branches that are required to support nests in more peripheral positions (Horn 1971; Hernandez-Aguilar et al. 2013).

Focusing on crown shape, bent-over crowns were found to be highly avoided in both sites which is likely due to their inherent instability from their lop-sided shape. Cone shaped and upside-down cone shaped crowns were found to be highly preferred as nest sites. Previous research into the nesting behaviours of chimpanzees (*Pan troglodytes*) has noted a similar preference for upside-down cone shaped crowns; with Samson & Hunt (2014) hypothesising that these are easiest crown shapes to form into a nest which would also maximise comfort and minimise energy expenditure (van Casteren et al. 2012). It is possible that the shape of upside-down shaped cones may also be better at supporting nests in more peripheral positions as the triangular shape could offer greater biomechanical strength and reduce the physical load of the nest compared to horizontally growing branches. This is an area which needs further investigation to determine if different crown shapes offer greater stability and ability to hold the weight of a nest.

Surprisingly, DBH was in both instances found to be negatively associated with the probability of holding a nest. This result may have arisen due to a number of nests being built within trees with DBH <10cm which in the non-nest data we did not measure. Also, when looking at the selectivity indices there is a large number of large size categories avoided whilst only the smallest size category of DBH was avoided. This result directly counters the conclusion of Cheyne et al. (2013) as it suggests that in Sikundur and Sei Betung taller trees with large crown sizes and crown areas but narrow diameters are preferred as opposed to the shorter trees with large diameters and large crown areas perferred in Sabangau. This is probably the strongest evidence for the predator avoidance hypothesis as narrow trunks would make the tree less stable but also make them more difficult to access for a predator due to the increased instability. Smaller trunk size would also make a predators silent approach more difficult as the smaller trunk is more liable to vibrate with movement and making noise through the movement of leaves (Anderson 1984, 2000; Fan & Jiang 2008; Teichroeb et al. 2012). Future research could look into how vibrations travel through the tree to the nest and whether such movements are detectable to a sleeping orangutan and whether certain tree sizes or species due to wood density and stiffness are better at conducting such vibrations.

Lastly, crown connectivity was found to be positively associated with the probability of being a nest tree. The Jacob's D scores for connectivity further supported this result with Sikundur showing a highly significant avoidance of areas with connectivity <50% and a small preference for areas with connectivity >50% which is the expected result as was found by Felton et al. (2003) and Cheyne et al. (2013). Nesting within more highly connected trees provides both greater cover and protection from wind and rain through the higher numbers of branches and leaves from neighbouring trees but also provides easier escape routes from the proximity to and overlap with connected trees (Anderson et al.

1983; Anderson 2000). These results also suggest that in Sikundur a reduction in crown connectivity through human actions such as selective logging could have a significant negative impact on orangutans through the reduction in the availability of suitable nesting sites.

However, the results from Sei Betung disagree with this conclusion. Conversely, they suggest that areas with the most connectivity are the most highly avoided and showed the only significant preference for areas with 25-50% connectivity. This result goes against what was expected and predicted from the GLM and suggests that though many of the other interactions were similar between both sites, for this variable they differ significantly. The preference for less connected trees in Sei Betung may be similarly due to facilitating escape routes as the forest is much more open in Sei Betung than Sikundur (see Chapter 4) and trees tend to be in small clusters where they maybe be connected locally but for an orangutan to flee further it must come to the ground. Therefore, it would be preferable in such an open habitat and particularly where tree heights are lower to have greater sight lines to give an earlier warning of a predator’s approach and have an easier escape route down from the tree to flee. The incorporation of escape routes within nests has been observed in chimpanzee nesting and in open habitats chimpanzees have also been observed to nest higher in the tree with no overhead vegetation which also limits the possibility of attack from predators travelling from nearby trees which maybe further explain the preference for less connected trees in Sei Betung (Baldwin et al. 1981; Anderson 2000). Further analysis of nest positions is needed to determine whether less connected trees also have higher and more peripheral nests as in chimpanzees.

When drawing the results of these important tree characteristics six variable together there appears to be support for the predation avoidance, sleep quality and nest stability hypothesis as well as the thermoregulation hypothesis. However, the preference for narrower trunks does not fit with the stability hypothesis and is directly in opposition to the conclusion by Cheyne et al. (2013) suggesting that unlike in Borneo predation avoidance may be the primary driver for nest site selection. Nest stability and comfort though maybe act as a limiting factor to how far an orangutan may select anti-predatory properties as safety from predators isn’t useful if the nest itself is unsafe and liable to fail. There must be a balance between safety from predators and safety from falling (Tutin et al. 1995). There are limitations to how much can be inferred from these results and as Stewart & Pruetz (2013) state it is only possible to assess whether predation avoidance is influencing nesting by investigating nest positions whilst controlling for cross-site differences in nest characteristics such as nest height correlates with tree height. This is where Chapter 3 will build upon the results of this study and aim to provide an answer to this question.

2.4.4 Species use

Species composition also differed greatly between the two sites with 184 species recorded at Sikundur from a sample of 873 trees sampled in phenology plots conducted by SOCP staff as opposed to 53 species identified at Sei Betung from the 720 trees sampled during the vegetation transects for this study. 107 species were recorded in the primary forest of Sei Betung in a study conducted by Hartini et al. in 2017 which suggests that the reforested sections of Sei Betung has an extremely low species diversity which is mostly likely due to the trees there being replanted by humans as opposed to being naturally seeded (Kettle et al. 2014) and is as expected in our hypothesis.

As with previous studies (Prasetyo et al. 2009, 2012; Cheyne et al. 2013), this study found that orangutans were selective of tree species when selecting nest sites. As expected, orangutans in Sikundur utilised a greater diversity of tree species for nesting than in Sei Betung. 44 species were utilised for nest building in Sikundur and 14 in Sei Betung, these account for only 23.9% and 26.4% of the total available tree species at each site respectively. Though a small difference, this shows that orangutans in Sie Betung are potentially more selective than in Sikundur, though this could be a product of the low diversity or differing growth patterns of the tree species planted in Sei Betung. The number of tree species used at each of our sites however, are lower than those in both Sabah (125 species) (Ancrenaz et al. 2004a) and Sabangau (52 species) (Cheyne et al. 2013). Orangutans in both our field sites sites showed a high degree of selectivity with the species *Shorea sp., Nephelium caspidatum, Eugenia sp., and Knema laterica* accounting for 41.39% of the total number of nests in Sikundur and in Sei Betung the four most used species; *Polyalthea sumatrana, Shorea sp., Endospermum diadenum and Macaranga gigantea* accounted for 54.76% of all nests.

The tree species preferred for nesting in Sikundur are large, slower growing species such as Shorea sp. whilst in Sei Betung the preference was for fast growing, pioneer species such as members of the genus Macaranga and Endospermum further supporting the conclusion that orangutan are selecting taller, larger trees to nest in which provide both added comfort and safety from predators (Slik et al. 2003; Okuda et al. 2003; Meijaard et al. 2005; Ancrenaz et al. 2010; Hardus et al. 2012a; Chin et al. 2013; Nguyen et al. 2014; Wich et al. 2016b). As well as being large and tall growing species there is also the potential that these tree species may also have a number of other preferential tree architecture properties such as branch strength, branch flexibility or chemical properties which deter biting insects and parasite (Prasetyo et al. 2009; Thorpe et al. 2009; Stewart 2011b; van Casteren et al. 2012; Samson et al. 2013). Future research could investigate the structural and chemical properties of these tree species to ascertain why they are so highly favoured as nest trees. Hernandez-Aguilar et al. (2013) also noted that when considering preference for tree species it is important to not only consider abundance but also understand more the tree's physical characteristics and growth patterns. Some tree species may be common but rarely used as nest sites as that tree species is an understory tree which doesn't grow tall enough to be selected often as a nest site (Hernandez-Aguilar et al. 2013).

Using such information, conservation managers could potentially identify tree species which may potentially be valuable nest sites and ensure that they are protected or that such species are planted in reforestation projects such as Sei Betung.

Table 2-17 Economic value and human uses of the most preferred and utilised species for nesting by orangutans in Sikundur and Sei Betung (Wang et al. 2004; Fern 2019).

TREE SPECIES	SIKUNDUR		SEI BETUNG		ECONOMIC VALUE AND USES
	Proportion %	Jacob's D	Proportion %	Jacob's D	
Aglaia tomentosa	0	0	2.3	1	Fruits are eaten and collected locally. Genus Aglaia only source of flavaglines compounds useful for medicine development, insecticides and potential as a cancer treatment Wood used in house building
Artocarpus dadah	2.3	-0.1	4.6	0.49	Fruits eaten locally used as food and medicine. Commonly exploited for timber which is traded internationally.
Calophyllum sp.	3.9	0.34	0	0	Harvested for timber which is used locally
Endospermum diadenum	0.8	1	13.9	0.52	Commercial source of the timber "Sesendok", commonly harvested for local use and trade
Knema sp.	10.2	0.22	0	0	Dependent on species, some harvested locally for wood, others harvested for oil and seeds for medicine
Lithocarpus sp.	7	0.19	0	0	Dependent on species some harvested locally for wood, others are timber species that are traded
Macaranga sp.	0	0	23.3	0.16	Harvested for wood locally and medicinal properties for treating diarrhoea. Also, *Macaranga sp.* are extremely useful for reforestation projects as pioneer species
Neolamarckia cadamba	0	0	7	-0.34	The wood is used for plywood. Very frequently planted species due to religious beliefs in SE Asia. Is a pioneer species.
Nephelium sp.	12.5	0.47	4.7	1	Fruit harvested and sometimes planted in local plantations and cultivated. Favoured for "wild taste" compared to domesticated rambutan
Polyalthia sp.	2.3	0.42	18.6	0.74	Some harvesting for wood and pulp
Quercus sp.	1.6	1	0	0	Timber species that is traded on a commercial basis under the name “Mempening”. Leaves, seed, bark and galls of value to local medicines due to tannins.
Shorea sp.	14.8	0.35	14	0.81	Timber species that is traded commercially with a number of Shorea species listed as endangered and critically endangers on the IUCN Red List. Traded under the name "Meranti".
Streblus elongatus	2.3	-0.11	2.3	1	Harvested for local medicinal use
Styrax benzoin	0.8	1	2.3	0.18	Gum from the bark is harvested as a food flavouring and traded internationally. Benzoin gum also has a number of medicinal properties. Also, benzoin is highly useful ingredient in cosmetics and a fixative in perfumes with high grades of benzoin being a prized fragrance note.

The four most used tree families in Sikundur (*Dipterocarpaceae , Myristacaceae*, *Myrtaceae* and S*apindaceae*) accounted for 52.4% of all nests whilst in Sei Betung the three most used families the *Euphorbiaceae*, *Annonaceae* and *Dipterocarpaceae* accounted for 69.03% of all nests which is a significantly higher amount of selectivity than what was found by either Ancrenaz et al. (2004), Cheyne et al. (2013) or Prasetyo et al. (2012). In fact, this level of selectivity is comparable to and greater than that of some of the African great apes (Kano 1982; Fruth & Hohmann 1993, 1996; Tutin et al. 1995; Hashimoto 1995; Brownlow et al. 2001). The high preferences for these species further provide a number of conservation implications as most of these species are of economic value to humans (see Table 16), leading to competition and conflict over these resources with humans, as well as the potential disappearance of preferred nest sites as these species are removed from the forest. Trees belonging to the genera *Shorea*, *Macaranga* and *Endospermum* are all valuable timber species (Ådjers et al. 1995; Okuda et al. 2003; Chin et al. 2013), *Nephelium caspidatum* produces a valuable fruit that is collected (Saw et al. 1991) and *Macaranga gigantea* and *Polyalthea sumatrana* both have medicinal properties which also gives them value to local communities (Table 2.17) (Eswani et al. 2010). Humans collecting from these species could disturb the orangutans or possibly attack them as they may perceive the orangutan as a threat to either themselves or to the valuable fruit and trees (Meijaard et al. 2011; Wich et al. 2011a; Davis et al. 2013).

Some of these tree species however also offer the potential to help promote the conservation of orangutans by protecting the habitats, in particular the trees due to their value to medicine and the discovery of new medicines and treatments for illnesses. Trees belonging to the genus Aglaia are the only known source of a group of around 50 compounds that bear a unique cyclopenta[b]tetrahydrobenzofuran skeleton. These compounds are more commonly known as rocaglate, rocaglamide derivatives or flavaglines, most of which have been found to have potent insecticidal properties, antifungal, antiviral, antibacterial and antihelminthic bioactivity. There is even the potential for new cancer treatments to come from these compounds as several have been found to exhibit pronounced cytotoxic activity against a range of human cancers (Wang et al. 2004; Li-Weber 2015; Fern 2019). By protecting the forests where these trees grow we also protect these potential sources for future medicines which can help to eliminate some of humanities worst illnesses.

2.4.5 Multiple nest trees

Of particular interest is the number of trees which held multiple nests in Sikundur and Sei Betung as Ancrenaz et al. in 2004 found increased numbers of trees with multiple nests was linked to the amount of disturbance a forest had experienced. Normally the reuse of nest trees or finding of multiple nests in the same tree is quite rare, 3% in Danum Valley (Kanamori et al. 2017), 14.6% in Sabah

(Ancrenaz et al. 2004a) and 9.51% and 10.9% in Tuanan (Prasetyo et al. 2009, 2012) and 5% in Suaq Balimbing in Sumatra (Singleton 2000). The proportion of trees in Sikundur with multiple nests was 11.1% which is similar to these previously published figures, whilst multiple nest trees accounted for 40% of all nest trees in Sei Betung which in unprecedented compared to what has been found in previous studies (Rijksen 1978; Ancrenaz et al. 2004a; Prasetyo et al. 2012).

When trees holding multiple nests were compared to single nest trees, those in Sei Betung were found to be significantly larger than single nest trees for crown size, crown area and crown volume whilst FBH was significantly lower in multiple nest trees and tree height and DBH showed no significant differences. In Sikundur tree height was the only variable found to be significantly different between single and multiple nest trees with multiple nest trees being significantly taller than single nest trees. Field site however, was found to have no significant effect upon the models. Crown size and connectivity were found to be the most influential variables based on their RI scores. Crown area and DBH however, were found to have much less significant influence upon models though they are still of importance to the interactions due to their presence within the top candidate models. Larger crown sizes as mentioned previously offer a greater number of potential nest sites and nesting material through an increase in the number of branches and is likely one of the primary reasons why these larger trees contain multiple nests.

Increases in both crown area and crown size showed positive associations with the probability of holding multiple nests. Conversely trees with larger DBH were found to have a lower probability of holding multiple nests and an increased probability of single nests. Again, as highlighted earlier, the trees with lower DBH but tall in height and large crowns may provide increased anti-predation benefits due to the greater difficulty a predator would face accessing nests in these trees stealthily (Anderson 1984, 2000; Fan & Jiang 2008; Teichroeb et al. 2012). At both sites trees with lower connectivity had much higher probabilities of holding multiple nests than those with higher connectivity. This result is likely due to a lower availability of large trees in areas with low connectivity so those few large trees that are present are significantly more likely to have multiple nests as the need for reuse arises and as Ancrenaz et al. (2004) noted, the more frequently a tree is reused for nests the more its structure is altered and becomes further preferable as a nest site. In areas with few potential nest sites, large trees with particularly large crowns would be valuable resources due to the potential number of nest sites. As such, these trees which are most frequently used and reused as nest sites should be protected as the loss of them cold severely lower the number of potential nest sites in such degraded and open areas and their loss could have negative effects upon the orangutan population.

2.4.6 Implications

The similarities in results for both datasets suggest that either conducting PCQM transects or measuring trees within 5m radius of the nest tree both produce similar results and that either could be used as potential methodologies when studying nest site selection and that previous prior studies which only measured average forest trees show a good representation of nest site selection. Further research could look to compare between data collected from plots against transects to determine which provides a better representation of forest structure for the site.

The tree size classes which orangutans showed the highest preferences for made up an extremely small proportion of the trees within the forest at each site, suggesting that there is significant pressure upon these trees as nest trees and that their removal would increase the pressure on the remaining preferred nest trees and lead to an increase in the reuse of these nest trees and clustering of nest sites. This provides further evidence for the need to protect these larger trees due to their significant value as nest trees, not only for their value for travel and canopy connectivity (Ancrenaz et al. 2004a; Prasetyo et al. 2012; Davies et al. 2017). It is unknown what effect such clustering of nests has upon the behaviour and health of orangutans as individuals potentially are forced into proximity than would normally be preferred for a species that is semi-solitary. Future research could look to take hair samples from nests in Sikundur and Sei Betung and look at cortisol levels to determine if the reduction in potential nest sites was increasing stress within the animals at this site.

The value of larger trees is particularly high in more open and degraded areas as nest site reuse and trees containing multiple nests were significantly more common in Sei Betung than Sikundur and at a higher incidence than has been reported in any prior study. Such a proportion of trees holding multiple nests shows that there is a high pressure upon preferred nest sites within such environments and that such trees much be protected. Looking at the tree species used, we saw that in Sei Betung, faster growing pioneer species were heavily favoured, likely because these are the first trees which grow to have a crown structure capable of supporting a nest. A focus should be on planting fast growing species such as those belonging to the genus *Macaranga* when conducting reforestation projects if one of the aims or goals of such a project is to encourage the recolonization of the site by orangutans. Orangutans also favoured a number of species which have significant economic value to humans and as such there is the potential of conflict over these resources (Table 16). Some tree species however have significant value to cosmetics and medicine and so these could offer potential backing for conservation or managed agroforestry projects where the sap, gum and resin from those trees are collected without removing trees or disturbing orangutans.

2.5 Conclusion

Other studies have concluded that orangutans prefer the largest available trees (Ancrenaz et al. 2004a; Cheyne et al. 2013) and our results agree with this to a point. Our findings suggest that orangutans do prefer to nest in larger, taller trees but they avoid extremely tall trees, whereas they prefer trees with the largest crowns in terms of size and area and this result of previous studies of preferring the largest trees is likely to be a function of orangutans selecting for trees with the largest crown and crown area. Larger, wider crowns are likely to hold a greater number of branches and this both provides a greater amount of building material for nesting but also provide greater protection from the wind, rain and overhead sun through the presence of a denser canopy. Trees with larger numbers of branches are able to reduce dangerous harmonic sway through the dynamic sway of the branches which also helps to dampen energy transfer from the wind down to the trunk and roots, thereby reducing the chances of the tree falling or breaking (James et al. 2006). Therefore, this supports the hypothesis that orangutans select nest sites based on comfort and stability rather than predator avoidance. Orangutans were also found to prefer nesting within crowns considered more stable and easier to build nests in further lending support to the idea that nest site selection in driven by safety and comfort (van Casteren et al. 2012; Samson & Hunt 2014). However, our study also found evidence for orangutans potentially selecting nest sites which have properties which reduce their risk from predation. In less disturbed forests with fewer gaps and higher connectivity orangutans selectively build nests in trees with greater connectivity that provide an increased number of escape routes. In more open and disturbed habitats orangutans select for trees which are less well connected as these allow for easier access to the ground and greater sightlines of a potential predator’s approach. Furthermore, we found evidence that there may be a selection for trees with smaller DBH in both sites which would reduce a predator’s access to the nest and give warning to the nesting orangutan through the vibration of branches and rustle of leaves. Therefore, not only is nest site selection in the lowland dipterocarp forests of Sumatra driven by comfort and stability as in Borneo but predator avoidance also plays a major role in determining where an orangutan builds their nests.

The larger trees which orangutans have been found to have high preferences for, only represent a small proportion of the trees within the forest. This means the removal of these preferred nesting trees poses another threat to their survival which must be considered. Such large trees are disproportionately favoured by selective logging operations (Felton et al. 2003) and as such could create added pressures on orangutans beyond the loss of habitat and potential food species. As well as the removal of preferred nesting trees the removal of these trees is likely to create gaps which lower the connectivity of the trees in the area which our study has shown to be highly avoided by orangutans and when tree with lower connectivity were used, they had a significantly higher probability of multiple nests being built in that tree as other quality nest trees become harder to find. This will lead to an increase in competition for nest sites and could lead to increases in confrontations between individuals over nest sites. The increasing reuse of nest trees could also lead to a change in the tree’s architecture as was noted by Ancrenaz et al. 2004 as the constant bending, breaking and healing of branches alters the shape of the tree into a more preferential one for nesting which then increases its rate of reuse and leads to the formation of “villages”. The frequent reuse of such trees in disturbed and open habitats shows that the loss of such large and preferred nest trees could have a greater impact upon orangutans within disturbed habitats as such trees represent a greater proportion of the overall potential nest sites than in more intact forests where orangutans have a greater choice of nest sites. Within such disturbed sites a focus should be placed on protecting large trees known to be frequently nested in and if such trees much be lost then they should be replaced with fast growing pioneers such as those belonging to the genus *Macaranga* which can provide alternative nest sites.

Future research could look into the characteristics of the tree species found to be nested in to identify species which would are most useful as nest sites through either large size, strong branches or fast growing. Another potential avenue of research would be to ascertain whether any of the preferred nest species have mosquito repellent properties which would allow us to then test the anti-vector hypothesis. The potential of this could also lead to the potential discovery of a new chemical for use in mosquito repellents should such a result be found. In Chapter 3 I will build upon the results of this study to provide a more definitive answer as to whether orangutans are selecting nest sites as a method of predator avoidance or comfort and stability or thermoregulation through my investigation of nest height and nest positions.

Chapter 3: The influence of forest structure on nest positioning of Sumatran orangutans (*Pongo abelii*)

3.1 Introduction

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Orangutans are the largest extant arboreal mammalian species (Cant 1987b, 1987a), spending almost all of their lives in the canopy with adults building nests almost daily for sleep and rest (Mackinnon 1974; Ancrenaz et al. 2004a; Russon et al. 2007; Prasetyo et al. 2009, 2012; Cheyne et al. 2013). Nest building is a behaviour that orangutans share with all other great apes (Hashimoto 1995; Hall et al. 1998; Blom et al. 2001; Mehlman & Doran 2002; Kouakou et al. 2011; Samson & Hunt 2014; Serckx et al. 2016). Orangutan nests are considered to be the most sturdy, complex and elaborately designed and longest lasting nests of all those produced by apes (Groves & Sabater Pi 1985; Ancrenaz et al. 2004a; van Casteren et al. 2012). They frequently include features such as pillows, blankets and roofs which increase comfort and secondary bunk nests for young individuals helping to give them further protection and comfort as well (MacKinnon 1971; Anderson 1984, 1998; Russon et al. 2007; Meijaard et al. 2011; van Casteren et al. 2012). There are a number of hypotheses suggested to be behind nest building in great apes, the primary ones are improved sleep quality through comfort and stability, improved thermoregulation, avoidance of biting insects and disease vectors and reducing the risk from predators.

Nests offer increased comfort and sleep quality by providing a comfortable platform to sleep in and cushioning through the weaving of small branches and the addition of soft leaves (Goodall 1962; Van Lawick-Goodall 1968; Stewart et al. 2007; Prasetyo et al. 2009, 2012). Nests also improve comfort through protection from adverse weather conditions such as rain and strong winds (Goodall 1962; Kano 1982; Anderson 1984; Prasetyo et al. 2012; Cheyne et al. 2013). Being able to relax and rest safely without concern of nest failure due to nest instability allows for improved and longer sleep periods which is why factors that improve nest stability and strength are considered in the comfort and sleep quality hypothesis. Orangutans and other apes are able to increase the safety and stability of their nests by selecting nest sites within taller trees with wider trunks (Ancrenaz et al. 2004a; Cheyne et al. 2013). They can also improve nest safety and stability by building their nests in more stable positions closer to the trunk and lower within the crown where wind speeds are lower and the weight of an orangutan produces less strain on the branch (Rayadin & Saitoh 2009; Samson & Hunt 2012; Hernandez-Aguilar et al. 2013). Male chimpanzees and orangutan have been reported to nest lower in trees and closer to trunk of trees (Brownlow et al. 2001; Rayadin & Saitoh 2009) and in the case of gorillas the silverback males produce significantly more ground nests than either females or immature individuals (Yamagiwa 2001; Mehlman & Doran 2002). This is most likely a product apes being sexually dimorphic with males being significantly larger than females and are therefore limited in nest sites due to their increased weight and need for extra strength and stability (Richmond & Jungers 1995).

Sleeping in nests can help to improve thermoregulation by aiding in the reduction of heat loss at night and experiencing lower humidity (Anderson 1984; Fruth & Hohmann 1993; Stewart 2011b). Chimpanzees have been observed to nest higher within trees during the wet season as higher altitudes have lower humidity (Koops et al. 2012a). Avoiding high humidity has benefits for thermoregulation as high humidity in high temperatures reduces the efficiency of heat loss through sweating and evaporation whilst in cooler temperatures high humidity and increase heat loss through convection (Bell & Greene 1984). Arboreal nest also help the nest builder to avoid the wet and damp ground in wetter habitats or during rainy seasons (Remis 1993). Stewart (2011) reported less heat loss during the night when sleeping in an arboreal nest compared to sleeping on the bare ground.

The building of nests has also been posited as a method of avoiding insect-borne pathogens by acting as a physical barrier to vectors such as mosquitoes as well as the use of certain tree species for nesting which contain chemicals which act as repellents to mosquitoes and other biting insects (Prasetyo et al. 2009; Stewart 2011b; van Casteren et al. 2012; Samson et al. 2013). Orangutans and chimpanzees have been observed to preferentially select nest sites in tree species known to have mosquito repellent properties (Largo et al. 2009). Furthermore, orangutans have been observed carrying branches and leaves from prior nest sites and trees that have mosquito repellent properties (Russon et al. 2007; Kuze et al. 2011). The daily movement and building of fresh night nests has also been posited as a method of reducing the possibility of infestation by ectoparasites (Mackinnon 1974; Anderson 1998). Empirical testing by Stewart (2011) found that the research was bitten less by mosquitoes and other biting insects when sleeping in arboreal nests as opposed to sleeping on the ground.

Nest building has also been suggested as a way to reduce the risk of predation by removing the risk from ground based predators and camouflaging the animal while they rest (Sugardjito 1983; Anderson 1984, 1998; Fruth & Hohmann 1993; Pruetz et al. 2008; Stewart & Pruetz 2013). Adult orangutans and other great apes have very few natural predators due to their large body size, but they are still at risk of predation from a small number of species including large pythons (*Python reticulatus*), Sunda clouded leopards (*Neofelis diardi*) and Sumatran tigers (*Panthera tigris sumatrae*) (Mackinnon 1974; Rijksen 1978; Sugardjito 1983; van Schaik & van Hooff 1996). The presence of tigers in Sumatra is the most widely accepted theory as to why ground nesting is almost completely unheard of in Sumatra compared to Borneo, as compared to the predators in Borneo, tigers are more than capable of preying upon orangutans with adult orangutans being in the lower part of the preferred prey size of tigers (60-250kg) (Markham & Groves 1990; Hayward et al. 2012a; Ashbury et al. 2015). With the presence of tigers in Sumatra, it should also be expected that orangutans should be altering their nest sites to reduce the threat from nocturnal predators.

Stewart & Pruetz (2013) in their study stated that studying nest positions is the only way to control for cross-site differences in correlate such as nest height and tree height. This is why in this Chapter we are building on the findings of Chapter 2 which found that there was some support for the predation avoidance hypothesis over comfort and nest stability and thermoregulation. Both Rayadin & Saitoh (2009) and Prasetyo et al. (2012) found that young orangutans built their nests higher in the canopy and in more peripheral positions whilst adults and in particular flanged males built their nests lower in the crown in more stable positions closer to the trunk. This was suggested to be both an adaptation for comfort and stability as well as an anti-predatory adaptation (Rayadin & Saitoh 2009) as large adult orangutans are generally too large to be predated on by clouded leopards but because of their extra weight are more susceptible to nest failure should they build a nest in a more peripheral position. Whereas juvenile orangutans are more susceptible to predation as they fall within the preferred prey size category and clouded leopards have been recorded predating on proboscis monkeys (*Nasalis larvatus*) which are comparable in size to juvenile orangutans (Wilting et al. 2006; Matsuda et al. 2008) and clouded leopards have been reported to have predated on rehabilitant orangutans in Sumatra (Rijksen 1978). Chimpanzees similarly have been observed to build nests higher in areas with greater predator pressures (Baldwin et al. 1981; Pruetz et al. 2008) as building nests higher in the canopy may increase the difficulty for a predator to reach them and provide more time for the ape to escape during attack even from a predatory species adept at climbing (Koops et al. 2012). Nesting in more peripheral positions however requires that either body size and weight are lower or that the individual builds the nests in a larger tree with greater biomechanical strength that can support their weight (Horn 1971; Hernandez-Aguilar et al. 2013). Therefore, the structural characteristics of the tree could have a significant influence upon nest positioning.

Nest height is generally considered to be linked to the height of the tree that the nest was built within and mean nest heights vary across field sites due to the differing forest structures and canopy heights (Prasetyo et al. 2009; Badji et al. 2017). However, the height of the nest within the crown can differ depending upon a number of factors. In their studies from Borneo both Ancrenaz et al. (2004) and Cheyne et al. (2013) found that nests were more frequently built in the upper crown of the trees they were built in, however Cheyne et al. (2013) concluded that nest site selection was not due to predator avoidance in their study but as preference for safer and more stable nest sites as extremely tall trees were not selected for in their study. Nesting higher in the canopy has also been suggested to offer improved comfort by reduced risk from airborne parasites such as mosquitoes (Prasetyo et al. 2009; Stewart 2011b) however this was not supported by Koops et al. (2012a) with mosquito densities not differing with height or nest densities, though this may have been due to site differences and study design. As Koops et al. (2012a) had significant difficulties in capturing mosquitoes and other vectors and we lacked the equipment and expertise for identifying such species we did not further pursue this hypothesis. Nest height has also been suggested to offer improved comfort through lower humidity which would aid in thermoregulation (Koops et al. 2012a; Samson & Hunt 2012). However higher nests also have the drawback of experiencing increased wind speeds which can cause sway increasing sleep disturbance (Samson & Hunt 2012) and in high winds potentially force the nest builder to abandon the nest in favour of a lower nest or even ground nesting (Tutin et al. 1995). This could suggest that nesting above the canopy should be avoided due to this increased exposure. However, chimpanzees in Assirik have been observed to preferentially build their nests in open positions at the top of tree crowns as this helps to reduce dripping from overhead vegetation from overnight rain and also gives them access to the early morning sun to help warm and dry their bodies (Baldwin et al. 1981; Anderson 2000). Increased nest height also offer the simplest method of reducing the risk of predation by both reducing access to the nest through the increased distance from the ground and reducing the possibility of being seen by a predator (Sugardjito 1983; Prasetyo et al. 2009; Stewart & Pruetz 2013).

Whilst differences in the proportional use of nest positions could be due to differences in body size and sex this still does not provide an explanation for all nest positions and why some nests are built at the top of the main stem (Position 3) and others at the ends of branches (Position 2) as both offer protection from predators. Therefore, there must be another explanatory reason for why certain positions are chosen over others other than anti-predation. It has been suggested that the different nest positions could also be product of the architecture of the tree that the nest is built within (Prasetyo et al. 2009) and that along with predator avoidance a nest must also be safe and stable as was found in the previous chapter in regards to nest site selection (Cheyne et al. 2013). One of the aims of this study is to understand which forest structure parameters influence nest position and to test whether these important parameters differ with site and differing forest structures.

Though the majority of nest positions and nest height can be linked to either environmental or sex and body size differences, there are some nest positions which have been suggested to differ due to cultural differences and forest structure differences. Position 4 nests (Fig 1.3) also known as tree tied nests are those where more than one tree is used for building the frame of the nest, this can either be through the tying together of branches or using the tops of smaller trees and bending and locking them together to form a stable platform (Prasetyo et al. 2009, 2012; Orangutan Network 2015). In most forests Position 4 nests are rarely found whilst the other three nest positions are the most common and are use in relatively similar proportions despite differences in canopy structures and frequencies of types of tree architecture such as dryland forest of Ketambe and swamp forest of Suaq Balimbing (both of which are in Sumatra) (Prasetyo et al. 2009). However, Position 4 nests are the most common nest positions in the peat swamps of Central Kalimantan at Sabangau and Tuanan (Prasetyo et al. 2010). It has been suggested that this may be due to the paucity of suitable larger nest trees at these field sites due to logging though it could also be due to differences in geography and populations with a preference for this nest position due to cultural preferences (Prasetyo et al. 2010). There is the potential that Position 4 nests could have arisen through mate guarding behaviour with males building nests below those of females in oestrus as suggested for chimpanzees in Nimba by Koops et al. (2007). However this theory was later contested by genetic analysis from the same field site which found that the majority of these lower nests were either built by the same individual or other maternally related males (Koops et al. 2012b). Though mate guarding is a behaviour known in orangutans with flanged males travelling in a consortship with a female in oestrus where they will travel together and nest in each other's vicinity (Schürmann & van Hooff 1986; Utami-Atmoko et al. 2009a). Due to the difficulty in conducting genetic analysis to determine the sex of the nest builders and the doubt surrounding the mate guarding hypothesis we have not further considered it in our study. Our research sites however offer the perfect opportunity to test the cultural difference and forest structure hypotheses as our field sites are within close proximity to each other and similar lowland forest however, they differ in disturbance levels as Sikundur was selectively logged 40 years ago (Knop et al. 2004; Priatna et al. 2006) and has since been allowed to naturally recover whereas Sei Betung was an illegal palm oil plantation that was cleared and replanted with native species over the last 15 years (Kettle & Koh 2014; Kettle et al. 2014). As such, we will be able to ascertain whether a paucity of large trees influences the building of these nests or if it is a local preference to Bornean orangutans in Tuanan and Sabangau.

These two field sites also offer us the invaluable opportunity to investigate how orangutan nesting is influenced by disturbance and how orangutans adapt to more open environments. This is of particular importance as currently Indonesia is experiencing the second highest rate of deforestation amongst all tropical countries and Sumatra stands out with 70% of its forested area having been converted through intensive forest clearance as of 2010 (Margono et al. 2012, 2014). Some provinces on Sumatra have lost nearly 50% of their forest cover between 2000 and 2012 (Margono et al. 2012; Supriatna et al. 2017). These forests are being cleared for conversion to agriculture and oil palm plantations as well as the extraction of valuable timbers through both clear felling and selective logging (Hall et al. 2003). Selective logging has been found to be result in more homogenous forests with lowered species richness and a more simplified vertical structure (Norris et al. 2010). The removal of larger emergent trees in particular leads to a reduction of continuous canopy and tree density which could possibly affect the availability of good nest sites as taller, larger trees were also preferentially selected for nests in Borneo (Ancrenaz et al. 2004a; Prasetyo et al. 2012; Cheyne et al. 2013). Reforestation efforts have been suggested as a method for reducing the impact of forest clearance and to restore previously lost forest lands (Parrotta et al. 1997b; Parrotta & Knowles 1999; Goosem & Tucker 2013; Kettle et al. 2014; Kettle & Koh 2014). However, these restorations take time to recover to pre-disturbance forest structure (Kanowski et al. 2003, 2005, 2006; Catterall et al. 2004; Erskine et al. 2005), during this recovery period it is unknown how orangutans utilise these restoration forests and in particular how their nesting behaviours adapt to these new and changing forest structures.

3.1.1 Hypotheses

- Given the confirmed presence of Sumatran tigers, clouded leopards at Sikundur and Sumatran elephants at both sites, few if any ground nests are expected to be found at either of our field sites.
- Regarding nest height, should thermoregulation be the most important factor we should expect to observe nests built in tall trees with nest heights above the height of the surrounding canopy. Should nest stability and safety be the most important we would expect to find the nests built lower in the canopy where branches are thicker and wind speeds are lower (Rayadin & Saitoh 2009; Samson & Hunt 2012; Hernandez-Aguilar et al. 2013). If predation avoidance is the principal driver, we would expect to see nests built high within the crown but within the level of the canopy as this would allow for easier escape from the nest.
- Nest heights should differ between the sites due to the differing mean tree heights of those forests as found in the previous chapter, though we expect the pattern for determining nest height to be similar across both sites.
- As Sikundur and Sei Betung have vastly different forest structures we would expect to see different proportions of each nest position used at each site. As trees are larger in Sikundur we expect to find a higher proportion of peripheral nest position on later branches (Position 2) used whilst in Sei Betung we expect to find more positions built against the main stem (Position 1 and 3).
- Should predation avoidance be a primary driver for nest placement in Sikundur and Sei Betung we would expect to find higher proportions of peripheral nest positions built at both sites; Position and Position 3 nests. If nest stability and sleep quality is the principal driver, we would expect to find more Position 1 nests at both sites where the nest is built against the main stem.
- With Sei Betung being a more open site and having a lower density of large trees we expect to find a higher proportion of tree tied nests (Position 4) in Sei Betung than Sikundur.
- As Position 2 nests require greater biomechanical strength to support them we should find that these are built in significantly larger trees than any other nest position whilst Position 4 nests should be built in the smallest trees.
- Both nest height and position are expected to be closely linked to tree architecture parameters and that is nest height and position are not determined randomly, tree height is also expected to be one of the most important factors in determining height and position as previous studies

into chimpanzee nesting have found nest height to be closely linked to the tree height (Badji et al. 2017).

3.2 Methodology

3.2.1 Study Sites

The fieldwork for this study was completed at two geographically close but structurally distinct field sites within the eastern borders of Gunung Leuser National Park and the larger Leuser Ecosystem of North Sumatra. These are Sikundur (also known as Sekundur in some papers) (3°1’N, 98°02’E) and Resort Sei Betung (4°3’N, 98°07’E) which are approximately 9km apart with Sei Betung 9km to the north of Sikundur (Knop et al. 2004; Wich et al. 2008; Marshall et al. 2010; Hartini et al. 2017; Szantoi et al. 2017). Sikundur experienced varying levels of selective logging until the late 1970’s with some sporadic logging into the 1980’s (Knop et al. 2004; Nowak & Singleton 2016), since then it has been allowed to recover naturally and is now classified as an area of diverse mixed dipterocarp lowland forest that also possesses rich alluvial forest along the rivers (de Wilde & Duyfjes 1996; Knop et al. 2004; Wich et al. 2008b). Unlike Sikundur, Sei Betung was almost completely clear felled and stands upon a former illegal oil palm plantation that has been actively restored and reforested through the planting of 500,00 seedlings of 97 indigenous tree species by the NGO OIC (Orangutan Information Centre) (Kettle et al. 2014). Replanting commenced in 2008 with different parts of the site replanted up until 2013 with the west of the site being less thoroughly replanted due to the stands of logged forest which remained there (Wich et al. 2016b). Though the two sites are close geographically they differ drastically in terms of human disturbance and the method and stage of regeneration which provides an invaluable opportunity to compare orangutan nesting behaviours between these two sites. The surveys were undertaken February-August 2015 and March-September 2016.

3.2.2 Data collection

Both nest and vegetation data were sampled using transects. In Sikundur these were 30 500m long transects and in Sei Betung 9 1km long transects. Transects in Sikundur were distributed using a stratified random grid where the first point was placed randomly and then the transects were plotted from this point on North-South bearings with each transect being separated by 300m to the East and West and 150m to the North and South from the next transect. All transects were placed to ensure that none were split by the Besitang river. Due to the disturbance that cutting new transects would bring to the Sei Betung study site, nine pre-existing transects of 1km length were used, these were 150m apart to the east and west and ran parallel to each other on a north-west south-east bearing (Fig

4.2.). The length and placement of the transects was designed to prevent an overlap of observations and with the intention of optimizing the trade-off between having a large number of independent samples and ensuring that transects were long enough to minimise the potential biases due to spatial heterogeneity from such things as the clumping of orangutan nests or variation in habitat and structure along the transect (Johnson et al. 2005). Transects were cut along these lines irrespective of topography or vegetation to ensure that they adhered to the line-transect method assumption that all transects be placed randomly in respect to terrain and were able to cover a representative sample of both field sites (Buckland et al. 2001; Mathewson et al. 2008). All transects were walked and used by the lead author with deviations from the transect due to obstacles kept as small a deviation as possible.

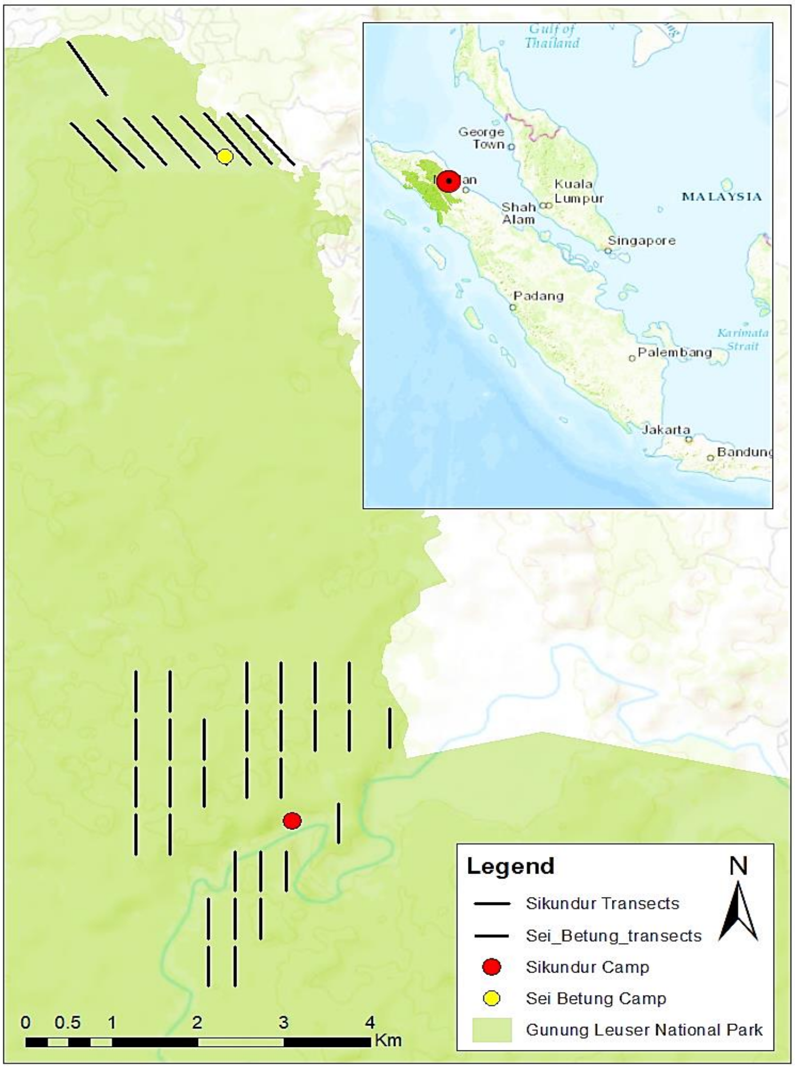

Figure 3-1 Locations of Sikundur and Sei Betung in North Sumatra. Both sites lie within Gunung Leuser National Park but are close to the edge and experience frequent encroachment and disturbance from local villagers

3.2.3 Nest transects

Nest transects were conducted in teams which consisted of the author and 1-2 well trained local field assistants from SOCP in Sikundur and OIC in Sei Betung. Transects were walked at a slow pace of no more than 1km/h to ensure the greatest opportunity for nest detection. Upon detection, the perpendicular distance from the transect to the nest (measured directly beneath it) was recorded in metres along with bearing to the transect in degrees. Nest heights were recorded using a Nikon ProForestry laser rangefinder to ensure accuracy, with the measurement being taken to the base of the nest and measured to the nearest 0.2m.

For every nest tree a number of tree architecture variables were measured and recorded which included; tree height, first bole height (FBH), diameter at breast height (DBH), crown radius to the north, south, east and west, crown shape and connectivity. Tree height was measured using the laser rangefinder and again measured to the nearest 0.1m, tree height was determined by measuring the highest visible leaf on the tree. FBH was measured at the point that the lowest bough or branch joined the main stem or trunk of the tree using either the laser rangefinder or if low enough a tape measure was used. Using tree height and FBH the crown size was calculated using the formula:

$$Crown\ size\ (cs) = Tree\ height(TH) - First\ branch\ height(FBH)$$

Using nest height and tree height we were able to calculated the amount of overhead canopy above the nest:

$$Overhead\ canopy = Tree\ height - Nest\ height$$

DBH was measured using a tape measure at chest height (1.4m) around the trunk of the tree to the nearest centimetre. The radius of the crown was measured in meters from the trunk of the tree to the edge of the crown to the North, East, South and West, these were recorded as the crown radius can be quite variable so this should eliminate any potential over or under estimates. Using these crown radius measurements, the crown area was calculated using:

$$Crown\ area = \sum \frac{\pi Nr^2}{4} + \frac{\pi Sr^2}{4} + \frac{\pi Wr^2}{4} + \frac{\pi Er^2}{4}$$

Nr= North radius

Sr= South radius

Wr= West radius

Er= East radius

Crown shapes were classified as either spheroid, elongated spheroid, cone, upside-down cone, umbrella, bent over, broken or palms (Table 4.1).

Using the crown shapes along with the crown radii and crown size measurements we are then able to calculate the crown volume:

Crown volume:

$$NS\,r\ (North - South\,radius) = \frac{Nr+Sr}{2}$$

$$EW\,r\ (East - West\,radius) = \frac{Er+Wr}{2}$$

$$CSr\ (Crown\,Size\,radius) = \frac{CS}{2}$$

Cone and upside-down cone crown volume:

$$V = \sum \frac{\pi NSr^2 \frac{CS}{3}}{2} + \frac{\pi EWr^2 \frac{CS}{3}}{2}$$

Spheroid, elongated spheroid and bent over crowns:

$$V = \frac{4}{3}\pi NSrEWrCSr$$

Umbrella shape crowns:

$$V = \frac{\frac{4}{3}\pi NSrEWrCSr}{2}$$

Table 3-1 Definitions of crown shapes adapted from *(Coder 2000; Manduell et al. 2012)*

CROWN SHAPE	DEFINITION
SPHEROID	Sphere shaped/ lollipop shape
ELONGATED SPHEROID	Crown with a height greater than its width and rounded ends
CONE	Cone shaped crown with a wide base that tapers to the top
UPSIDE-DOWN CONE	Crown which dove tails from the first branches, inverse of the cone (also known as inverse tripod)
UMBRELLA	Similar to spheroid or cone but lowest branches tips hang further down than the base of the branch
BENT-OVER	Tree with trunk or crown growing significantly in one direction, typified by lack of crown in one direction

BROKEN	Tree where the crown has broken off leaving either a splintered top or new growth if still alive
PALM	If the tree is a palm species there is no crown but series of large palm leaves

Crown connectivity was estimated visually by estimating the proportion of the crown in contact or enclosed by neighbouring crowns using a four point scale; 0-25%, 26-50%, 51-75% and 76-100%, the inverse of this gives the exposure of the crown (Whitten 1982; Manduell et al. 2011; Cheyne et al. 2013).

Observed nests were placed into age classes by the lead author and if there were uncertainties a consensus would be reached with the trained field assistants; these classes were reflective of the decay rate. The classes were; 1- fresh leaves, still green; 2- mix of green and brown leaves; 3- all leaves turned brown and some holes forming; 4- all leaves gone and nest falling apart (van Schaik et al. 1995; Hashimoto 1995; Russon et al. 2001; Felton et al. 2003; Johnson et al. 2005; Spehar et al. 2010). Nest position was recorded following the standard methodology set out by the University of Zurich's Department of Anthropology (Orangutan Network 2015) and used in Prasetyo et al. 2012; Rayadin & Saitoh 2009. These positions are defined as follows; Position 1- at the base of the branch and close to the main stem; Position 2- at the end of a branch; Position 3- top of the tree crown; Position 4- using the branches of two different trees weaved together (there were no Position 0 recorded at either site; Position 0 are nests that are found on the ground) (Fig 1.3).

All nest trees species were identified by trained field assistants. All trees within a 5m radius of the nest tree were recorded as these were used to provide a control against the nest tree to determine whether nests were built within the surrounding canopy or above or below it. For each of these trees the distance to the nest tree, direction with a compass, DBH, first bole height, tree height, crown shape, connectivity and species were recorded. All nests were recorded with GPS points using a Garmin GPSmap 60Cx.

3.2.4 Data analysis

A generalised log linear model with a Gamma distribution was ran using R (R Core Team 2017) and the lme4 (Bates et al. 2015), Matrix (Bates & Maechler 2017) and car (Fox & Weisberg 2011) packages to understand the relationship between nest height and the structure of the nest tree and the height of the canopy surrounding the nest trees. All model iterations were run including an intercept only model using the dredge function of the MuMIn package (Barton 2018). The models were ranked by their AICc (corrected Akaike Information Criterion) scores which compensates for small sample sizes. A subset of these models was then extracted using the maximum delta ∆AICc values (which is the difference between the AICc of each model from the best performing model) that are <2. This threshold was used as models with AICc values <2 all have substantial support and perform equally well (Burnham et al. 2002; Burnham & Anderson 2004). From this subset of best performing models' parameter estimates were averaged and parameters were weighted by the proportion of models that the parameter was present in. These weights allow for the relative importance of each parameter to be assessed and understand which of the tree structure characteristics have the greatest influence upon nest height. The graphical outputs of these models were produced using the sjlabelled (Lüdecke 2018a), sjPlot (Lüdecke 2018b), sjmisc (Lüdecke 2018c), dplyr (Wickham et al. 2017) ggplot2 (Wickham 2009), texreg (Leifeld 2013) and snakecase (Grosser 2018) packages.

To investigate nest position, a PCA (Principal Component Analysis) was used to determine which variables were important in determining nest position and simplify the model if any variables were not significant or not present in any of the best principal components (Hotelling 1933). To select the most important principal components, two criteria were considered; the Kaiser contribution criterion (Yeomans & Golder 1982) and the interpretability criterion of Hatcher and Stepanski (Echeverry-Galvis et al. 2014), in addition to the percent of variance that each of the principal components explained. Using the Kaiser criterion an important principal component should explain at least one original variable and have a corresponding eigenvalue >1. The interpretability criterion however, states that an important principal component is a linear combination of original variables which all represent the same latent concept (Echeverry-Galvis et al. 2014). Following what Echeverry-Galvis et al. (2014) suggested, an original variable was determined to be influential or important if its weight in the principal component was >0.3. An original variable is defined as a variable that only appears once and is included in the first instance that it has a weight >0.3. The PCA biplot allows for the effects of each of the variables that influences each of the nest positions to be visualised and determined. PCA analysis was performed using the ggbiplot (Vu 2011) and factoextra packages (Kassambara & Mundt 2017). Following this a multinomial logistic regression was run for nest position against the tree architecture variables and tree height and FBH of the surrounding canopy as this allowed for the differences between each nest position to be compared against a reference sample which was selected as position 1 nests. This analysis was ran using the nnet (Venables & Ripley 2002) and AICcmodavg (Mazerolle 2017) packages. As with nest height all model iterations were ran and the best performing models were selected based upon AICc scores <2. The models were model averaged and the parameters were weighted by the proportion of models which they were present in to give relative importance (RI) scores to determine their influence on the model using the MuMIn package in R (Barton 2018). The figures for this were produced using the ggplot2 (Wickham 2009), snakecase (Grosser 2018), plyr

(Wickham 2011), sjlabelled (Lüdecke 2018a), sjPlot (Lüdecke 2018b) and sjmisc (Lüdecke 2018c) packages.

3.3 Results

A total of 199 nests were found and recorded across both sites with 153 found in Sikundur and 45 in Sei Betung. 1200 trees were measured on vegetation transects in Sikundur and 720 in Sei Betung, 62 trees were recorded within 5m of nest trees in Sei Betung and 598 were recorded and measured in Sikundur. However, trees with broken crowns and palms were removed from the comparisons as they were significant outlier's and heavily affected the interactions as no nests were recorded in either crown shape and both were extremely rare and heavily skewed analyses for crown volume, crown size and crown area.

3.3.1 Nest height

Nest heights were found to differ significantly between Sikundur and Sei Betung (Welch's $t_{113} = -9.63$, $P= <0.001$) with mean nest height significantly higher in Sikundur (14.53m±4.71m) than Sei Betung (8.85m±3.02m). Crown volume, surrounding FBH and FBH of nest tree were all removed from the analysis due to overdispersion with all having VIF scores >4 suggesting multicollinearity. When field site was tested as a random effect within a mixed effects model, no significant effect was found upon the model with no significant difference found in AIC scores when using a Likelihood-ratio test ($X^2_{df1}=1.961$, $P=0.161$). Therefore, the simpler generalised linear model was used for the further analysis. Model selection presented 8 candidate models with ∆AICc scores <2 (Table 4.2). From these candidate models four variables were found to be present in every model therefore having relative importance's (RI's) of 1. These highly important variables were connectivity, crown shape, overhead canopy and the nest tree height. Crown area was also a highly important variable with a RI of 0.64 whereas the surrounding tree height only had an RI of 0.44 whilst crown size and DBH both had RI's <0.3.

Table 3-2 *Top performing models of nest height based on ∆AICc scores <2 and the full model containing all variables and null model*

Model	**Adj R^2**	**df**	**logLik**	**AICc**	**delta**	**weight**
Nest height~Connectivity+Crown shape+Overhead canopy+Tree height	0.9522	12	-295.37	616.43	0	0.17
Nest height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown area+Surrounding tree height	0.9534	14	-293.101	616.5	0.06	0.17
Nest height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown area	0.9528	13	-294.27	616.52	0.09	0.16
Nest height~Connectivity+Crown shape+Overhead canopy+Tree height+ Surrounding tree height	0.9526	13	-294.55	617.07	0.64	0.12
Nest Height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown area+Crown size	0.953	14	-293.75	617.79	1.36	0.09
Nest Height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown area+Crown size+Surrounding tree height	0.9536	15	-292.67	617.97	1.54	0.08
Nest Height~Connectivity+Crown shape+Overhead canopy+Tree height+ Crown area+Surrounding tree height+DBH	0.9535	15	-292.76	618.17	1.73	0.07
Nest Height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown area+DBH	0.9529	14	-293.95	618.2	1.76	0.07
Nest height~Connectivity+Crown shape+Overhead canopy+Tree height+Crown size	0.9523	13	-295.23	618.43	2.00	0.06
Nest height~Connectivty+Crown shape+Overhead canopy+Tree height+ Crown area+Crown size+Surrounding tree height+DBH (Full model)	0.9539	19	-292.302	619.6	3.18	0.028
Null model	0	2	-591.533	1187.1	570.7	0

Table 3-3 *Model averaged parameters of the top performing models for nest height determined by ∆AICc scores <2*

Parameters	Estimate	Std Error	Adj SE	Z value	Pr(>|z|)	RI	2.5% CI	97.5% CI
Intercept	1.259	0.061	0.061	20.522	**<0.001**	-	1.138	1.379
Connectivity 25-50%	0.07	0.038	0.038	2.058	**0.039**	1	0.004	0.153
Connectivity 50-75%	0.125	0.036	0.037	3.433	**<0.001**	""	0.0538	0.197
Connectivity 75-100%	0.122	0.036	0.036	3.383	**<0.001**	""	0.0514	0.193
Crown shape C	0.176	0.047	0.048	3.699	**<0.001**	1	0.083	0.269
Crown shape ES	0.115	0.048	0.049	2.367	**0.018**	""	0.02	0.210
Crown shape S	0.182	0.045	0.046	3.975	**<0.001**	""	0.092	0.271
Crown shape UC	0.124	0.047	0.047	2.635	**0.008**	""	0.032	0.216
Crown shape UM	0.108	0.055	0.055	1.972	**0.049**	""	0.0007	0.216
Overhead canopy	-0.072	0.003	0.003	23.238	**<0.001**	1	-0.078	-0.066
Tree height	0.073	0.002	0.002	41.911	**<0.001**	1	0.069	0.076
Crown area	0.0002	0.0002	0.0002	0.939	0.348	0.64	<0.001	0.0007
Surrounding tree height	0.001	0.002	0.002	0.654	0.513	0.44	-0.0008	0.006
Crown size	-0.0004	0.0015	0.002	0.327	0.744	0.23	-0.007	0.0028
DBH	-0.0001	0.0004	0.0004	0.246	0.806	0.14	-0.002	0.001

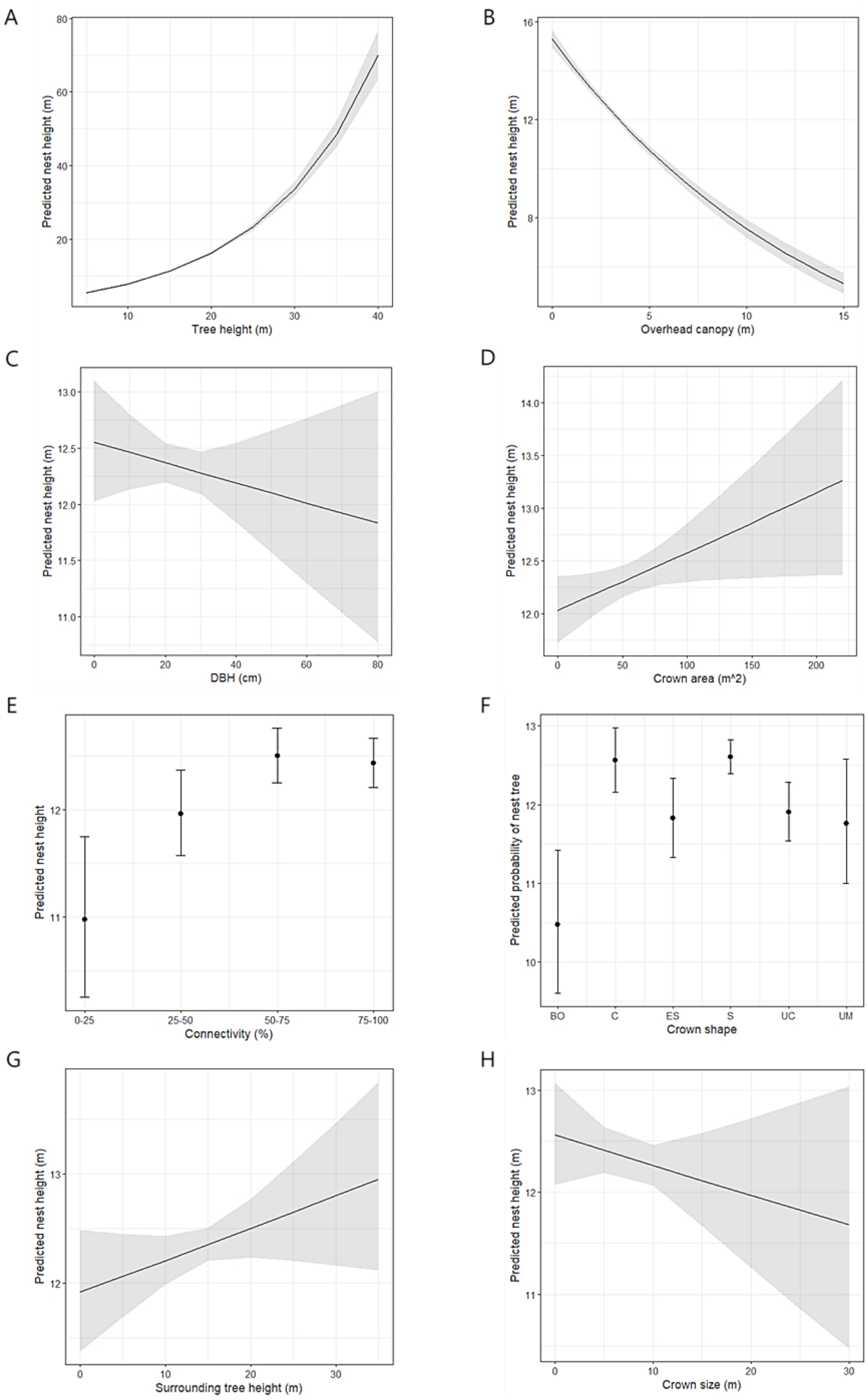
A
Predicted nest height (m)
80
60
40
20
10
20
30
40
Tree height (m)
B
Predicted nest height (m)
16
12
8
0
5
10
15
Overhead canopy (m)
C
Predicted nest height (m)
13.0
12.5
12.0
11.5
11.0
0
20
40
60
80
DBH (cm)
D
Predicted nest height (m)
14.0
13.5
13.0
12.5
12.0
0
50
100
150
200
Crown area (m^2)
E
Predicted nest height
12
11
0-25
25-50
50-75
75-100
Connectivity (%)
F
Predicted probability of nest tree
13
12
11
10
BO
C
ES
S
UC
UM
Crown shape
G
Predicted nest height (m)
13
12
0
10
20
30
Surrounding tree height (m)
H
Predicted nest height (m)
13
12
11
0
10
20
30
Crown size (m)

Figure 3-2 *Marginal effects plots of the most influential variables found through multi-model inference and how they influence Sumatran orangutan nest height*
A- Tree height, B- Overhead canopy, C- DBH, D- Crown area, E- Connectivity, F-Crown shape, G-Surrounding tree height, H-Crown size
**Crown shape classes: BO= Bent-over, C= Cone, ES= Elongated Spheroid, S= Spheroid, UC= Upside-down cone, UM= Umbrella*

The marginal effects plots in Fig 3.3 displays that nest height is strongly positively associated with tree height and show strong negative association with overhead canopy suggesting that nests are generally built in the upper canopy. Nest height is also observed to be negatively associated with both DBH and crown size, suggesting that nests are built higher in trees with smaller crowns and lower DBH. Crown area was positively associated with nest height suggesting that nests are built higher in wider crowns. A weaker positive relationship between surrounding tree height and nest height was also found. Increasing connectivity is strongly associated with increasing nest height with nests in trees with connectivity <25% predicted to be built 1.5m lower than those in tree with connectivity >50%. Nests were built highest in spheroid and cone shaped trees with bent-over trees having significantly lower nest heights than any other crown shape. From slope and effects of each parameter it is evident that changes in tree height, overhead canopy connectivity and crown shape have the greatest influence upon nest height.

Further in-depth comparisons of the effect of connectivity upon nest heights when compared to surrounding trees further agrees with what was identified by the marginal effects of the model revealing that for nest trees with connectivity >25% and <75% nest heights are found within the upper canopy and close to the mean height of the surrounding trees with no significant differences detected (25-50% Nest height vs Surrounding tree height $t_{58} = -0.47$, $P= 0.64$, 50-75% Nest height vs Surrounding tree height $t_{139} = -0.14$, $P= 0.89$). Whereas in trees with connectivity <25% and >75% nest heights were found to be significantly lower than the surrounding tree heights (<25% Nest height vs Surrounding tree height $t_7 = -2.63$, $P= 0.03$, >75% Nest height vs Surrounding tree height $t_{164} = -2.24$, $P= 0.03$) and in the case of <25% connectivity the nests were also lower than the surrounding FBH as well (see Supplementary materials Fig.S8).

Crown shapes also agree further with what was found in the model and marginal effects of Fig 3.4. Nests built in elongated spheroid and umbrella shaped crowns were all found to be significantly lower than the height of surrounding trees (ES $t_{31} = -2.36$, $P= 0.02$, UM $t_{11}= -3.68$, $P= 0.004$). Nests within bent over crowns were close to being significantly different and were much lower than the surrounding tree heights but due to the small sample size significance was not found (BO $t_4= -2.66$, $P=0.056$) (see Supplementary materials Fig S8.). There was no significant difference between the height of nests built within cone, spheroid and upside-down cone shape crowns and the surrounding tree heights (C $t_{52}= -$

1.01, P= 0.32, S t_{212} = -0.15, P= 0.88, UM t_{62}= -1.29, P= 0.2), suggesting that these are built within the upper canopy and are also within the upper canopy of the nest trees (see Supplementary materials Fig S8.). Higher proportions of nests within cone shaped crowns were found in trees with connectivity <25% than any for trees with any other level of connectivity. Spheroid crowns were found in roughly similar proportions no matter the connectivity (see Supplementary materials Fig. S9).

3.3.2 Nest position

No position 0 nests were recorded at either site, whilst position 4 nests were the rarest of those found accounting for 8.6% of all nests with the other three positions used in roughly equal proportions in Sikundur (Fig. 3.5). In Sei Betung position 4 nests were even rarer than in Sikundur, contributing only 2.22% of all nests built at the site. Position 1 nests were also far less common in Sei Betung than Sikundur, decreasing from 31.4% of nests in Sikundur to only 20% of nests in Sei Betung. Conversely Position 2 and Position 3 nests were far more common in Sei Betung contributing 37.8% and 40% respectively compared to 28.1% and 30.1% in Sikundur. Therefore, we can see that site differences have produced differences in the proportions of nest positions used. Further observation of the distributions of the parameters in Figure 4.6 further display the differences between the nest positions. Position 4 nests are both built lower and in smaller trees than all other nest positions which are relatively similar in terms of nest and tree height. Position 2 nests have the largest DBH and largest crowns in terms of area, volume and size of all the nest positions, whilst Positions 1 and 3 are very similar in respect to these parameters whilst Position 4 are again the smallest. The overhead canopy and canopy below measurements provide information about both a nests positions within a crown but also the size of crown. Position 4 nests have the smallest numbers for both as they are built in the smallest crowns and conversely Position 2 have the highest amount of canopy above and second highest amount of canopy below due to these nests being built around the mid-point of trees with very large crowns. Position 1 nests as expected were found to be built lower in the crown and Position 3 nests in the upper crown with very little overhead canopy. All positions appear to have similar surrounding tree heights though so surrounding crown height may not have much of an impact upon nest position.

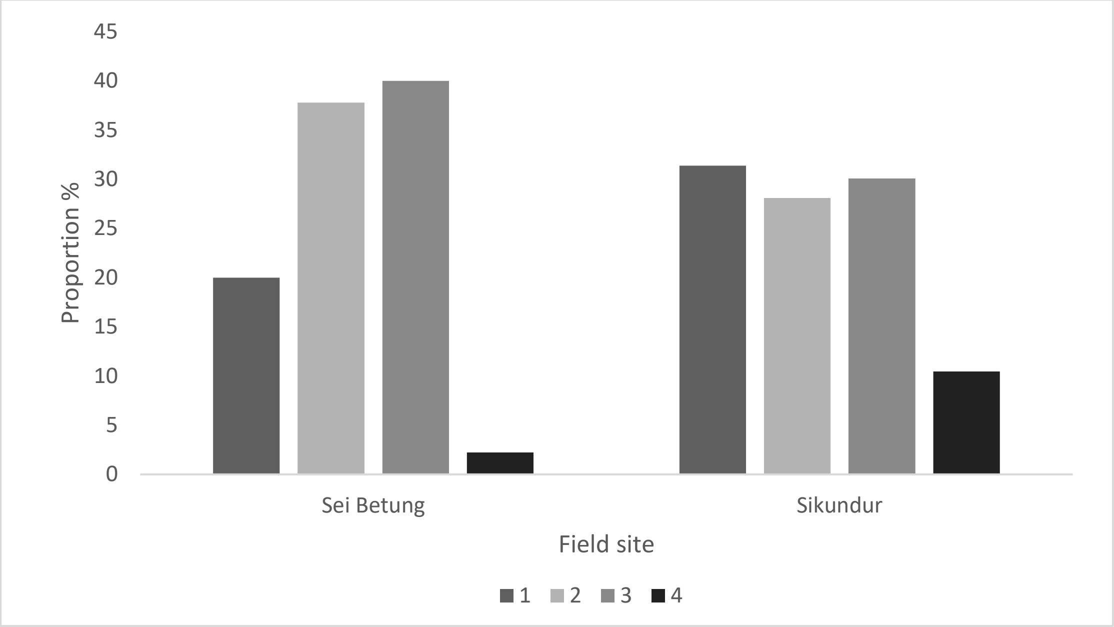

Figure 3-3 Proportion of each nest position in Sikundur and Sei Betung

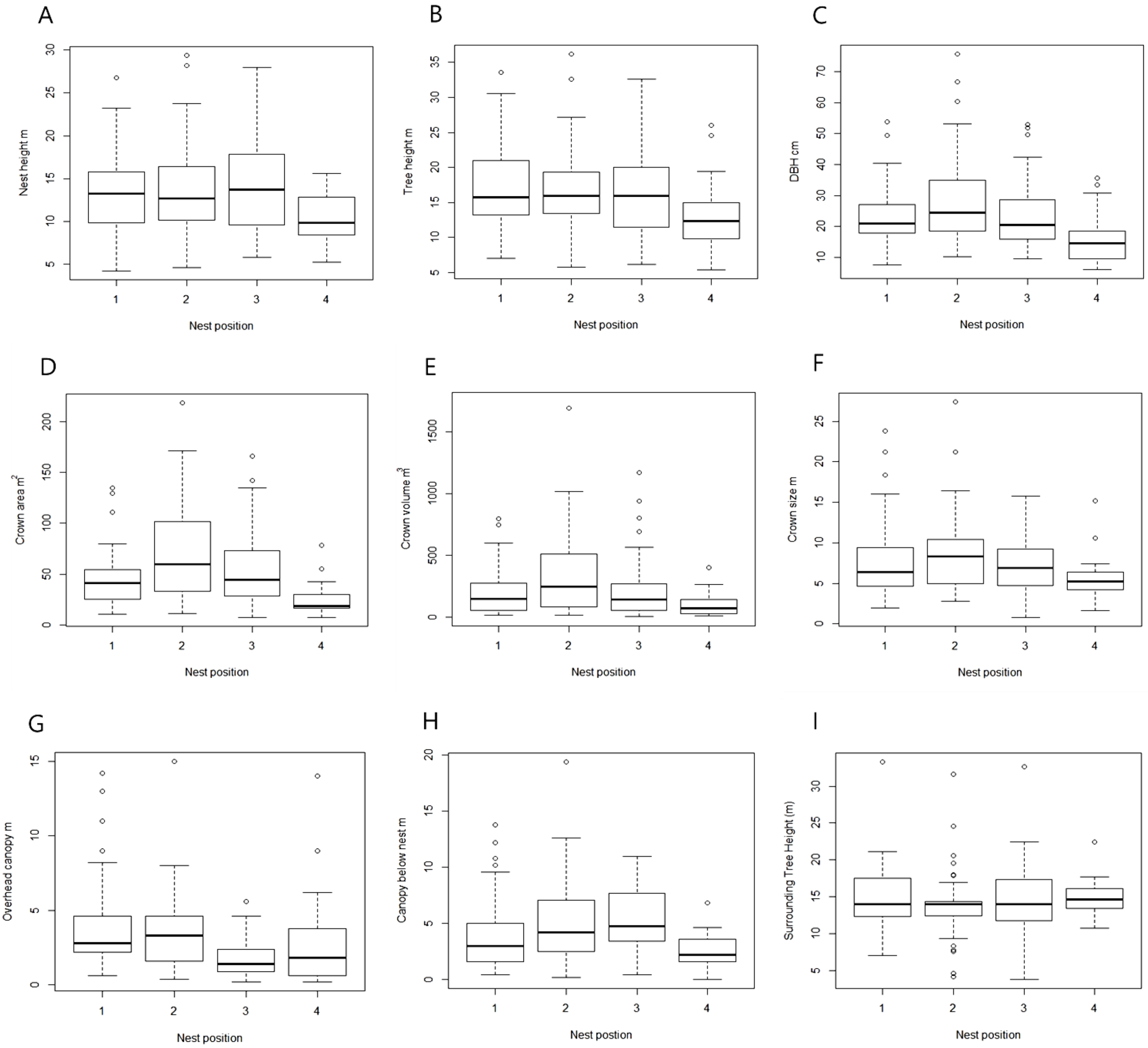

Figure 3-4 Boxplots of the differences between nest positions with nest data pooled from both Sikundur and Sei Betung: A- Nest height, B- Tree height, C- DBH, D- Crown area, E- Crown volume, F- Crown size, G- Overhead canopy, H- Canopy below nest and I- Surrounding tree height

To better understand, quantify and visualise how these differences in tree architecture differentiate nest positions a PCA analysis was run and the PCA will help us to identify variables with high overlap which can then be removed to assist later modelling. The scree plot in Figure 4.7 shows a marked decrease in the variance between the top principal components. Using Kaiser's criterion and the interpretability criterion both agreed that from the ten principal components only the first three were of significant interest. This was determined due to the first three PC's being the only components to have eigenvalues >1 (PC1- 4.84, PC2- 1.99, PC3- 1.14) fulfilling the requirements of the Kaiser criterion and these PC's were the only ones to contain unique variables with loadings >0.3 as all other PC's contained variables which were already significant in one of the first three PC's. This analysis suggests that all variables play some determinant role in nest position as none were excluded from the important principal components.

Table 3-4 Selected observed variables and corresponding coefficients based on interpretability and Kaiser criterion for PCA analyses Sumatran orangutan nest position

Component	Variable	Coefficient
1	Crown volume	-0.407
	Tree height	-0.397
	Crown size	-0.379
	DBH	-0.365
	Nest height	-0.357
	Crown area	-0.322
2	Surrounding Tree Height	0.634
	Surrounding Tree FBH	0.632
3	Overhead canopy	0.811
	Canopy below	-0.359

The first PC accounted for 48.39% of the total variance, PC2 accounted for 19.86% and PC3 accounted for 11.42%, therefore in total these three principal components accounted for 79.67% of the total variance. In the biplot of the interaction of PC1 and PC2 (Fig 3.6) crown size and crown volume were found to show considerable overlap as did tree height, nest height and overhead canopy and surrounding tree height and surround FBH suggesting that in the interaction between these principal components they have similar influence. Due to this significant overlap and VIF scores from analysis in previous chapters suggesting overdispersion, nest height, crown volume and surrounding FBH were removed from the analysis and a further biplot was produced (Fig 3.7). The removal of these variables reduced the number of important principal components from 3 to 2 with overhead canopy moving into PC1 and surrounding tree height being the sole parameter in PC2. The new simplified important principle components of PC1 and PC2 accounted for a combined 69% of the total variance which is a small improvement on the previous analysis. The biplot in Figure 8 shows the resulting biplot from this reduction in parameters. Little has changed between this and the more complex biplot in Fig 3.8 showing that the removal of the overlapping variables has had little influence upon the analysis.

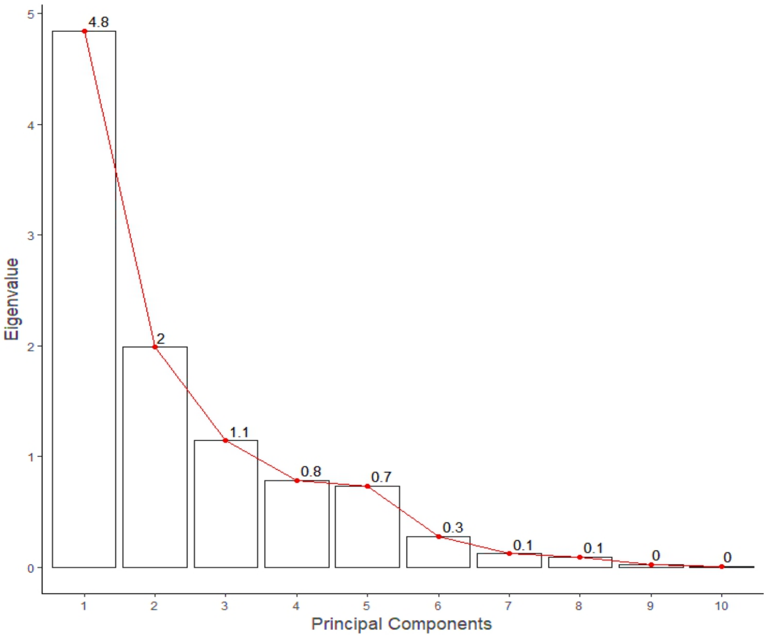

Figure 3-5 Scree plot of PCA of nest position showing corresponding variance of components. The cut off for the Kaiser criterion variance is 1 so three principal components are of significant interest in this analysis

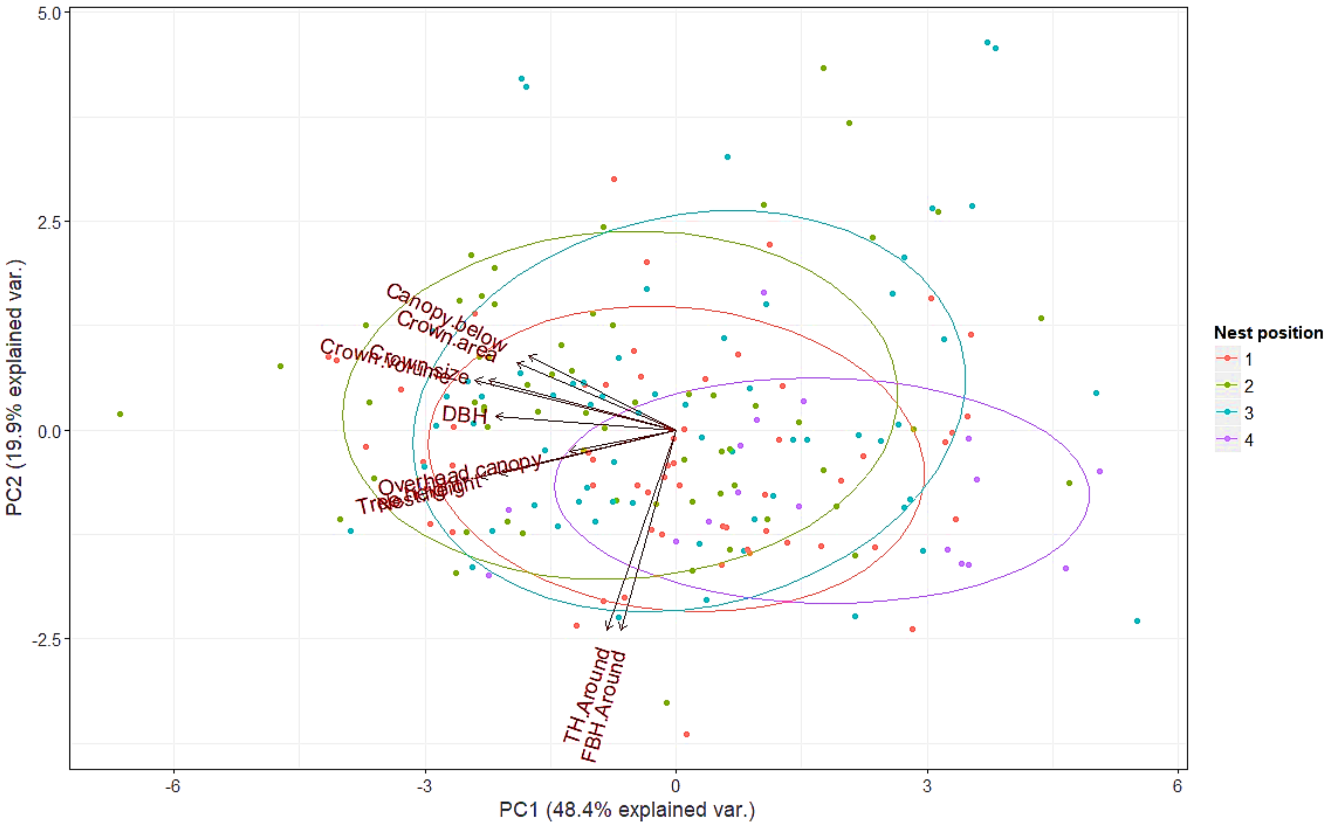

Figure 3-6 PCA biplot of the interaction of PC1 and PC2 for nest positions. Crown size and crown volume show considerable overlap as do Tree height, Nest height and Overhead canopy suggesting that in the interaction between these principal components they have similar influence.

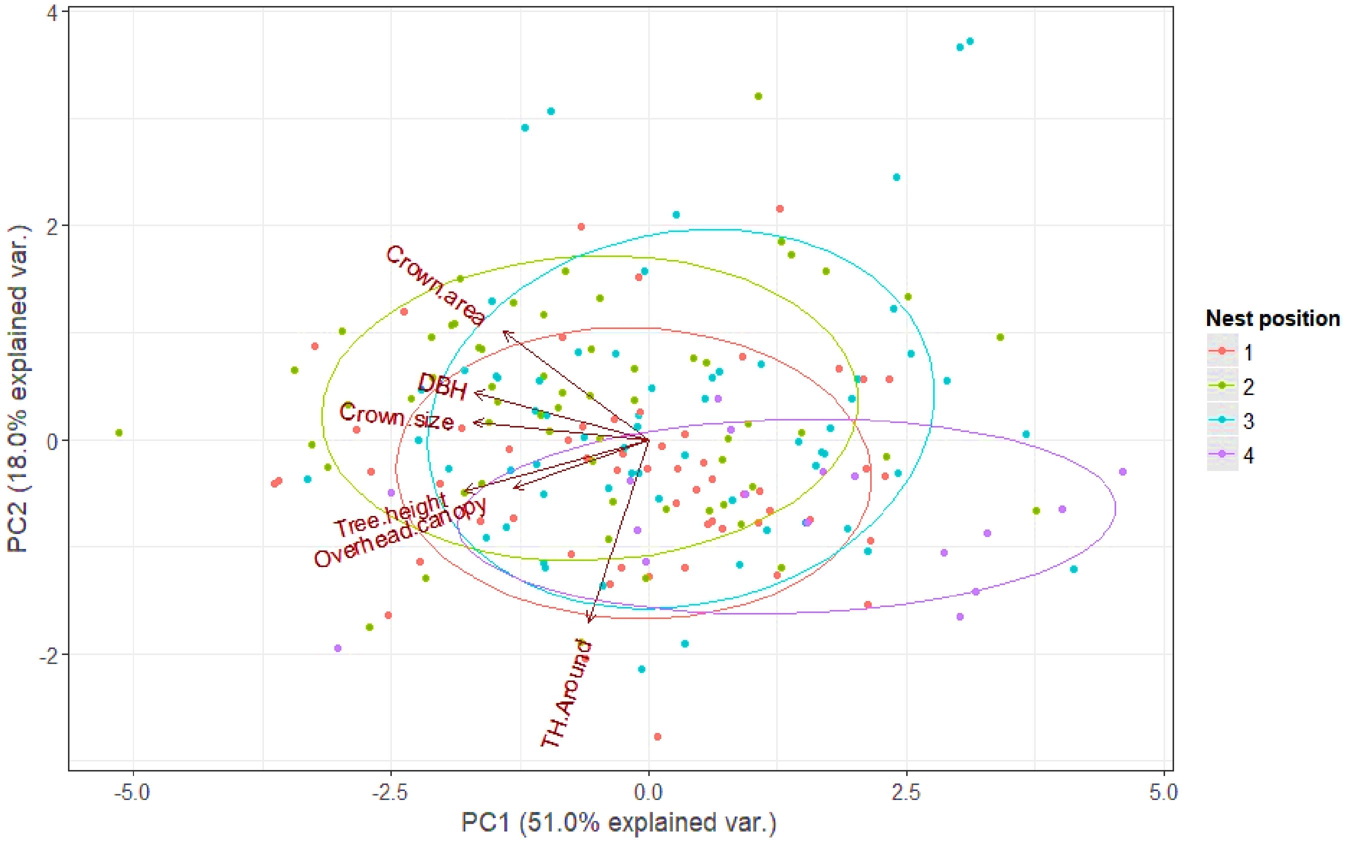

Figure 3-7 PCA biplot of the interaction of PC1 and PC2 for nest positions for the simplified data set following the removal of overlapping variables from initial analysis as can be seen in Fig S5.

The biplot in Figure 3.7 shows that Position 4 nests are built in trees surrounded by taller canopies compared to Position 2 and 3 which generally have lower surrounding canopies and are in built in significantly smaller trees and smaller crowns than all other nest positions. Figure 3.7 also suggests that Position 4 nests are built lower in the canopy of the tree that they were built in as position 4 nests are more positively linked with increased overhead canopy and conversely a lower amount of canopy below them. This is also true for Position 1 nests which is expected as these are built at the base of the branch near to the trunk and lower in the tree by definition. Position 2 nests have the largest crowns, DBH and crown area as was previously evidenced in Figure 3.7, whilst Position 3 nests are least associated with overhead canopy as to be expected by their definition of being built at the top of the main stem.

Following the PCA analysis a multinomial logistic regression was run to determine which parameters were the most influential upon nest positions, it also allowed us to test whether crown shape or connectivity were influential as they had been found to for nest height. The multinomial logistic regression presented two candidate models with ΔAICc scores <2 out of 256 potential models. Both of these candidate models contained crown area and overhead canopy, with the top performing model also containing the added effect of crown size. Model averaging showed that crown area and overhead canopy are the two most important variables when determining nest position with both having RI's of 1 and crown size having an RI of 0.52. DBH, tree height, connectivity, crown shape and surrounding tree height were all found to have no significant influence on determining nest position. Position 1 nests were used as the reference group for the model with all other positions tested against this reference group. The model averaged parameter estimates show that when differentiating between Position 1 and Position 2 the most significant variable is crown area with a P value <0.001. By observing both the parameter estimates in Table 3.7 and the log odds in Figure 3.8, it is evident that the trees which Position 2 nests are built in have significantly greater crown area and greater crown size than those position 1 nests are built in. Position 2 nests however, also have less overhead canopy than Position 1 nests and are therefore built higher within the crown than Position 1 nests. Position 3 nest trees also have greater crown area and crown size than position 1 nests but have significantly less overhead canopy which suggests as expected that position 3 nests are built higher in the canopy than Position 1 nests. Position 4 nests display the opposite of this trend having significantly smaller crown areas and crown sizes than the trees that nest Position 1 are built in but have significantly more canopy overhead suggesting that in these smaller trees, nests are built lower down in the canopy than those nest positions in trees with deeper and wider crowns.

Table 3-5 Top performing models for nest position using a multinomial logistic regression with candidate models identified by ΔAICc scores <2, as can be seen by the extremely low weight and high ΔAICc scores the full model and null model both performed poorly

Model	*df*	*logLik*	*AICc*	*ΔAICc*	*weight*
Nest position~Crown area+Overhead canopy+Crown size	12	-217.72	461.13	0	0.32
Nest position~Crown area+Overhead canopy	9	-221.17	461.29	0.16	0.29
Nest position~Crown area+Overhead canopy+Crown size+DBH+Tree height +Surrounding tree height+Crown shape+Connectivty(Full model)	51	-196.01	509.25	48.12	<0.001
Null model	3	-256.63	519.38	58.25	<0.001

Table 3-6 Model averaged parameter estimates of the top performing models of the multinomial logistic regression of nest position. Crown area and overhead canopy were the most influential parameters in determining nest position.

Nest position	*Parameters*	*Estimate*	*Std Error*	*Z value*	*Pr(>|z|)*	*RI*	*2.5% CI*	*97.5% CI*
2	Intercept	-0.885	0.446	1.986	**0.047**	-	-1.758	-0.011
2	Crown area	0.021	0.006	3.435	**<0.001**	1	0.009	0.033
2	Crown size	0.028	0.056	0.506	0.613	0.52	-0.079	0.188
2	Overhead canopy	-0.131	0.096	1.363	0.173	1	-0.319	0.057
3	Intercept	0.649	0.505	1.286	0.199	-	-0.34	1.639
3	Crown area	0.013	0.007	1.785	0.074	1	-0.001	0.026
3	Crown size	0.084	0.098	0.861	0.389	0.52	0.012	0.31
3	Overhead canopy	-0.687	0.16	4.297	**<0.001**	1	-1.001	-0.374
4	Intercept	0.553	0.659	0.84	0.401	-	-0.738	1.844
4	Crown area	-0.044	0.02	0.22	**0.026**	1	-0.083	-0.005
4	Crown size	-0.065	0.119	0.55	0.582	0.52	-0.399	0.148
4	Overhead canopy	0.033	0.161	0.204	0.838	1	-0.283	0.349

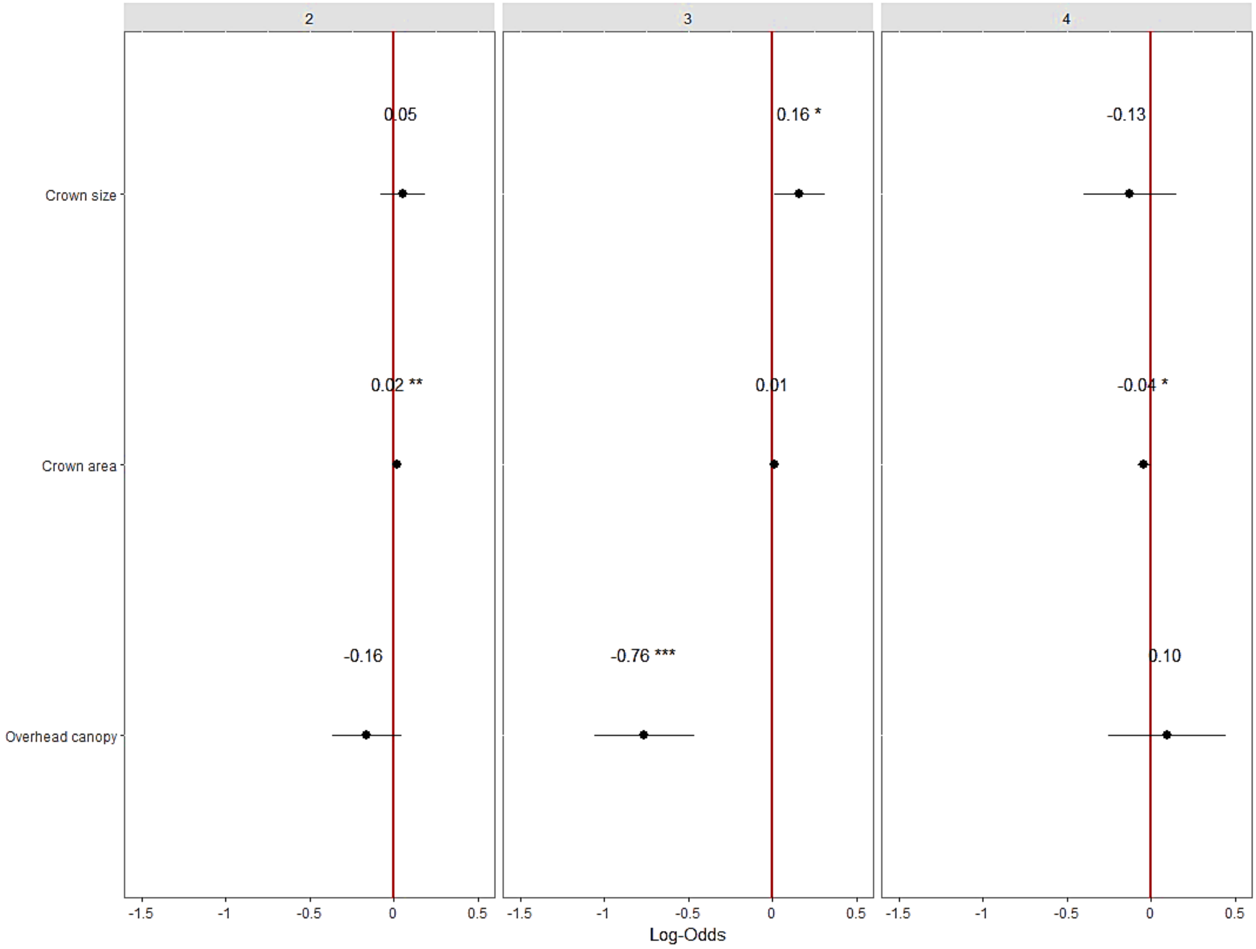

Figure 3-8 Forest plot of the log odds of the variables from the top performing models and how they differ for each nest position compared against position 1

3.4 Discussion

In this study we set out to further understand how when building a nest, nest height and nest position are influenced by the structural characteristics of the nest tree and how this may differ with changes in forest structure. Our aims were also to understand what may have been the principal driver determining selection for nest height and nest positions whether it be improved nest stability and comfort, thermoregulation or predator avoidance.

3.4.1 Nest height

No ground nests (Position 0) nests were found at either field site as had been expected. Tigers have been recorded in the vicinity of our field sites (Luskin et al. 2017) and camera traps within Sikundur recorded both tigers and clouded leopards so we know that there is a potential predation pressure in Sikundur and possibly Seprasetyo(Prasetyo et al. 2009; Badji et al. 2017)i Betung (Abernethy et al. 2016). Elephants and their signs were encountered a number of times at both Sikundur and Sei Betung as well as images of them on camera traps, so there is also the potential that the presence of elephants may also influence nest patterns in orangutans as has been observed with gorillas (Tutin et al. 1995; Anderson 1998).

Site differences were found with nests heights, supporting our hypotheses. As expected, nests in Sikundur being built significantly higher than those in Sei Betung. Differences in nest height were expected as nest height is known to be correlated with tree height (Prasetyo et al. 2009; Badji et al. 2017) and in Chapter 2 we showed that the forest structure differed significantly between both sites, with Sikundur having significantly taller mean tree height. When modelling the effect of the tree architecture variables field site was found to have no significant effect upon the interaction, as such suggesting that the variables which influence nest height carry across sites and differences in forest structure. Tree height, overhead canopy, crown shape and connectivity were the variables found to have the greatest influence upon nest height being present in all top performing models and RI values of 1. Model averaging also suggested that crown size, crown area, DBH and the height of the surrounding trees were also influential upon determining nest height. The results of these models also suggest that the determination of nest height is more complex than has previously been suggested (Ancrenaz et al. 2004a; Prasetyo et al. 2009; Cheyne et al. 2013; Badji et al. 2017). Rather than being simply a function of tree height as has been suggested in previous literature (Badji et al. 2017) .

The models showed a strong association between nest height and tree height however we also see that surrounding tree height also increases with nest height and when looking at both Figures S8 and S9 we find no instance in which nests are built above the level of the surrounding canopy though nests are built in significantly taller trees than the average. By avoiding nesting in extremely tall trees as noted in Chapter 2 and not nesting above the canopy this could be seen as rejecting the thermoregulation hypothesis, however nesting within the upper canopy would still provide a reduction in humidity (Koops et al. 2012a; Samson & Hunt 2012). By nesting within the height of the surrounding canopy though nests are offered greater protection from wind and rain as well as from strong sunlight which could offer a more comfortable nest site and with reduced wind sway also a safer and more stable nest site. Nesting lower in the canopy would have offered greater stability and reduction in wind sway though (Samson & Hunt 2012), therefore nesting within the upper canopy must be an anti-predatory response. Nesting within the upper canopy potentially offers a "goldilocks height" whereby the nest is not too high that it is exposed to strong winds which may dislodge the nest, but it is not to low that it experiences higher humidity and offers easy access to ground predators. Nesting within the upper canopy also offer a greater potential to escape from the nest should a predator discover its location as by nesting within the canopy the nest has close access to other branches and trees and escape routes (Baldwin et al. 1981; Anderson et al. 1983).

Unsurprisingly, nest height was also found to be strongly linked with increased crown connectivity. Nests built in trees with low connectivity were found to both built below the height of surrounding trees but also in much smaller trees. This could be a method of reducing the impact of the wind and rain which would be significantly more intense due to the lack of surrounding trees to act as windbreaks. However, this could also be a product of availability as trees which are less connected may be in more open areas and as such have less ned to compete for light and thus less need to grow tall compared to growing a wider crown to maximise light capture (Yoda 1974; Hartshorn 1978; Clark & Clark 1992; Ackerly 1996; Sterck & Bongers 2001). Conversely, within more connected trees, nests were found to be built higher in the crown of the nest tree. This could be due to trees with higher connectivity scores being found in denser stands of forest and as such the surrounding trees provide added shelter by acting as windbreaks as well as providing further shade and protection from rain. The reduction in the impact of the wind through the shelter provided by the surrounding trees reduces branch sway and the chance of branch failure which is one of the major dangers of nesting higher within the tree, the removal of this risk allows for nests to be built higher within the crown and in positions further from predators (Peltola 1996; Moore & Maguire 2004; Samson & Hunt 2012)

Unlike chimpanzees in the open habitat of Assirik, nests in Sei Betung were not built on the top of the crown with no overhead branches (Baldwin et al. 1981; Hernandez-Aguilar et al. 2013; Hunt & Mcgrew 2014). Instead, orangutan nests in Sei Betung as in Sikundur tended to be built within the upper canopy as this still provides the nest with shade and protection from wind, rain and overhead sunlight whilst still raising the nest high from the ground and potential predators (Anderson 1984, 1998; Ancrenaz et al. 2004a; Cheyne et al. 2013). Knowing that orangutans in both open habitats such as Sei Betung and closed habitats such as Sikundur suggests that the use of drones to survey orangutan densities at both sites is a viable option. An assessment of such methods has been conducted at Sei Betung by Wich et al. (2016) who found that the drone was able to find all but one of the nests identified on through ground transects. However Wich et al. (2016) had reservations the use of drones as they produced lower estimates per transect due to the higher number of transects that they completed and as such would have a serious effect upon density estimates. There was also concern about the initial purchasing cost of drone equipment, training required to use one and the methods for identifying nests from the still photos from the drone, though an early pilot by Chen et al. (2014) showed promising results of a user friendly method for identifying orangutan nests from such drone data. Should the technology improve and become cheaper then there is the potential for it to be extremely useful in surveying orangutan densities within habitats such as Sikundur and Sei Betung.

Crown shape plays a significant part in determining nest height. Nests built within upside-down cone shaped crowns along with cone and spheroid shaped crowns were all found to be built within the upper canopy of the nest trees and near to the top of the surrounding tree heights (Fig S9). These are all relatively stable crown shapes with their wide crown areas and in the case of upside-down cone crowns are shapes which have been noted as being both relatively easy to form into a nest but also produce particularly stable and safe nests due to their concave shapes (van Casteren et al. 2012; Samson & Hunt 2014). In Chapter 2 we found that the crown shapes were also highly preferred as nest sites and it is likely that some structural aspect which allows nests to also be built high within these trees is why they are preferred. Nests within bent-over crowns were found to be much lower than the surrounding canopy which is likely due to small size of these trees and with the inherent instability of the bent-over shape it is safer to nest lower to avoid the effects of wind and the danger of nesting within the weaker upper branches. Similarly, bent-over trees were also highly avoided as nest sites in Chapter 2 as such, the smaller size and lower nests further suggests that such trees are not preferred or “quality” nest sites.

A similar trend was found for elongated spheroid crowns with nests being built low within the crowns of nest trees. The reasoning behind nesting low within trees with crowns of this shape can potentially be down to two reasons based around the openness of the forest. In more closed sites such as Sikundur where tree densities are high, crowns tend to be narrower due to the decrease in growing space. However, because of the decrease in light availability, the trunks also tend to be longer and first branch height higher in more dense forest stands to increase photosynthetic efficiency and limit wasted energy by avoiding growing foliage that does not receive light (Iwasa et al. 1984; Jung et al. 2011). As such, trees in such dense environments should have higher first branch heights which is a favourable property for predation avoidance and would be particularly beneficial to large males who require more stable positions lower in the crown and closer to the main stem as it would improve their safety from potential predators (Rayadin & Saitoh 2009; Prasetyo et al. 2012; Hernandez-Aguilar et al. 2013).

Nests in umbrella shaped cones were found to have the least overhead canopy suggesting that nests in these trees tend to be built in the upper crown. Unusually, 42.9% of all nests built in umbrella shaped cones were position 4 nests using another tree and position 3 were the second most common for umbrella crowns accounting for 28.6% of nests in these trees and position 1 and 2 both accounting for 14.3% of nests. It could be suggested that crowns of this shape are relatively weak as evidenced by the shape of the branches which are bent downwards creating the umbrella shape, along with the frequent use of either the main stem or support from another tree for building a nest within these trees. Nest are built within umbrella shaped crowns only in areas with connectivity >50% and tend to be built in the lower canopy which is likely a way of reducing the risk of building nests within these trees by reducing the impact of wind and rain (Samson & Hunt 2012).

The results from this study show that the pattern for nest height selection is similar across both and that nest height is a product of the interaction between the trees structural properties, an orangutan's desire for a nest furthest from potential ground predators but limited by the need for a safe and stable nest by avoiding strong winds and rain. Though there is this preference for nesting higher which would aid in predator avoidance, in areas where forest height and in turn nest heights are lower and the forest is more open so connectivity for escape routes are lower, nest height may not be enough to deter a predator. Though tigers terrestrial and do not climb often as adults they can still climb in search of prey (Gonyea & Ashworth 1975; Bhattarai & Kindlmann 2012) and lower nest heights in Sei Betung may not be enough to deter a tiger compared to the significantly higher nests of Sikundur, thus, other adaptations such as nest position must be used as well to reduce the risk from predators (Anderson 2000; Pruetz et al. 2008; Stewart & Pruetz 2013).

3.4.2 Nest position

The proportions of each nest positions used differed across sites. Orangutans used all positions expect Position 4 nests in relatively equal proportions whereas more peripheral nest positions of Position 2 and Position 3 were more frequently built in Sei Betung. As the lower tree heights and lack of connectivity in Sei Betung may offer nest sites that provide less protection from predators and as such orangutans have been required to nest in more peripheral positions to provide that added protection from predators. Stewart & Pruetz (2013) noted that by building nests apes are able to create a safe place to rest where otherwise they would not be able to stand safely. Without the construction of the nest a single branch would not be able to support the weight of a sleeping ape but the collective strength of the branches formed into the nest offers the necessary strength and support and allows an ape to rest safely in a peripheral position out of the reach of predators. The results in Sei Betung appear to give evidence to this hypothesis. These results point to predator avoidance being the primary driver for nest site selection in Sei Betung as with its more open forest structure, wind would have a greater impact upon nests and in particular those in more peripheral positions (Flesch & Wilson 1999; James et al. 2006). Orangutans in Sei Betung are at greater risk of nest failure and potentially lower sleep quality due to wind sway due to their nest position preferences, given such risk there must be some advantage to outweigh the risk and the only advantage available is predator avoidance (Samson & Hunt 2012; Cheyne et al. 2013; Hernandez-Aguilar et al. 2013).

The forest in Sikundur has greater closure than in Sei Betung and higher tree height and first branch heights so trees are generally harder for predators to climb than in Sei Betung. This is potentially one of the reasons as to why there is little difference in the use of nest positions in Sikundur. However, when the nest heights of each position are observed (Fig 3.6B), it is apparent that all except for position 4 nests are built at roughly similar heights. This matches with the earlier result of the “Goldilocks height” in that there is a preferred for nests within the canopy and that the orangutans are tailoring their nests to match this height with the tree structure they are given. When comparing between the three 3 most used nest position in Sikundur using the PCA analysis and multinomial model it becomes apparent how each nest position is suited to the tees structural properties to allow it to fit within the “Goldilocks range” to maximise distance from predators, nest stability and avoiding strong winds and rain.

Both the PCA analysis and multi-model inference found that Position 4 nests were the most distinct nest position, differing greatly from all other nest positions by being built much lower and in the smallest trees whereas the other three positions showed greater similarities and overlap in structure of the tree that they were built in. Position 1 and 3 nests showed the greatest similarities with Position 3 nests differing by being built in trees with larger crown sizes and larger crown area as well as having significantly less overhead canopy which is expected by the definition of each nest and their position within the crown. The largest trees were associated with Position 2 nests, with Position 2 nests being built in trees with the largest crown areas, crown size, crown volume and DBH, but not the tallest. Trees with larger crown areas and DBH have been found to have greater stability and a reduction of sway in the wind (Nicoll & Ray 1996; Soethe et al. 2006; Cheyne et al. 2013). Trees with larger crown areas and crown sizes are also likely also have a higher number of branches which has also been found to reduce harmonic sway (James et al. 2006). This increased number of branches and in particular thick branches would also provide a greater amount of building material for the nest which would allow for more complicated and stable nests to be built such as those built at the ends of branches and at the top of the crown (Horn 1971; Rayadin & Saitoh 2009; van Casteren et al. 2012, 2013; Samson & Shumaker 2013; Stewart & Pruetz 2013; Samson & Hunt 2014). This suggests that although Position 2 nests are more precarious due to their position, similarly to chimpanzees minimise the risk of building these positions by only building them in the largest crowns which are most likely to have thick enough branches capable of supporting the weight of a nesting orangutan (Horn 1971; Rayadin & Saitoh 2009; Stewart & Pruetz 2013; Hernandez-Aguilar et al. 2013).

Position 1 nests were built in the tallest trees with relatively small DBHs' which is as expected as nesting higher within these trees would be problematic due to the reduced stability because of their tall, thin shape therefore the position of the nest within the crown would have to be lower (Nicoll & Ray 1996; Soethe et al. 2006; Cheyne et al. 2013). By being built in shorter trees, Position 3 nests are able to be built at the top of the main stem of the nest tree but still be within the upper canopy of the surrounding canopy. Both Position 1 and Position 3 nests tend to be built in trees with relatively small DBHs' and similarly sized crowns in terms of size, volume and area. It is possible that by nesting in trees with smaller trunks orangutans are increasing the difficulty for a potential predator to climb and reach the nest unnoticed. Smaller trunks is more liable to vibrate with the movement causing branches to shake and leaves to rustle which would warn a nesting orangutan of a predator attempting to reach the nest (Anderson 1984, 2000; Fan & Jiang 2008; Teichroeb et al. 2012). Unlike in the study by (Cheyne et al. 2013) which concluded that nest height and nest site selection was only driven by comfort, both Sumatran tigers and Sunda clouded leopards are have being recorded in the area of where our study was conducted (Rijksen 1978; Sugardjito 1983; Luskin et al. 2017). Both species and were recorded on camera traps in Sikundur in 2015 (Abernethy et al. 2016) confirming the presence of potential predation pressures on orangutans at these field sites. Sumatran elephants (*E. maximus sumatrensis)* were also recorded at our sites on both camera traps as well as being encountered by the lead author. Gorillas in Lopé, Gabon are known to avoid ground nesting in areas where elephants occur and build their arboreal nests higher to avoid disturbance by elephants (Tutin et al. 1995), there is potential that orangutans could exhibit similar behaviour. Future research is required to understand the interactions between orangutans and elephants. The presence of these species however, along with the significant numbers of human hunters recorded on the camera traps and large number of snare traps in Sei Betung which were personally observed suggest that there is a high risk associated with ground nesting or nesting lower in these sites, especially when compared to Cheyne et al's (2013) study in Sabangau or Ashbury et al's (2015) in Tuanan. Orangutans are known to exhibit predatory response behaviours(Rijksen 1978; Lameira et al. 2013) and orangutans in Borneo still produce alarm calls at a model of a tiger even though tigers have been potentially extinct on the island since the Late Pleistocene or Early Holocene (10,000-12,000 years ago) (Piper et al. 2007; Lameira et al. 2013), therefore orangutans must also exhibit other anti-predatory behaviours if such a response is so ingrained in the species behaviour.

Countering the hypothesis that greater proportions of Position 4 nests are built in more heavily disturbed forests (Prasetyo et al. 2009, 2012), Position 4 nests were far more common in Sikundur than Sei Betung; contributing 10.5% and 2.2% of nests at each site respectively. Furthermore, no Position 4 nests were built in a tree with connectivity <50% suggesting that because these nests are so low in height that adequate escape routes from this nest position are a necessity. The smaller proportion of Position 4 nests in Sei Betung further supports the predator avoidance hypothesis as this nest position is built lowest to the ground and in the smallest trees so would provide the least protection from ground predators of all nest position other than ground nesting. Rather than being a product of a paucity of large trees, it appears more likely that as Prasetyo et al. (2009) alternately hypothesised that increased use of Position 4 nests is due to differences between species or cultures as only populations in Central Kalimantan have been found to show a preference for building nests through tree tying. However, another potential theory as to the building of Position 4 nests is the associated with stem density and the availability of small trees in close vicinity to each other. Sikundur unlike Sei Betung has a relatively closed structure and so there is a higher density of stems which could be used to build a nest with whilst in Sei Betung with its more open habitat there may be too few neighbouring trees to safely build such nests. The forests in Tuanan and Sabangau though disturbed likely have a more closed secondary forest structure as opposed to the open habitat in Sei Betung, thereby facilitating the building of such nests (Husson et al. 2009; Prasetyo et al. 2009).

Though differences in forest structure and predation avoidance may provide an explanation for the differences in proportions of nest positions used at each site there is also the potential that it could be due to sex and age preferences in nest positions. Rayadin & Saitoh (2009) and Prasetyo et al. (2012) found that there appeared to be age and sex differences in the nest positions used due to the differences in body size, with younger individuals preferring to nest in more peripheral and unstable positions whilst large adults nested closer to the main stem. It is possible that these differences in nest positions could tell us about the population demographics in a site as generally flanged males would ordinarily be restricted to Position 1 nests but potentially in a site such as Sei Betung where Position 1 nests are rarer that flanged males are either leaving the site or utilising more unstable nest positions due to a dearth in taller trees for building Position 1 nests in. This could be a potential avenue for future research using genetic methods with hair samples taken from these nests we could potentially identify whether these nest positions do represent the demographics of a population. If so, this could provide an easy and quick method of assessing population health through estimates of breeding males, females and young that could be used for strategic conservation plans.

3.5 Conclusion

The findings of our study show that the parameters that determine nest height and nest position in Sumatran orangutans is far more complicated than previous studies have suggested and is not merely a function of the height of the nest tree. Instead, nest height and nest position are determined by using the trees architecture to achieve a nest in a “Goldilocks range” that maximises the nests safety from predators using height and position in conjunction with the trees architecture to ensure the nest is both safe from predators, stable and protected from strong winds or rain. Orangutans appear to prefer nesting within the upper canopy as this both limits access to ground predators, offers potential easy escape routes through the connecting canopy and also increases comfort and stability by sheltering the nest from the wind and rain. In Sikundur where the forest is denser and trees are taller all nest positions except Position 4 were used in roughly equal proportion whereas in Sei Betung, where tree heights are lower and easier for predators to access a significantly greater proportion of peripheral positions (Position 2 and Position 3) were used. This suggests that predator avoidance may have a significant influence upon nest heights and nest positions of orangutans in the lowland dipterocarp forests of Sumatra though this needs further testing with sites in Sumatra where tigers may be absent.

Observations by Rayadin & Saitoh (2009) and Prasetyo et al. (2012) suggest that there is a body size and sex basis to nest positions and potentially the proportions of nest positions could reflect population demographics as large flanged males are required to nest in more stable positions near to the main stem due to their large body size. Potentially this could mean that in Sei Betung there is either a lower proportion of males in the site due to the lack of suitable nest trees or that these large flanged males are having to alter their nesting behaviours and utilise more unstable positions which could put them at greater risk of nest failure in strong winds. Further study of the nest position preferences of individuals through nest to nest follows or genetic analysis is required to understand the relationship between body size, sex, nest position and forest structure. Though there is the potential that nests could provide a quick method of assessing a populations demographics should this theory be proved true.

The increased rarity of Position 4 nests in Sei Betung; an area which has experienced severe human disturbance and has a very open forest structure refutes what has been previously published that this nest position is used most often in disturbed forests with few large trees. Instead, our study suggests that this may be a geographic difference and that it is a cultural preference of the orangutans in Central Kalimantan or could be a product of the open habitat in Sei Betung that there are few trees close enough to produce Postion 4 nests whilst the studies in Borneo may have been conducted in more dense secondary forest where nesting material is more readily available.

Given the use of more peripheral positions in Sei Betung and the high rate of reuse of nests in Sei Betung found in Chapter 2 this reaffirms the need to protect larger trees and preferred nest sites within site open and disturbed site. As orangutans are prioritising more peripheral and potential unstable nest positions to reduce their risk from predation, they are more susceptible to nest failure or falling from the nest in strong winds. The removal of large trees and preferred nest trees could force orangutans in Sei Betung to utilise smaller trees which are even less capable of supporting their weight and offer less protection from predators. This could create more stress for the orangutans and affect their health as well as creating more risks with the potential for injury or death which could lead to orangutans dispersing from such areas in search of better forest but also potentially into neighbouring plantations.

Chapter 4: The influence of forest structure on orangutan densities in the recovering forests of North Sumatra

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4.1 Introduction

Habitat loss and habitat change driven by climate change and the spread of human influence are threats currently facing species globally and are exacerbating the threats of extinction to those species (Mantyka-Pringle et al. 2015). Understanding how habitat change may affect a species and how they utilise this space is key to developing effective conservation and management plans to ensure the continued survival of these species (Levin 1992). Orangutans are one of the many faunal species threatened with extinction due to habitat loss and landcover change as the forests in Sumatra and Borneo are cleared for agriculture, mining and timber extraction (Ancrenaz et al. 2016; Singleton et al. 2017; Voigt et al. 2018; Wich et al. 2016). With the decreasing proportion of pristine and undisturbed forests, orangutans and other forest species are needing to use and adapt to living in more disturbed habitats (Rao & van Schaik 1997; Felton et al. 2003; Knop et al. 2004; Ancrenaz et al. 2010; Mohamad et al. 2015). Reforestation and enrichment projects offer the potential to help disturbed and logged forests to recover to similar levels of structural diversity and complexity in a shorter time period than through natural recovery alone (Ådjers et al. 1995; Parrotta et al. 1997a; Vallauri et al. 2002; Kanowski et al. 2003, 2005, 2006; Catterall et al. 2004; Fagan et al. 2016). This decreased recovery time for forests could potentially be a valuable tool for orangutan conservation by working to slow or even reverse habitat loss in key forest areas (Meyfroidt & Lambin 2011; Kettle et al. 2014; Wills et al. 2017), though the use and value of these reforestation sites to orangutans are still poorly studied (Wich et al. 2016b).

Orangutans are the only great ape found in Asia, formerly they were found across South East Asia during the Pleistocene period but are now restricted to the two islands of Sumatra and Borneo (von Koenigswald 1982; Jablonski et al. 2000; Bacon & The Long 2001; Ibrahim et al. 2013). Three species are currently recognised with a single species on Borneo (*P. pygmaeus*) which is split into three recognised subspecies (Warren et al. 2001) and two species on Sumatra. On Sumatra there is the Sumatran orangutan (*P. abelii*) found to the north and the Tapanuli orangutan (*P. tapanuliensis*) restricted to the south of Lake Toba in Batang Toru, the southernmost range of orangutans in Sumatra (Nowak et al. 2017; Nater et al. 2017). All three species of orangutan are currently listed as critically endangered on the IUCN Red List (Ancrenaz et al. 2016; Nowak et al. 2017; Singleton et al. 2017) with habitat loss, habitat degradation, and hunting being the primary reasons for their decline in numbers (Ancrenaz et al. 2016; Nowak et al. 2017; Singleton et al. 2017).

Habitat loss has been driven by the rapid conversion of forest land for agricultural purposes in particular the planting of oil palm plantations, rubber plantations, candlenut plantations and mixed agroforestry (Wich et al. 2011; Robertson & van Schaik 2001; Voigt et al. 2018). Both protected and non-protected areas are experiencing forest loss, with areas at elevation below 500m above sea level experiencing the most rapid levels of forest loss. Selective logging is less destructive than clear felling and conversion to plantations, but it still has a negative impact upon orangutan densities on Sumatra (Rao & van Schaik 1997; Hardus et al. 2012a), but to a lesser extent on Borneo (Felton et al. 2003; Husson et al. 2009; Ancrenaz et al. 2010).

Although forest loss is still prevalent throughout the tropics, some countries have now transitioned from net deforestation to net reforestation (Meyfroidt & Lambin 2011; Wills et al. 2017). However, in many cases reforestation in former rainforest landscapes has taken the form of planted monocultures of fast-growing timber species, pulp and paper acacia plantations and oil palm plantations which lack the diversity of the rainforest which they replace (Lugo 1997; Lamb et al. 2001, 2005; Kanowski et al. 2003). Therefore caution is needed when defining forest land as not all forest has the same quality for biodiversity (Lugo 1997). As a consequence, mixed-species plantations are being established to meet both conservation and socio-economic needs (Harrison et al. 2000; Kanowski et al. 2003; Nguyen et al. 2014; Wills et al. 2017). Other projects have used planting of a diverse mix of native tree and shrub species to attempt ecological restorations of rainforests on cleared land along with revitalising degraded forest areas (Kanowski et al. 2006; Goosem & Tucker 2013; Lamb 1998; Parrotta & Knowles 1999; Parrotta et al. 1997a; Kettle et al. 2014; Parrotta et al. 1997b). Along with active reforestation there are many areas that through neglect, abandonment or through the active assistance of landholders have been able to revert to secondary forest naturally, this method offers potentially the cheapest in terms of financial and labour, and the most passive form of reforestation (Brown & Lugo 1990; Kanowski et al. 2003; Lugo & Helmer 2004; Wills et al. 2017).

The method of reforestation has a significant impact upon the area's value to conservation through its ability to approximate the original forest structure and biodiversity pre-clearance (Vallauri et al. 2002; Kanowski et al. 2003). The rate of colonisation and the floral and faunal diversity of the area are significantly influenced by the method of reforestation with monocultures offering little for native species to feed on or use and have generally low recruitment levels of species diversity as opposed to mixed plantations and logged areas (Stuebing & Gasis 1989; Lamb 1998; Kanowski et al. 2005, 2006; Beehler et al. 2008; Wills et al. 2017). Given time older, mature timber plantations (>50 years in age) have been found to develop similar forest structure to pre-clearance forests and host a significant diversity of species though still lower than pre-disturbance levels (Kanowski et al. 2003, 2005, 2006;

Catterall et al. 2004; Erskine et al. 2005). Through the extensive replanting of native tree and shrub species, ecological restorations host similar levels of diversity and canopy closer as old plantations but within a significantly shorter time scale (~-10-20 years) due to the large number of native species that are initially planted (Kanowski et al. 2003, 2005, 2006; Catterall et al. 2004). Similarly, assisted natural regeneration methods such as enrichment planting help forests to develop greater levels of diversity and structural complexity within a shorter period than by natural regeneration alone (Ådjers et al. 1995; Shono et al. 2007). Ecological restoration and assisted natural regeneration methods offer a significant tool in the recovery and restoration of the world's forests and forest species, though the increased cost and effort involved in implementing ecological restorations currently prohibits their wider use (Erskine et al. 2005)

Reforestation and forest restoration projects do have benefits for reptiles, birds, mammals and various invertebrate groups (Stuebing & Gasis 1989; Lamb 1998; Catterall et al. 2004; Kanowski et al. 2005, 2006; Beehler et al. 2008; Castillo et al. 2018). Plantations, in particular old plantations, are used by prosimian species in Madagascar and serve as both an extension to the habitat of lemurs as well as a buffer from human disturbance (Ganzhorn 1987). Ecological restorations have also to be successfully aided the conservation efforts of other primates and is the focus of other conservation plans for promoting primate species recovery through the restoration and linking of isolated forest habitats (Manjaribe et al. 2013; Allgas et al. 2017; Li et al. 2017; Chapman 2018). Primate species are particularly important to the regeneration of these forest through their role as seed dispersers, helping to accelerate regeneration and the recolonization of areas by native plant species (Parrotta et al. 1997b; Shono et al. 2007; Manjaribe et al. 2013; Tarszisz et al. 2018).

Forests which have experience low level disturbance are utilised by orangutans and are of conservation significance with orangutans being found in areas which have been selectively logged along with areas naturally regenerated after fires, though frequently at lower densities in disturbed areas than undisturbed areas (Rao & van Schaik 1997; Felton et al. 2003; Husson et al. 2009; Prasetyo & Sugardjito 2011; Cattau et al. 2015; Russon et al. 2015). Areas which had low levels of disturbance or have had significant time to recover have been found to host similar densities of orangutans to those which are undisturbed (Knop et al. 2004; Ancrenaz et al. 2004a, 2010; Marshall et al. 2006). Secondary regrowth forests are utilised by orangutans, and in some cases orangutans use to a greater extent than other mammalian species within the area (Gregory et al. 2012; Spehar & Rayadin 2017). Orangutans are known to highly utilise plantations including oil palm plantations (Ancrenaz et al. 2015), paper and pulp plantations (Meijaard et al. 2010) and agroforestry areas used for fruit production (Campbell-Smith et al. 2011b). Orangutans have been reported to utilize reforested areas and display significant clustering of nests, where nests are found in high densities in small pockets of sites rather than being evenly distributed throughout the site, this clustering is similarly found in heavily logged forests (Wich et al.

2016; Prasetyo & Sugardjito 2011; Ancrenaz et al. 2004). Davies et al. (2017) observed than in disturbed forests orangutans were selective of which areas of forest they used and travelled through and that this was linked to forest structure. Their results found that orangutans preferred forests with increased canopy closure, taller trees, uniform height and generally moved away from gaps and towards emergent trees.

A number of variables have been suggested and found to be useful in predicting or explaining orangutan nest densities. Both Marshall et al. (2006) and Wich et al. (2012) found that hunting has a significant effect on orangutan densities, orangutans are also killed in retaliation for crop raiding and damaging economically valuable trees and plants in plantations as well as being hunted for food and the pet trade (Meijaard et al. 2011; Campbell-Smith et al. 2011a, 2011b, 2012; Davis et al. 2013; Freund et al. 2017). As a consequence orangutan densities tend to be lower nearer to human settlements known to hunt orangutans likely as a result of the hunting by these settlements (Marshall et al. 2006; Wich et al. 2012b). Hunting orangutans for food is generally unheard of the North Sumatra outside of Batang Toru due to the Islamic religious beliefs of the locals that the meat of primates is “haram”. However, this does not discount potential poaching for the pet trade (Rijksen & Meijard 1999). Yet the pet trade in orangutans disproportionately affects Bornean orangutans, with Borneoan orangutans even appearing in Sumatran wildlife markets (Nijman 2009), therefore hunting pressures on orangutans in Sikundur and Sei Betung can generally considered low if any.

The availability of fruit such as figs and soft-pulp fruits are strong predictors of orangutan densities (van Schaik et al. 1995; Buij et al. 2002; Wich et al. 2004a) though this is not the case in all field sites in particular Sikundur where this study took place (Knop et al. 2004). Knop et al. (2004) in their study found that there was no correlation between orangutan densities and fruit availability in Sikundur. However, these results were disputed by Kanamori et al. (2017) as they noted that the survey period of 1 year may have been too short to detect any correlation due to the supra-annual nature of mast events. A such the research period could have missed any periods of peak fruit availability or the spatial differences in fruit availability may not have differed enough to cause the long-distance movement of orangutans (Kanamori et al. 2017).

As the rates of human disturbance across orangutan habitats are expected to continue (Wich et al. 2016; Voigt et al. 2018), it remains necessary to understand how changes to forest structure influence orangutan densities. As the extent of undisturbed, pristine habitat declines the importance of logged forests, secondary regrowth forest and restoration forests as habitats for orangutans will increase. Therefore, it is important that we understand how orangutan densities are affected by changes to the forest structure through logging or replanting so that conservation and habitat management plans can be better informed upon these impacts. In Chapter 2 and Chapter 3 of this thesis we showed the high degree of selectivity displayed by orangutans in relation to forest structure in determining nest site selection, nest position and nest height. In this study, we will investigate whether orangutan densities differ between a naturally regenerated selectively logged site which has regenerated over 40 years and a site where intensive reforestation efforts began 15 years ago and are still ongoing. Following this, we will investigate which forest structure variables influence nest densities in both sites and whether the influential forest structure parameters differ between the sites to determine why orangutan densities may differ between the sites. We will also measure the distance from the edge of the forest closest to plantations to determine whether the proximity to human disturbance influences orangutan nest densities and whether this has a greater influence than forest structure.

4.1.1 Hypotheses:

- As Chapters 2 and 3 have already shown, we expect to find significant differences between the forest structure of Sikundur and Se Betung. Based on the results from Chapters 2 and 3, Sikundur should have greater tree heights, higher canopy density, canopy closure, higher ratio of large tree and more heterogenous tree heights that are more evenly spread throughout the forest. Sei Betung should have more, larger gaps, smaller trees that are more homogenous in height that is representative of their similar age. Generally less disturbed areas should have greater canopy densities or canopy closure, more disperse gaps so therefore a lower Morosita index and intact places would have a greater ratio of large trees to small ones and a higher proportion of small trees could be a sign of natural regrowth (Mohamed et al. 2013).
- Orangutan densities are expected to be higher in Sikundur than Sei Betung. As Sei Betung is more disturbed, nests should appear to be clustered in small pockets of the site whilst those in Sikundur should be more evenly spread throughout the site.
- As alluvial soils have higher productivity, there should be higher orangutan densities found in the alluvial landunit compared to the hills or plains.
- Orangutan densities should remain similar between the survey periods as orangutan densities in Sikundur are not supposed to be linked to fruit availability.
- As prior studies have found that orangutan densities are negatively associated with human disturbance, we expect to find that orangutan densities are negatively associated with distance to the forest edge.

4.2 Methodology

4.2.1 Study Sites

Field research for this study was conducted at two field sites found within the eastern border of the Gunung Leuser National Park in Langkat District of North Sumatra; Sikundur also known as Sekundur in some papers (3°1’N, 98°02’E) and Resort Sei Betung (4°3’N, 98°07’E) ((Knop et al. 2004; Wich et al.

2008b; Marshall et al. 2009; Hartini et al. 2017; Szantoi et al. 2017). The Sikundur research site is found in an area of diverse mixed dipterocarp lowland forest that also possesses rich alluvial forest along the rivers, with part of it having been subjected to selective logging 40 years ago (de Wilde & Duyfjes 1996; Knop et al. 2004; Wich et al. 2008b). Sei Betung is approximately 9km north of Sikundur on the site of a former illegal oil palm plantation that has been actively reforested through the planting of 500,000 seedlings of 97 indigenous tree species by the NGO OIC (Orangutan Information Centre) (Kettle et al. 2014). Though the two sites are relatively close geographically, they differ considerably in terms of forest structure and the levels of anthropogenic disturbance that they have experienced as Sikundur has stands of primary forest and selectively logged areas which have had over 30 years to recover (Knop et al. 2004; Priatna et al. 2006; Marshall et al. 2009); whilst Sei Betung is just at the start of recovery with some areas replanted in 2007 and the most recent in 2013 and areas of secondary forest which was less intensively replanted to the west of the site (Kettle et al. 2014; Wich et al. 2016b). Data collection was undertaken from February-August 2015 and March-September 2016.

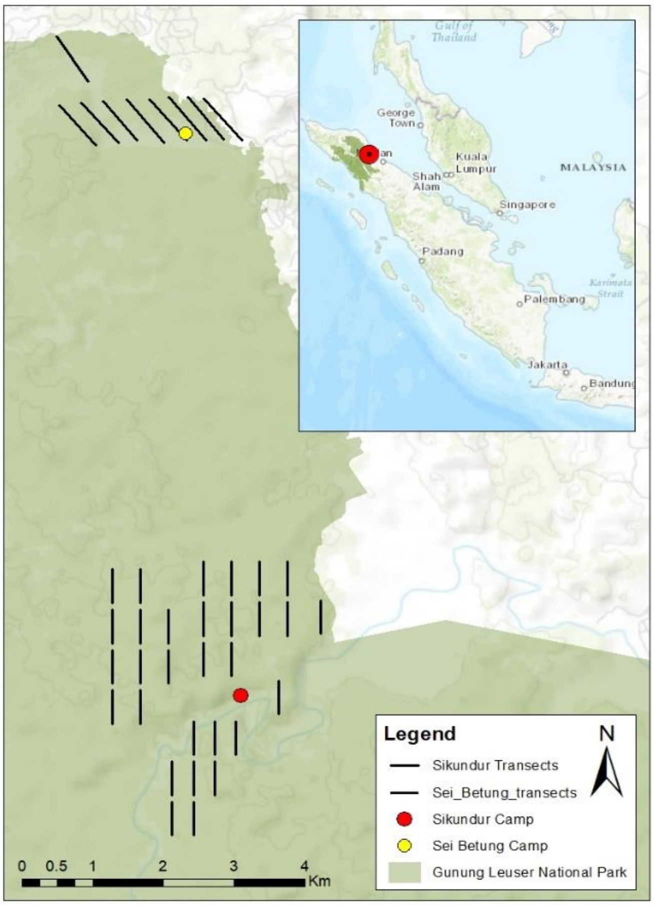

Figure 4-1 Locations of Sikundur and Sei Betung field sites in North Sumatra

4.2.2 Data collection

Transects were used in both sites for sampling nests and forest structure parameters. In Sikundur 30 transects, 500m in length were set out using a stratified random grid with the first point being placed randomly and the first transect measured 500m north from this point. All other transects were arranged around initial transect on north-south bearings and spaced 150m apart to the north and south and 300m to the east and west. The transects were placed to ensure that none were split by the Besitang river or that any crossed outside of the boundaries of the site. Underlying land units identified by Laumonier in 1997 (alluvial, hills, plains) were used to equally split the transects across the site with 10 transects being placed within each land unit. The land units were categorised by slope, elevation and soil profile, with the plains and alluvial areas having experienced greater levels of exploitation in the past due to their greater accessibility (Laumonier 1997; Consiglio 2015; Slater 2015). The three land units are defined as follows; Alluvial, characterised by low-lying land located next to rivers with fine-textured, poorly drained soils; Plains, typically consists of flat to undulating land at low elevations with porous, acidic soils; and Hills, as suggested by the name are found at higher elevations (100-500m), and are comprised of fine-medium textured, leached soils with low organic content (Laumonier 1997; Slater 2015). Existing transects were used in Sei Betung to eliminate the disturbance that cutting new transects would have produced. 9 transects 1km in length were used which were spaced 150m apart running parallel on north-west south-east bearings. For later analysis these transects were split in half to provide better comparisons with Sikundur. As Sei Betung is a smaller site and we were limited to using pre-cut transects there, we did not consider any differences in land unit or soil type in Sei Betung. Furthermore, the differences in planting age across Sei Betung are more likely to influence the data than the underlying soil types within Sei Betung.

The interval between parallel transects and length of transects was designed to prevent any overlap of observations and with the intention of optimizing the trade-off between having both a large number of independent samples and ensuring that transects were long enough to minimise the potential biases due to spatial heterogeneity from such things as the clumping of orangutan nests or variation in habitat and structure along the transect (Johnson et al. 2005). The transects were cut along lines irrespective of topography or vegetation to ensure that they adhered to the line-transect method assumption that all transects be placed randomly in respect to terrain and were able to cover a representative sample of both field sites (Buckland et al. 2001; Mathewson et al. 2008). All transects were walked and used by the lead author with deviations from the transect due to obstacles kept as small a deviation as possible.

Forest structure

Forest structure data such as tree height, DBH, crown radii to the North, South, East and West, crown shape and canopy photographs for later analysis were collected by the lead author, R. Consiglio and H. Slater together with field assistants from SOCP in both Sikundur and in Sei Betung data was collected by the lead author and field assistants from OIC. The point centre quarter method (PCQM) was used for surveying forest structure data at 50m intervals as this method also allowed for calculations of stem density to be produced for each transect (Cottam & Curtis 1956; Cannon & Leighton 1994; Ganzhorn et al. 2003; Manduell et al. 2012). Transect for collecting forest structure data were conducted only once at each site, in 2015 in Sikundur and 2016 in Sei Betung. Each sampling point was split into four quadrants set at 90˚ to each other and perpendicular to the transect. For each point the nearest tree with a diameter at breast height (DBH) >10cm (measured at 1.3m above the ground) was sampled with the distance to the centre point being recorded for each quadrant to the nearest 0.1m. GPS points were collected at each sampling point with a Garmin GPSmap 60Cx to ensure that transects were following the correct predetermined paths and that nest transects followed this pathway accurately.

A Nikon forestry Pro laser range finder was used to measure the height of the crown of each tree sampled to the nearest 0.1m, with the height of the tree being measured at the highest visible leaf. First bole height (FBH) was also measured by measuring to the base of where the first branch attached to the trunk, these measurements are used to obtain crown size and are also used to calculate crown volume. The radius of the crown was measured in meters from the trunk of the tree to the edge of the crown to the North, East, South and West, these were recorded as the crown radius can be quite variable so this should eliminate any potential over or under estimates. Diameter at breast height (DBH) was recorded for each tree using a tape measure at a height of 1.3m and measured to the nearest centimetre. Crown shapes were classified as either spheroid, elongated spheroid, cone, upside-down cone, umbrella, bent over, broken or palms (definitions in Table 4.1). Crown connectivity was estimated visually by estimating the proportion of the crown in contact or enclosed by neighbouring crowns using a four point scale; 0-25%, 26-50%, 51-75% and 76-100%, the inverse of this gives the exposure of the crown (Whitten 1982; Manduell et al. 2011; Cheyne et al. 2013).

Table 4-1 Definitions of crown shapes adapted from Coder 2000 and Manduell et al. 2011

CROWN SHAPE	DEFINITION
SPHEROID	Sphere shaped/ lollipop shape
ELONGATED SPHEROID	Crown with a height greater than its width and rounded ends
CONE	Cone shaped crown with a wide base that tapers to the top
UPSIDE-DOWN CONE	Crown which dove tails from the first branches, inverse of the cone (also known as inverse tripod)
UMBRELLA	Similar to spheroid or cone but lowest branches tips hang further down than the base of the branch
BENT-OVER	Tree with trunk or crown growing significantly in one direction, typified by lack of crown in one direction
BROKEN	Tree where the crown has broken off leaving either a splintered top or new growth if still alive
PALM	If the tree is a palm species there is no crown but series of large palm leaves

Measures of canopy density and Morosita index (an index for the dispersion of gaps) were obtained through canopy photography and processing with the CanopyDigi software (Goodenough & Goodenough 2012; Williams et al. 2013). Photographs were taken in each quadrant of the PCQM, at 45˚ angles to the transect, and 5m from the centre point of the PCQM to avoid overlap and maximise coverage. Photographs were taken using a Nikon D7200 DSLR with a Nikkor 18-55mm lens set to 35mm with the focus set to infinity. A tripod was used to take all photographs with the camera set facing straight up using a digital angle gauge to ensure that it was level on the x and y axis. The height of the camera was set at 1.3m or at the full extent of the tripod if on uneven ground. Photographs were processed in the CanopyDigi software using the methodology stated by (Goodenough & Goodenough 2012).

4.2.3 Nest transects

Nest transects were conducted on the same transects as the vegetation transects by JA and a team of 1-2 well trained local field assistants from SOCP in Sikundur and OIC in Sei Betung. Nest transects in Sikundur were completed in May 2015, April 2016 and August 2016 and in Sei Betung in August 2016. The transects were walked at a pace of no more than 1km/h. When located, the perpendicular distance from the transect to the centre of the nest was measured using a tape measure to the nearest

0.1m along with the direction as this is utilised along with age of nest and decay rate. Along with these distances the DBH, first bole height, height of tree, crown shape, connectivity, crown radius from the trunk to the edge of the crown for the north, south, east and west of the tree were recorded along with support availability using the same methodology as vegetation data. Nest height was recorded using the Nikon forestry Pro laser rangefinder to ensure accuracy.

Observed nests were placed into age classes by trained observers, these classes were reflective of the decay rate. The classes were; 1- fresh leaves, still green; 2- mix of green and brown leaves; 3- all leaves turned brown and some holes forming; 4- all leaves gone and nest falling apart (van Schaik et al. 1995; Hashimoto 1995; Russon et al. 2001; Felton et al. 2003; Johnson et al. 2005; Spehar et al. 2010).

4.2.4 Data analysis

Covariates

For each transect the ratio of large trees (DBH >40cm) to small trees (DBH <20cm) (rDBH) was determined as this can be used along with canopy density and Morosita index as a measure of disturbance that an area has experienced (Mohamed et al. 2013). Stem density of trees was determined using the methodology stated in Mitchell (2010) and Manduell et al. (2012) whereby 1 is divided by the square of the mean of all distances (measured in meters) ($\bar{r}$).This is calculated using the following formulae:

$$\bar{r} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{4} Rij}{4n}$$

Absolute density $\bar{\lambda}$, is then calculated via:

$$\bar{\lambda} = \frac{1}{\bar{r}^2}$$

This is then multiplied by 10,000 to convert the results from m^2 to ha^2. A correction factor for missing quadrants where no tree was recorded within a quadrant was used as detailed in Warde & Petranka (1981) which relies on identifying the proportion of vacant quarters and identifying the correction factor within correction factor table in Warde & Petranka (1981). The formula for calculating using the correction factors is as follows:

$$\bar{r}' = \frac{\sum_{m=1}^{4n-n_0} R_m}{4n - n_0}$$

Absolute density (corrected) $\bar{\lambda}_c$ is then calculated using:

$$\tilde{\lambda}_c = \frac{1}{(\bar{r'})^2} \cdot CF$$

Mean crown area, crown size and crown volumes were determined for each transect with areas with crown area being calculated using:

Crown area:

$Crown\ area = \sum \frac{\pi N r^2}{4} + \frac{\pi S r^2}{4} + \frac{\pi W r^2}{4} + \frac{\pi E r^2}{4}$

Nr= North radius

Sr= South radius

Wr= West radius

Er= East radius

Crown size is calculated with:

Crown Size:

$Crown\ size\ (CS) = Tree\ height - First\ branch\ height$

Crown volume is calculated using the crown radii measurements, crown size and the crown shapes to give more accurate estimates of crown volume in m^2:

Crown volume:

$NS\,r\ (North - South\ radius) = \frac{Nr+Sr}{2}$

$EW\,r\ (East - West\ radius) = \frac{Er+Wr}{2}$

$CSr\ (Crown\ Size\ radius) = \frac{CS}{2}$

Cone and upside-down cone crown volume:

$V = \sum \frac{\pi NSr^2 \frac{CS}{3}}{2} + \frac{\pi EWr^2 \frac{CS}{3}}{2}$

Spheroid, elongated spheroid and bent over crowns:

$V = \frac{4}{3} \pi NSrEWrCSr$

Umbrella shape crowns:

$$V = \frac{\frac{4}{3}\pi NSrEWrCSr}{2}$$

The distance to the edge of the forest was measured using satellite and aerial imagery from the ArcGIS world imagery basemap. The distance was measured from the mid-point of each transect to the closest edge of the forest irrespective of geographic barriers such as rivers as suggested by Wich et al. (2012) with the edge of the forest being considered to be where forest cover ends and either continuous open areas or plantations begin. The river was not considered as an edge as little to no hunting is expected within the site and the forest is readily accessible at both sites without the need of the river as Sei Betung is surrounded by plantations on three sides and Sikundur is surrounded by plantations to the East and West and has a number of old logging roads running through the site which provide access to locals on motorbikes as well as on foot. Our main consideration was on edges where humans had removed forest cover and that the forest bordered plantations or logged areas rather than the natural succession as found at river banks.

Rugosity (Tree height diversity) and evenness

Measures of tree height were used to the calculate estimates of the Shannon-Wiener index of diversity *H'* and Pielou's evenness index *J'*. The Shannon-Wiener index (Shannon & E. 2001) has been used in a number of forestry papers (Kuuluvainen & Pukkala 1987, 1989; Kuuluvainen et al. 1996; Pretzsch 1997, 1998; Varga et al. 2005; Rouvinen & Kuuluvainen 2005) to assess the diversity of tree heights within a stand and used for a number of purposes such as assessing a forest stand's quality for wildlife, monitoring the changes in tree size diversity over time, assessing the impact different silvicultural treatment have on stand structure and defining the appropriate silvicultural treatments for different stands (Lexerød & Eid 2006; Ozdemir et al. 2008). The index depends on a selected size class width (Staudhammer & LeMay 2001), for this we followed what was used in Kuuluvainen et al. 1996 using size class widths of 2m (eg. 0-2m, 2-4m…etc). The Shannon-Wiener index is calculated using the following formula:

$$H' = -\sum_{i=1}^{N} p_i \ln(p_i)$$

For this formula p_i refers to the proportion of trees in each height class *i* and *N* refers to the number of height classes. Pielou's *J'* also known as Shannon's evenness index or Shannon's equitability is frequently used along with the Shannon-Wiener diversity index to determine how evenly species are distributed throughout a site and like the diversity index can also be applied to tree height (Rennolls & Laumonier 2000; Vieira et al. 2004; Lexerød & Eid 2006; Ozdemir et al. 2008; Lindner 2011; Symonds & Moussalli 2011; Little et al. 2016). It is calculated using the formula:

$$J' = \frac{H'}{H_{max}}$$

Where H_{max} is found by finding the natural log of the total number of size classes;

$$H_{max} = lnS$$

Orangutan densities

Orangutan densities were calculated using the methodology set out in van Schaik et al. (1995) and improved upon by Buij et al. (2003) using the line transect method. Orangutan densities are calculated using the formula:

$$d = N/(L \times 2w \times p \times r \times t)$$

In this formula *d* = orangutan density (individual/km^2), *N*= number of nests observed along the transect, *L*= the length of transect covered in km, *w*= estimated strip width (ESW) of habitat actually covered (km), *p*= proportion of nest builders in the population, *r*= rate of which nests are produced (nests per day per individual) and lastly *t*= the decay rate for the nest or the time which it is visible (in days). Values for *p* and *r* were obtained from previous studies which state that there is little variation for these across sites in Sumatra where these variables have been measured which are *p*= 0.9 and *r*= 1.7 (van Schaik et al. 1995; Knop et al. 2004; Wich et al. 2004a). The value for *t* for Sikundur was take from Wich et al. 2004 (*t*=231.3 days) and for Sei Betung the rate of decay for logged areas in Sikundur was used from Knop et al. 2004 (*t*= 248 days). Estimated strip width (*w*) was calculated using the perpendicular distances of the nests to the transects. Kolmogorov-Smirnov tests were used to compare the distribution of perpendicular distances of nests for each land unit in Sikundur as well as testing between Sikundur and Sei Betung. No significant differences were found between the land units in Sikundur, therefore the perpendicular distances of all transects in Sikundur were pooled together which increases accuracy (Knop et al. 2004; Wich et al. 2004a). The perpendicular distances for Sikundur and Sei Betung were found to be highly different so the ESW was calculated separately for each site. The ESW was found using the software package Distance 7.1, which is described in detail in Buckland et al. (2001), (2010). Perpendicular distance data were truncated at 5% of the largest values to minimise the influence of outliers and the most extreme values. Different models were tested which include; half-normal with cosine, hermite and simple polynomial expansions, uniform with cosine, hermite and simple polynomial expansions and hazard rate with cosine, hermite and simple polynomial expansions and the best fitting model with the lowest AIC value was used.

To compare between the Shannon-Wiener indices for the different field sites and land units within Sikundur the Hutcheson t-test was used. This test was developed to compare the diversity of two community samples using the Shannon-Wiener index (Hutcheson 1970; Gardener 2017). It is calculated using the formula:

$$t = \frac{H_a - H_b}{\sqrt{S_{H_a}^2 + S_{H_b}^2}}$$

H refers to the Shannon index for each site, with $_a$ and $_b$ referring to each site or land unit being compared. The bottom half of the formula refers to the variance for each sample. The variance of the Shannon index is calculated using:

$$S_H^2 = \frac{\sum p.(\ln p)^2 - (\sum p.\ln p)^2}{N} + \frac{S-1}{2N^2}$$

In this formula *S* refers to the number of size classes and *N* is the number of individuals, in this instance the number of trees recorded and *p* is the proportion that each size class contributes to the total. The final variable needed to test between Shannon indices is the degrees of freedom which is calculated using:

$$df = \frac{(S_{H_a}^2 + S_{H_b}^2)^2}{(\frac{(S_{H_a}^2)^2}{N_a} + \frac{(S_{H_b}^2)^2}{N_b})}$$

For this, the variance and the total abundance (number of trees) are needed (Gardener 2017).

Statistical analysis

The Mann-Whitney U test was used to compared forest structure attributes between Sikundur and Sei Betung, whilst the Kruskall Wallis test with Dunn's post hoc test was used to test the differences in forest structure variables between the three land units in Sikundur. These calculations were made in R (R Core Team 2017) using the PMCMR (Pohlert 2014) package.

Principal Component Analysis (PCA) was used to investigates the differences in forest structure between the two sites as well as the different land units in Sikundur. The PCA was also used to help determine which variables were correlated and test whether any variables were non-significant and could be removed from further testing (Hotelling 1933). Selection of the most important principal components was performed using percent of variance that each principal component explained along with using two criteria; the Kaiser contribution criterion (Yeomans & Golder 1982) and the interpretability criterion of Hatcher & Stepanski (Echeverry-Galvis et al. 2014).The Kaiser criterion states that an important principal component should explain at least one original variable and have a corresponding eigenvalue of >1 (Echeverry-Galvis et al. 2014). The interpretability criterion however, states that an important principal component is a linear combination of original variables which all represent the same latent concept (Yeomans & Golder 1982; Al-Hassan & Al-Kassab 2009; Echeverry-Galvis et al. 2014). In this study we followed what was suggested by (Echeverry-Galvis et al. (2014) where an original variable was determined to be influential or important if it's weight in the principal component was >0.3, an original variable is defined as a variable that only appears once and is included in the first instance that it has a weight >0.3. Using a PCA biplot allows for the differences and similarities between the field sites and land units and the effect each variable has on these to be visualised. PCA analysis was performed using the ggbiplot (Vu 2011) and factoextra packages (Kassambara & Mundt 2017).

A negative binomial regression was run using R following the PCA analysis to investigate the relationship between nest numbers/ orangutan densities and forest structure variables to determine which have the greatest influence upon nest densities. Nest numbers were used as they are highly correlated with nest densities and orangutan densities but does not require the other variables to be rescaled for comparison. Using the dredge function of the MuMIn package in R (Barton 2018) all model iterations including an intercept only model was run. The models were ranked by their AICc (corrected Akaike Information Criterion) scores which compensate for small sample sizes. Using the maximum delta ∆AICc (the difference between the AICc of each model from the best performing model), a subset of models can be extracted with ∆AICc values <2. Values <2 is used as a threshold as models with ∆AICc values <2 all have substantial support and can be considered to perform equally well (Burnham et al. 2002; Burnham & Anderson 2004). From this subset of models, the parameter estimates were averaged and parameters weighted by the proportion of models that the parameter was present in, these weights allow for the relative importance of each parameter to be determined. Model averaging and the graphical output of this were produced using the MuMIn (Barton 2018), ggplot2 (Wickham 2009), snakecase (Grosser 2018), plyr (Wickham 2011), sjlabelled (Lüdecke 2018a), sjPlot (Lüdecke 2018b) and sjmisc (Lüdecke 2018c) packages.

4.3 Results

4.3.1 Orangutan densities

In this section, we provide estimates for orangutan densities in Sei Betung and Sikundur and further break the data down to determine whether orangutan densities differed across land units in Sikundur. The best model found for calculating estimated strip width for Sikundur nests in 2015 was a Half normal model with cosine adjustments (AICc= 585.24, p=0.7), ESW was estimated to be 13.34m, 95%

CI (10.99-16.19). For Sei Betung, a negative exponential model with cosine adjustments was found to best fit the data (AICc= 296.31, p= 0.7) with an ESW of 23.79m, 95% CI (15.41-36.74). As expected Sikundur was found to hold a significantly higher orangutan density compared to Sei Betung (Table 4.2). Within Sikundur, comparing orangutan densities across land units for 2015; no significant difference was found between alluvial, plains and hills (Table 4.3).

Half normal models with cosine adjustments were also found to be the best performing models for Sikundur nest surveys in April 2016 (AICc= 115.59, P= 0.76) and August 2016 (AICc= 86.16, P= 0.94), producing ESW's of 13.37m, 95% CI (8.23-21.74) for April 2016 and 18.75m, 95% CI (11.17-31.47) in August 2016. Orangutan densities subsequently were found to be significantly lower in Sikundur between 2015 than those in 2016 (2015 vs April 2016 t_{36df} =5.45, P= <0.001, 2015 vs August 2016 t_{32df} =6.81, P= <0.001), with 0.18 ind/km^2 ±0.04 found in April 2016 and 0.07 ind/km^2 ±0.02 in August 2016 which was found again to be significantly lower between seasons in 2016 (t_{45df} =2.3, P=0.03. Nests in Sei Betung showed high levels of clustering with 82.2% of all nests recorded in Sei Betung found on only 2 transects, OIC4A and OIC4B (Fig 4.2). Nests in Sikundur were far more evenly spread with only two transects found to hold no nests across the three sampling periods (Fig 4.3). As with 2015, no significant differences were observed in orangutan densities between land units in either April 2016 or August 2016 (see Table 4.2).

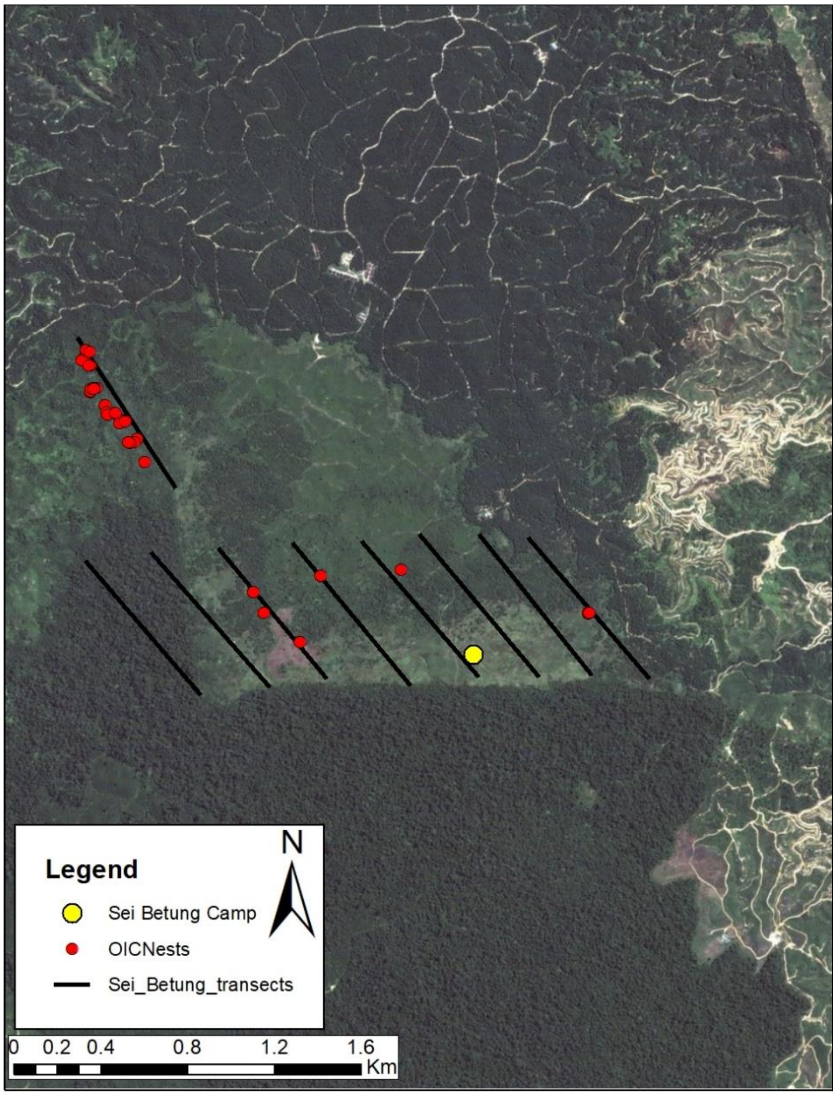

Figure 4-2 Map of transects and nests recorded in Sei Betung. Areas to the north and east of the field site are oil palm plantations whilst to the south is intact forest which connects the site to Sikundur. Nests in Sei Betung show significant clustering on one transect.

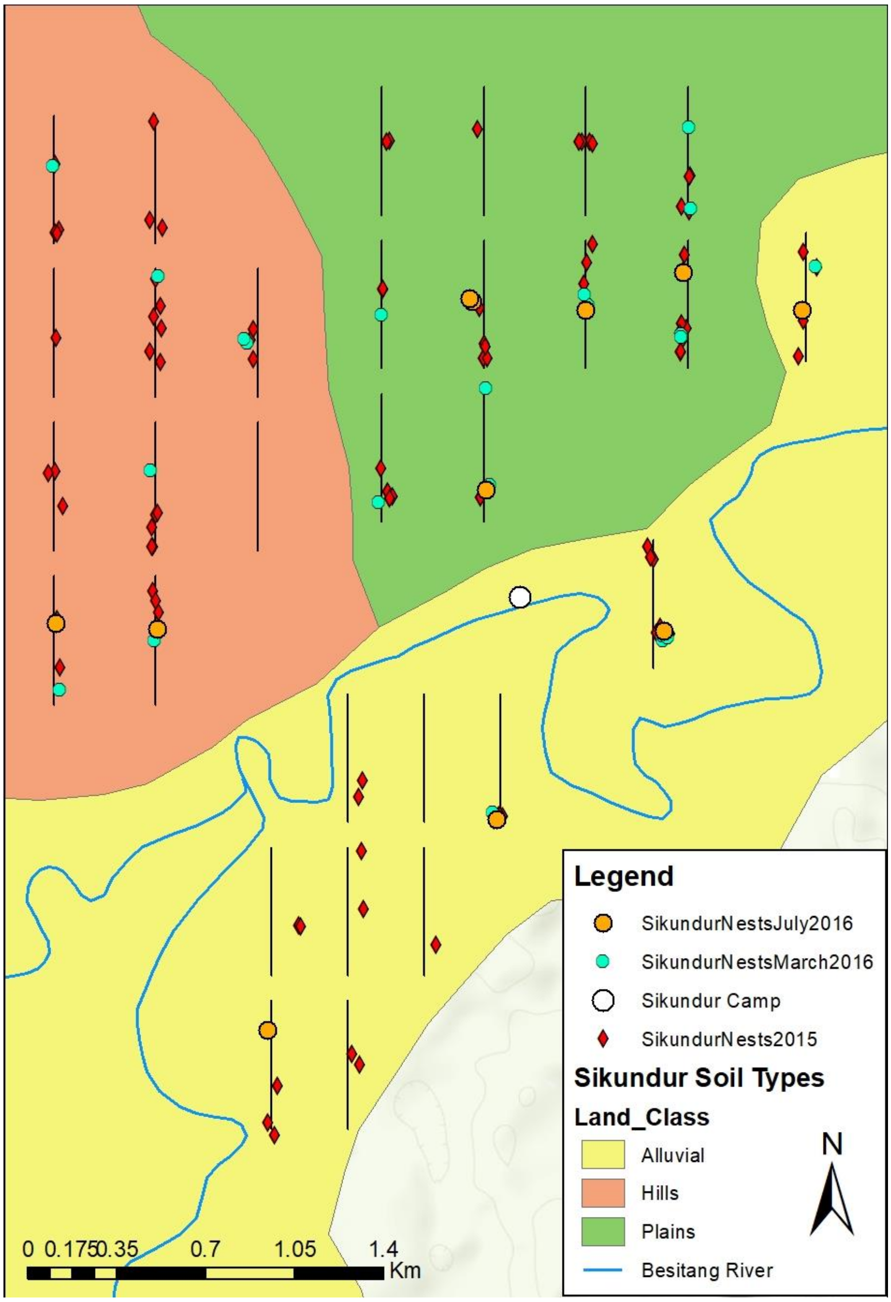

Figure 4-3 Map of transects and nest locations in Sikundur across three sample periods: May 2015, March 2015 and July 2016. The transects were evenly distributed across three land units; Alluvial, Plains and Hills as defined by (Laumonier 1997).

4.3.2 Forest structure and nest densities

4.3.2.1. Sikundur versus Sei Betung

The forest structure differed significantly between Sei Betung and Sikundur for all variables except crown size and crown area (p= >0.05) (Table 4.2). Trees in Sikundur were found to be significantly larger than those in Sei Betung in terms of, tree height and crown volume. The canopy structure differs significantly between both sites with Sikundur having significantly higher canopy density more dispersed gaps due to a lower Morosita index. Tree heights were found to be significantly more heterogenous in Sikundur using the Shannon-Wiener diversity index H' (Hutchesons $t_{1671.02\text{df}}$ = 105.24, *p*= <0.001). Though tree heights were more heterogenous in Sikundur they were more evenly distributed throughout the site with Sikundur having a significantly higher mean for Pielou's *J'* index of evenness. The composition of the forest also differed significantly between both sites with the ratio of large to small trees being significantly higher in Sikundur and Sikundur also having a significantly higher stem density of trees with DBH >10cm. The average distance of the transect from the edge of the forest also differs significantly between both sites with the average distance in Sikundur being 1.7km whilst in Sei Betung the mean is only 0.55km.

Table 4-2 Comparison of mean (SE) forest structure, canopy variables and nest densities between Sikundur and Sei Betung using Mann-Whitney U test

	Sikundur	***Sei Betung***	***U***	***p***
DBH (cm)	21.55±0.61	16.98±0.64	79	**<0.001**
Tree height (m)	14.9±0.29	9.21±0.45	4	**<0.001**
Crown size (m)	5.42±0.16	5.11±0.14	225.5	0.348
Crown area (m^2)	36.7±2.35	36.35±1.91	283	0.792
Crown volume (m^3)	152.76±20.37	94.81±7.81	146	**0.008**
Canopy density (%)	90.63±0.43	67.01±3.47	1	**<0.001**
Morosita index	1.1±0.003	1.71±0.29	525	**<0.001**
rDBH	0.15±0.02	0.04±0.01	75.5	**<0.001**
Shannon-Wiener H'	2.18±0.03	1.68±0.05	25	**<0.001**
Evenness J'	0.88±0.01	0.86±0.01	155	**0.014**
Stem density (stems per ha)	630±36.18	404.99±41.97	98	**<0.001**
Distance to edge of forest (m)	1698.03±115.23	553.89±79.84	33	**<0.001**
Nest density (nest per km^2)	9.33±1.22	5.97±3.48	104	**<0.001**
Orangutan density (OU per km^2)	0.79±0.1	0.28±0.17	85	**<0.001**

4.3.2.2. Sikundur land units

The land units in Sikundur were defined by Laumonier (1997) based on their soil profile, slope and elevation. Little statistical differences were found between the underlying land units of Sikundur in terms of forest structure, canopy structure or forest composition (Table 4.3). The DBH of trees in each land unit was found to differ significantly (H= 13.54, df=2, p= 0.001) with trees in the Alluvial land unit having the largest mean DBH (22.99±1.85cm) and differing significantly from those in both the Plains (p= <0.05) and Hills land units (p= <0.001). Crown size and crown volume were also found to differ significantly between land units (crown size H= 13.86, p= <0.001, crown volume H= 11, p= 0.004), in both instances significant differences were found between the Alluvial land unit and the Plains and Hills land units whereas no significant different was detected between Hills and Plains (p= >0.05). Crown sizes were largest in the Alluvial land unit whilst crown volumes were larger in the Plains land unit. A slight difference was found for canopy density (H= 6.24, p= 0.04) with only alluvial and hills being found to have a significant difference (p= <0.05) with canopy densities being greater in the hills land unit. The distance to the edge of the forest for the transects in each land unit was the only other variable which differed significantly between the three land units (H= 33, p= 0.002) with transects in the Plains land unit being significantly further from the forest edge than those in the (p= <0.001).

Table 4-3 Comparison of forest structure variables across the three land units in Sikundur using the Kruskal-Wallis test and the Dunn's post hoc test with means and standard errors presented

Variable	*Alluvial (1)*	*Hills (2)*	*Plains (3)*	*Kruskal-Wallis test*			*Dunn test*		
	Mean	**Mean**	**Mean**	**H**	**df**	**p**	**1 vs 2**	**1 vs 3**	**2 vs 3**
DBH (cm)	22.99±0.99	20.48±0.88	21.17±1.21	13.544	2	**0.001**	***	*	ns
Tree height (m)	15.17±0.38	14.84±0.46	14.7±0.65	1.467	2	0.48	ns	ns	ns
Crown size (m)	5.9±0.32	5.17±0.21	5.2±0.26	13.864	2	**<0.001**	**	***	ns
Crown area (m²)	37.04±2.41	36.85±2.33	36.2±6.51	3.247	2	0.197	ns	ns	ns
Crown volume (m³)	147.72±14.45	141.8±19.23	168.77±58.19	10.995	2	**0.004**	*	***	ns
Canopy density (%)	90.34±0.58	90.65±0.97	90.89±0.69	6.239	2	**0.044**	*	ns	ns
Morosita index	1.02±0.003	1.02±0.01	1.02±0.004	0.421	2	0.81	ns	ns	ns
rDBH	0.19±0.04	0.12±0.03	0.12±0.03	2.849	2	0.241	ns	ns	ns
Shannon-Wiener H'	2.24±0.04	2.22±0.04	2.08±0.05	0.241	2	0.089	ns	ns	ns
Evenness J'	0.91±0.01	0.89±0.01	0.89±0.01	2.403	2	0.301	ns	ns	ns
Stem density (stems per ha)	609.62±28.87	678.83±89.55	601.55±58.32	98	2	0.879	ns	ns	ns
Distance to edge of forest (m)	1638±242.38	2205±70.67	1251.1±116.03	33	2	**0.002**	ns	ns	***
Nest density (nest per km²)	3.1±2.28	3.6±1.72	4.5±2.33	1.825	2	0.402	ns	ns	ns
Orangutan density 2015 (OU per km²)	0.66±0.19	0.76±0.15	0.95±0.2	85	2	0.402	ns	ns	ns
OU density April 2016 (OU per km²)	0.118±0.08	0.177±0.06	0.217±0.07	2.1478	2	0.342	ns	ns	ns
OU density Jul 2016 (OU per km²)	0.086±0.04	0.03±0.02	0.09±0.04	1.367	2	0.505	ns	ns	ns

*Dunn test df= 1, ns= not significant, * = P <0.05, **= P <0.01 ***= P <0.001*

When comparing between the age classes of the nests in each sampling season the age distribution is found to be significantly different between the three sampling seasons X^2_{6df}= 19.4, P= 0.004. Surveys in 2015 show a considerably higher proportion of older nests with twice as many category 4 nests as was recorded in April 2016 and significantly fewer newer nests in 2015 compared either seasons in 2016 (Fig. S16). With the long decay rate in Sikundur of ~231.3-248 days (Knop et al. 2004; Wich et al. 2004a) it is likely that a number of these nests were built during mid-2014.

4.3.3 PCA analysis of field sites and land units

Principal component analysis were run for the forest structure variables and the data points were grouped by site and land unit to determine how each differs based upon their forest structure. The first three principal components of forest structure were found to be of interest using the Kaiser criterion as these were the only principle components to have eigenvalues >1 (PC1- 6.19, PC- 2.35, PC3- 1.45) (Fig 4.2). In addition, each of these variables contains only original variables with loadings exceeding 0.3. Each principal component also fits to the interpretability criterion whereby each important principal component represents a linear combination of original variables representing the same latent concept (Table 4.4) (Echeverry-Galvis et al. 2014). PC1 can be categorised as focused on tree size (DBH and height). PC2 is more focused on the canopy in regards to its depth, density and the distribution of gaps. PC3 could be considered as the level of disturbance by the distance from the edge of the forest and the evenness of tree sizes across the site.

There is no overlap in forest structure properties between Sei Betung and Sikundur whereas the land units in Sikundur display considerable overlap which further evidences the previous conclusion upon the similarity of the three land units (Fig 4.3). The Plains data is closest to that of Sei Betung in terms of forest structure, as can be seen by the proximity of the ellipses in Figure 4.3.

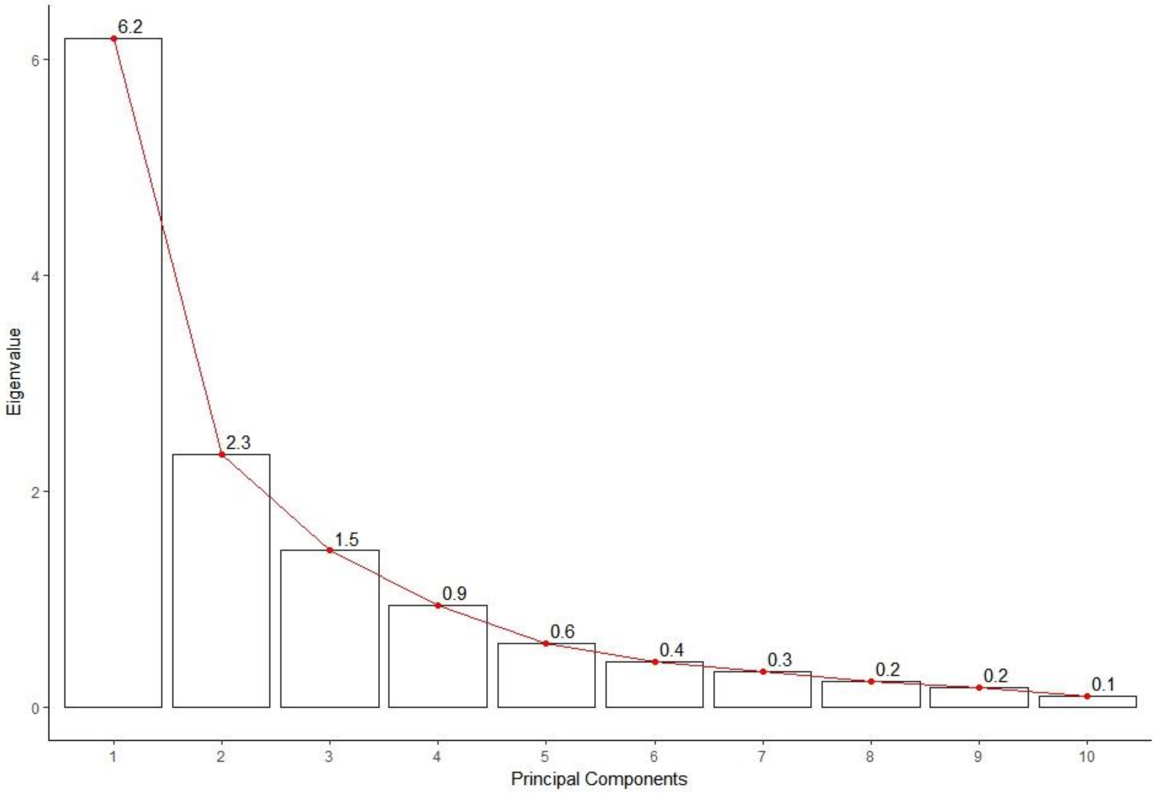

Figure 4-4 Scree plot of principal components of forest structure in Sikundur and Sei Betung, the eigenvalues show that only the first three principal components are of interest as their values are >1.

Table 4-4 Selected observed variables and corresponding coefficients based on interpretability and Kaiser criterion for PCA analyses of Sumatran orangutan nest densities in Sikundur and Sei Betung

Component	***Variable***	***Coefficient***
PC1	DBH	0.367
	Tree height	0.372
	DBH <20cm	-0.319
	rDBH	0.323
	Shannon-Wiener	0.326
PC2	Crown size	-0.328
	Crown Area	-0.379
	Crown volume	-0.307
	Canopy density	0.349
	Morosita index	-0.412
	Stem density	0.436
PC3	Evenness	-0.635
	Distance to edge	-0.322

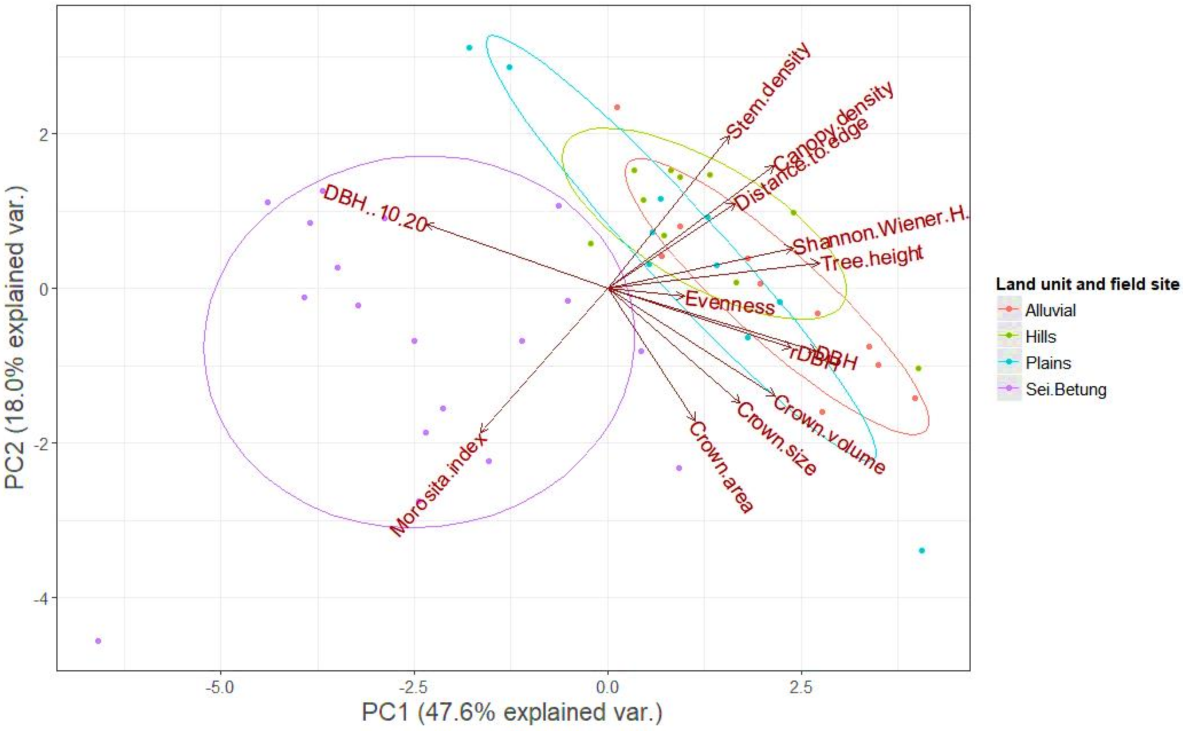

Figure 4-5 Biplot of the first and second principal components of the PCA analysis for forest structure variables across Sei Betung and the three soil type land units in Sikundur.

4.3.4 Modelling of the influence of forest structure parameters upon nest numbers

Following the PCA analysis, models were run to determine which forest structure parameters were most influential in determining nest numbers. Tree height, DBH and crown volume were removed from the models due to VIF scores >5 suggesting multicollinearity along with the PCA biplot suggesting the high level of collinearity between rDBH and DBH, and tree height with the rugosity (Shannon-Weiner H' for diversity of tree heights). The effect of field site was tested as a random effect in a generalized linear mixed effect model (GLMM) against a generalised linear model (GLM), however it was found to have no effect upon the model with both being considered identical by using a Likelihood ratio ANOVA chi square test (X^2=0, df=1, p= 1) with both having identical log likelihoods and deviance, and the simpler model also had both lower AIC and BIC values (GLM AIC= 251.89, BIC= 272.47, GLMM AIC= 253.89, BIC= 276.34). Therefore, the simpler GLM was used for further analysis. The negative binomial regression found 11 candidate models with AICc scores <2, which included the null model, these candidate models are presented in Table 4.5. From these models, 5 variables were found to be recurrent and of importance to determining nest densities in Sikundur and Sei Betung, these variables are canopy density, Morosita index, rugosity (Shannon-Wiener H' tree height diversity), stem density and distance to the edge of forest (Table 4.6).

Table 4-5 Top candidate models (AICc <2) of the forest structure variables which influence nest densities of Sumatran orangutans in Sikundur and Sei Betung

Model	*Adj R^2*	*df*	*logLik*	*AICc*	*ΔAIC*	*weight*
Total nests~Canopy Density+Distance to edge	0.121	4	-117.329	243.6	0	0.031
Total nests~Morosita index	0.069	3	-118.72	244	0.4	0.025
Total nests~Distance to edge+Morosita index+Shannon Wiener	0.158	5	-116.315	244.1	0.47	0.024
Total nests~Distance to edge+Shannon Wiener	0.107	4	-117.712	244.4	0.77	0.021
Total nests~Distance to edge+Morosita index	0.104	4	-117.799	244.5	0.94	0.019
Total nests~Canopy Density	0.054	3	-119.092	244.7	1.14	0.018
Total nests~Distance to edge+Shannon Wiener+Stem density	0.142	5	-116.753	244.9	1.34	0.016
Total nests~Canopy density+Distance to edge+Shannon Wiener	0.141	5	-116.806	245	1.45	0.015
Null model	0	2	-120.413	245.1	1.5	0.015
Total nests~Shannon Wiener	0.042	3	-119.396	245.3	1.75	0.013
Total nests~Canopy density~Distance to edge+Stem density	0.131	5	-117.062	245.6	1.96	0.012
Full model	0.205	11	-114.943	259.2	15.63	0

Model averaging found that of these five important variables, distance from the forest edge was the most important variable with a RI (relative importance) score of 0.66, which was found to be negatively associated with nest densities. The other variables were found to be positively associated with nest densities with higher Shannon-Wiener values, increased canopy and stem densities and lower Morosita index values all being associated with increasing nest densities (Fig 5.4). Of these, stem density was of the least importance, whilst canopy density and Morosita index had similar RI values and the Shannon-Wiener index was the second most important.

Table 4-6 Model averaged parameters from the top performing models (ΔAIC <2) of the multi-model inference of the influence of forest structure parameters on orangutan densities in Sikundur and Sei Betung

Variables	***Estimate***	***Std Error***	***Adj SE***	***z value***	***P***	***RI***	***2.5% CI***	***97.5% CI***
Intercept	-0.373	2.22	2.238	0.167	0.868		-4.76	4.014
Canopy Density	0.013	0.021	0.021	0.611	0.542	0.36	-0.004	0.074
Distance to edge	-0.373	0.369	0.373	1	0.317	0.66	-1.192	0.067
Morosita index	-0.282	0.491	0.495	0.569	0.569	0.33	-1.843	0.143
Shannon-Wiener H’	0.711	1.003	1.011	0.703	0.482	0.43	-0.102	3.424
Stem density	0.0001	0.0005	0.0005	0.273	0.785	0.13	-0.001	0.003

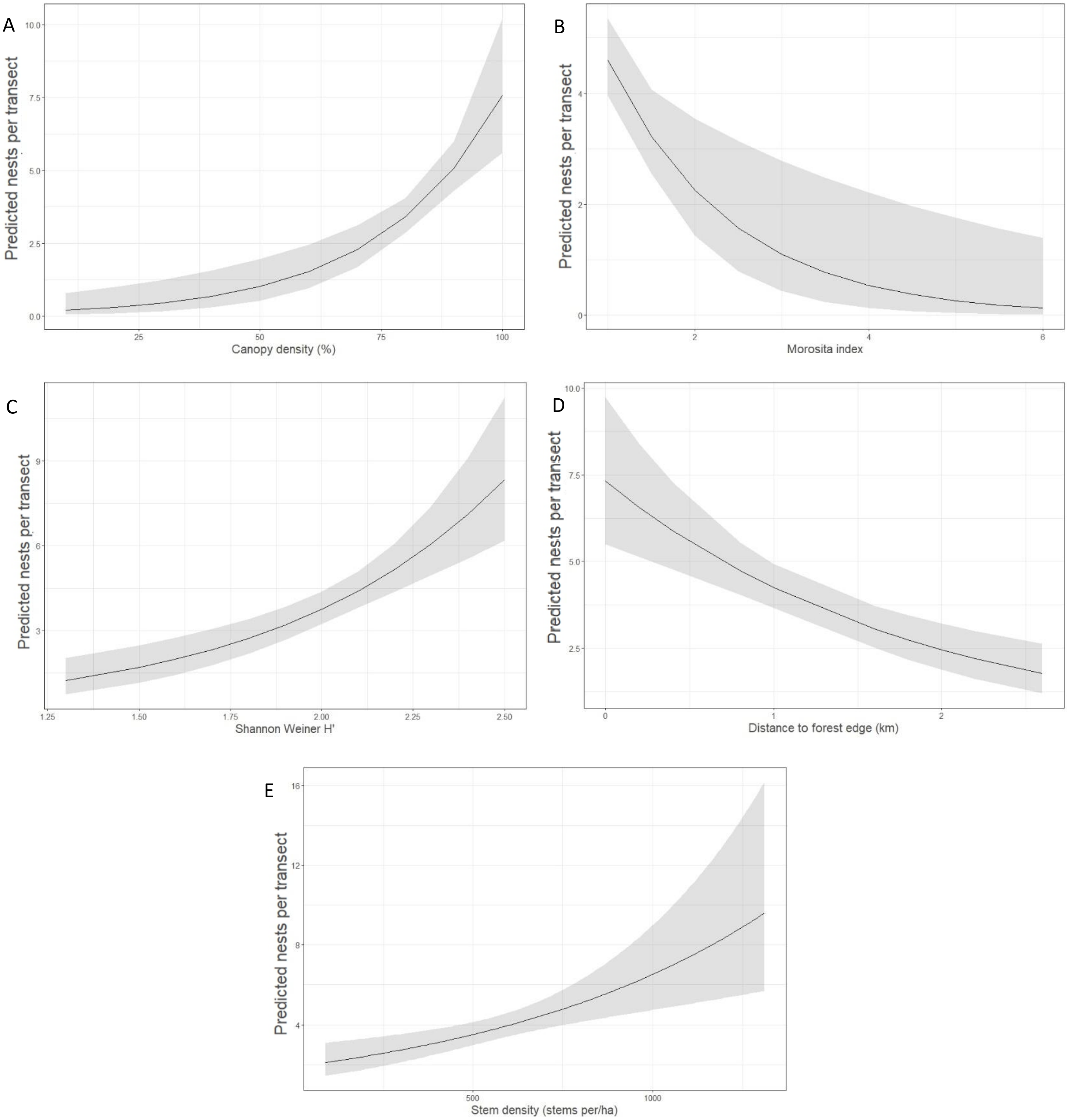

Figure 4-6 Marginal effects plots of canopy density, Morosita index, Shannon-Wiener H', distance to the edge of forest and stem density upon predicted orangutan nest densities. A- Canopy density (%), B- Morosita index, C-Rugosity (Shannon Wiener H' diversity of tree heights), D- Distance to forest edge (km), E- Stem density (stems per/ha)

4.3.5 Influence of forest structure on nest site clustering in Sei Betung

Due to the significant clustering of nests in Sei Betung, a PCA analysis was run to determine whether the transects with nests present differed significantly in terms of forest structure from transects where nests were absent. The analysis was run using all variables and the five important variables from the earlier GLM for determining nest site selection; canopy density, Morosita index, stem density, rugosity and distance to forest edge. Both offered similar results, with a large number of variables overlapping in the more complex analysis, thus the simpler analysis based on the model results was used and is reported below. Based on the Kaiser and interpretability criteria only the first two principal components were found to be of importance with only the first two principal components having eigenvalues >1 (Fig 4.5) and both components containing each of the variables with coefficients >0.3 (Table 4.6).

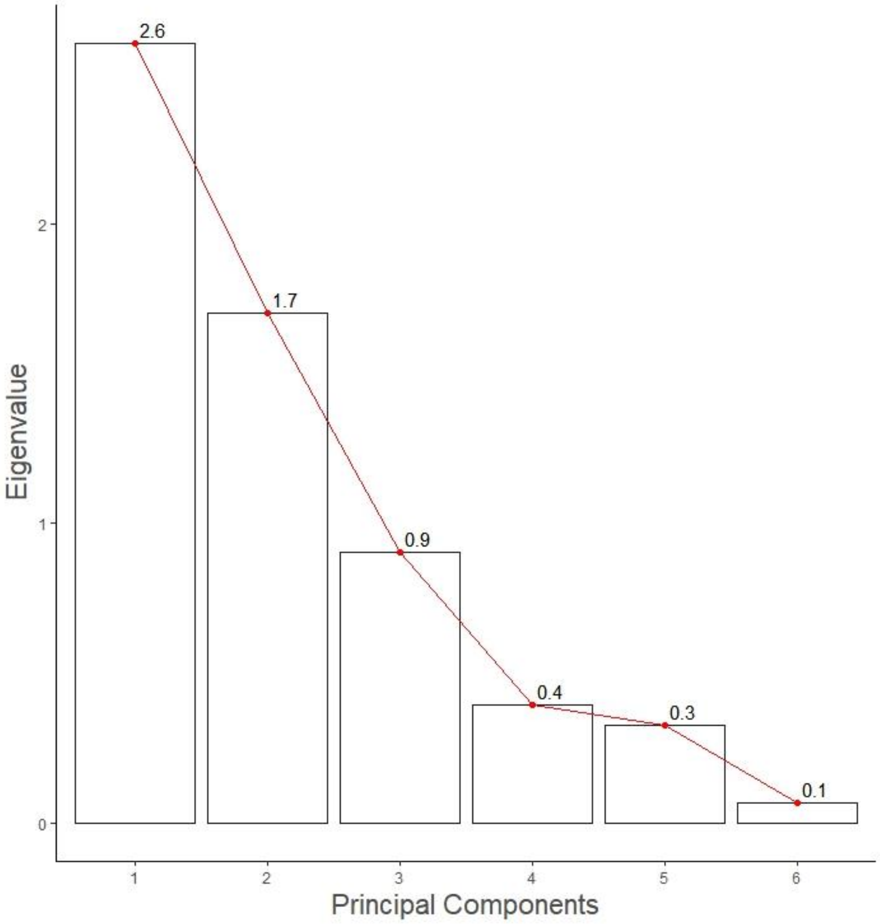

Figure 4-7 Scree plot of principal components for the interaction of forest structure on the presence and absence of nests

Table 4-7 Table 5.6 Variables and their loading for the important principal components for the PCA of forest structure on the presence and absence of nests on transects in Sei Betung

Component	***Variable***	***Coefficient***
PC1	Canopy density	-0.597
	Morosita index	0.573
	Stem density	-0.507
PC2	Rugosity (Shannon Wiener H' tree height)	0.838
	Distance to forest edge	0.492

Based on the results of the PCA in Figure 5.6 it is evident that there is significant overlap in the forest structure properties of transects where nests are present and those where no nests were found. The only visible difference is in the absence of transects with extreme values for nest transects, with the majority of nest transects being in the centre of the interaction having more “average” values.

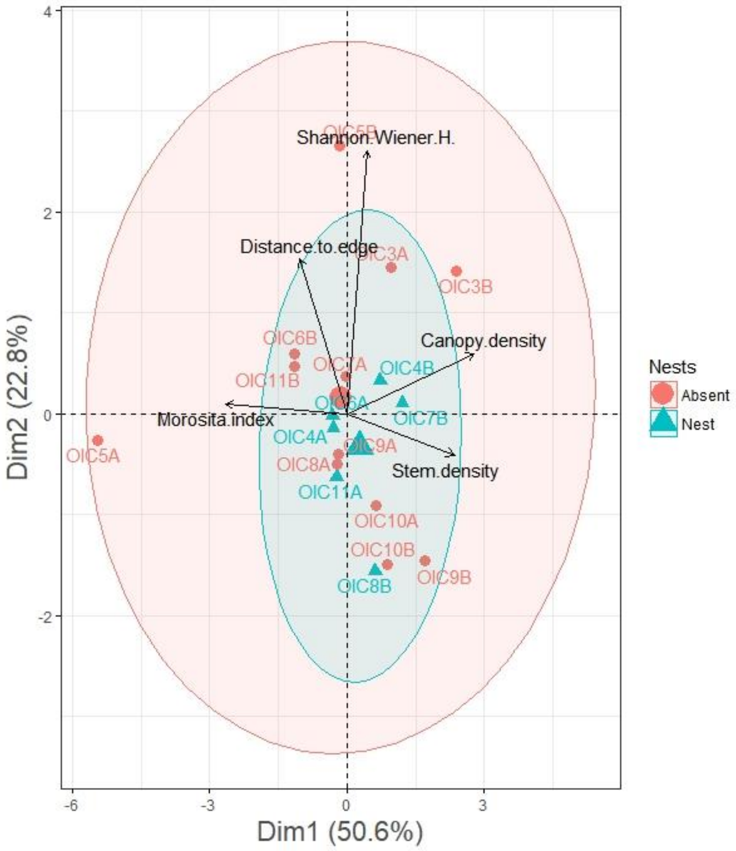

Figure 4-8 PCA biplot of the influence of important forest structure variable upon the presence or absence of nests on transects in Sei Betung

4.4 Discussion

Forest structure in Sikundur and Sei Betung were found to be significantly different for all structural variables except crown size and crown area echoing the results of Chapter 2. Forests in Sikundur exhibited higher canopy density, fewer and smaller gaps, more heterogenous and evenly distributed tree heights as well as taller trees and a higher ratio of trees with large trunks. The similarity in crown size and crown area for trees which otherwise would be considered significantly smaller in Sei Betung is likely a product of the lower stem density in Sei Betung compared to that in Sikundur. The lower stem density would allow for greater space for the trees to spread out horizontally and reduce the need to compete for light vertically as is required in more dense forests such as Sikundur and allows for the trees in Sei Betung to more quickly shade out their competitors (Yoda 1974; Hartshorn 1978; Clark

& Clark 1992; Alvarez-Buylla & Martinez-Ramos 1992; Ackerly 1996; Clark et al. 1996; Sterck & Bongers 2001)

As was expected, orangutan densities were found to be significantly lower (65% lower) in the restoration forest in Sei Betung in comparison to the naturally recovered forest of Sikundur. The significantly lower orangutan density in Sei Betung is likely due to the significant differences in forest structure between the two sites. Distance to forest edge and therefore human influence was found to differ significantly between sites with nests in Sei Betung built considerable closer to the forest edge than Sikundur. However, the models found that increased distance from the forest edge was negatively associated with nest densities. Therefore, should distance from forest edge have been the most influential variable in differentiating Sikundur from Sei Betung in terms of nest densities then we would have expected to find higher nest densities in Sei Betung than Sikundur. As the opposite was found then we must conclude that it is the differences in forest structure which have led to the differences in nest densities.

The forest structure results showed that Sikundur had a more closed structure with more large trees and fewer gaps whilst Sei Betung has significantly more large gaps and is much more homogenous in terms of tree heights. Indicating that the forest condition in Sei Betung has yet to recover to a level which could be compared to the recovering selectively logged forest of Sikundur and that these changes in forest structure directly influence the orangutan densities in the field site. These results further support what was found by Felton et al. 2003 that when a forest has experienced considerable human disturbance orangutan densities decline along with the forests condition, however the disparity in orangutan densities between Sikundur and Sei Betung was much larger than what was found by Felton et al. (2003) who observed a drop of 21% between their field sites in Gunung Palung National Park and a nearby site that had been selectively hand logged. The difference in disturbance levels between Felton et al's (2003) study and ours may be why the decrease in orangutan densities is more pronounced in our study. Felton et al. (2003) reported that the logging had occurred two years prior to their study and that loggers had extracted on average 7 trees/ha with a range of 0-30 trees/ha. Sei Betung however was previously an illegal oil palm plantation that was cleared and replanted over the last 15 years. Observing the difference in stem densities between Sei Betung and Sikundur (Table 4.2) we see that Sei Betung has considerably fewer than Sikundur (404.99 stems/ha versus 630 stems/ha) so the effect on orangutan densities should be higher as was observed.

Nests in Sei Betung showed considerable clustering with 82.2% of all nests in Sei Betung found on two adjacent transects. These clusters of nests corroborate what was found by Wich et al. 2016 with the greatest concentrations of nests found in the same area of the site; to the west and near to the primary forest to the south which had never been previously cleared (Hartini et al. 2017). This area has experienced less severe degradation and as such had only received enrichment planting (~400 seedlings per ha) compared to the other areas of the site which had been more thoroughly replanted (~1100+ seedlings per ha). Initially, the clustering of nests was thought to be due to a higher density of preferred nesting trees on these transects which would have followed the results from Chapter 2 and Ancrenaz et al. 2004 with “high quality” nest trees holding multiple nests suggesting potential reuse of these preferred nesting trees. However, PCA analysis of the transects in Sei Betung showed that in terms of forest structure, transects where nests were present did not differ significantly from those transects where nests were absent. The only transects where extreme scores for forest structure variables were found were also those found to have no nests. Thereby suggesting that although forest structure may explain why some forest areas are avoided for nesting it does not help to explain why some areas are preferred over others when forest structure appears similar. Therefore, another factor which we did not measure must be drawing orangutans to those transects and not others.

This could potentially be the presence or greater densities of preferred food species on those transects which are not found elsewhere within Sei Betung or in as great densities. The transect with the greatest nest density in Sei Betung (OIC4A) runs through the region of the site where Wich et al. (2016) also found the highest densities of orangutans in their study. This region of Sei Betung is the less disturbed area referred to as secondary forest which received only enrichment planting (~400 seedlings per/Ha) rather than the completely clear felled sections which were more densely replanted (~1100 seedlings per/Ha) (Wich et al. 2016). There is the potential that due to the complete removal of the forest in the other parts of Sei Betung that certain species are missing or may be slower growing so are not available to orangutans for nesting or food as they would be in the less disturbed areas where they may not have been removed during the initial logging and clearance. Further testing is needed to assess whether the presence or absence of particular tree species could influence orangutan densities, in other forests orangutan densities are known to be highly influenced by the densities of soft-pulp fruits (Djojosudharmo & van Schaik 1992) and figs which provide an important fall back food for orangutans but are known to be found in particularly low densities in Sikundur and Sei Betung (Wich et al. 2004a). The densities of figs and fleshy fruits weren’t surveyed as initially as prior research by Knop et al. (2004) on orangutan densities in Sikundur had found no correlation between orangutan densities and fruit availability. However, since the field research was completed Kanamori et al. (2017) have published their study where they discounted Knop et al's (2004) results due to the short period that their study was conducted over (1 year) as this could miss potential peak fruit periods of masting species as well as not detect the movement of orangutans into the area. Not surveying for fruit availability was a significant oversight and in future research should be an essential parameter to record.

In contrast to Sei Betung, no significant differences were observed between the three land units in Sikundur and nests were found to be generally well spread throughout the transects. Though no significant difference was detected between land units for any of the sampling periods, the Alluvial transects were found to have a mean orangutan density 30.53% lower than that of the Plains in 2015 and similarly for both samples in 2016. This difference in orangutan densities is larger than what was reported by Felton et al. 2003 between their logged and unlogged sites. The lack of any significant difference in orangutan densities between land units could be due to the similarities between the land units in terms of forest structure or potentially due to sampling size being too small in regards to the number of nests per land unit and transect which could be masking the difference between the land units. Both Cannon & Leighton (1994) and DeWalt & Chave (2004) found that within sites, soil types had little influence upon forest structure. The lack of significant difference in orangutan densities between the land units and lower nest density in the Alluvial land unit contrasts with the results of Vogel et al. (2015). Their study found that between the two geographically close peat swamp sites of Tuanan and Sabangau, orangutan densities were twice as high in Tuanan than Sabangau. Vogel et al. (2015) theorised that this difference was due to differences in soil nutrients influencing fruit productivity of the sites. In the more nutrient rich Tuanan, higher fruit productivity would lead to orangutan diets being of more nutritional quality, thereby allowing for greater orangutan densities than in the nutritionally deficient Sabangau. Tuanan had higher soil nutrient as it is in a seasonally rheotrophic area with shallower peat and having a more alluvial flooding regime whilst Sabangau is in an ombrotrophic bog which receives limited nutrient input from rain only (Vogel et al. 2015). There is also the potential that their results could be due to potential differences in forest structure as the higher levels of soil nutrients in Tuanan may also allow for higher densities of large trees which would be preferred for nest sites (Paoli et al. 2008). Our results suggest that the differences in forest structure and productivity for soil types in Sikundur are markedly less than was observed between Tuanan and Sabangau by Vogel et al. (2015) which is potentially why no significant difference was found in orangutan densities between the land units in Sikundur.

The orangutan densities differed significantly between sampling seasons with significantly more orangutans found in 2015 than in either April or August 2016. These significant differences in orangutan densities could be linked to the seasonal changes in fruit availability and the rainy seasons. Buij et al. 2002 found that orangutan densities closely followed fruit availability in the Sumatran field site of Ketambe, with orangutans being observed feeding on fruiting fig trees in a group of up to 9 individuals (Rijksen 1978; Sugardjito et al. 1987; Utami et al. 1997). A mast which happened in mid-2014 (Nowak & Singleton 2016) potentially could be the cause for the significantly higher densities of older nests recorded in early 2015. Surveys in 2015 show a considerably higher proportion of older nests than either survey in 2016, with twice as many category 4 nests recorded in 2015 than April 2016. With the long decay rate in Sikundur of ~231.3-248 days (Knop et al. 2004; Wich et al. 2004a) there is the potential for these nests to have been built during this mast period (Nowak & Singleton 2016). Following the masting event, the fruit availability dropped and this is most likely why the orangutan densities also dropped so significantly (Fig 4.9).

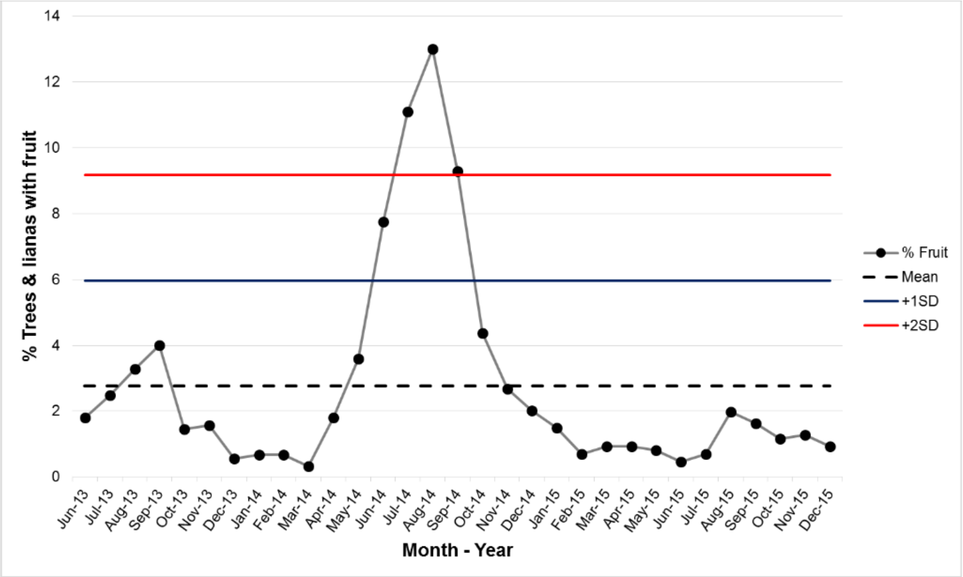

Figure 4-9 The average monthly percent of liana/tree stems with fruit for Sikundur from June 2013- December 2015, including the mean, +1 and +2 standard deviations from the mean. This shows a potential mast event occurred in mid-2014 which may be responsible for the higher density of old nests found in early 2015. Taken from Nowak & Singleton (2016).

This seasonality of fruit availability likely explains why the orangutan densities for Sikundur also differ significantly across the three sampling periods as well as from prior studies in Sikundur; Wich et al. 2004 gave an estimate of 1.04 ind/km^2 whilst Knop et al. 2004 gave estimates of 0.21 ind/km^2 for the primary forest and 0.3 ind/km^2 for the logged forest where our surveys took place which also show significant variation. Given the timescale between the studies and the fluctuations in fruit availability, it is likely that it is not seasonal changes but supra-annual fluctuations in fruit availability from periodic events suggest masting events which are influencing the variability in orangutan densities and therefore nest densities in Sikundur. Generally, Sumatran forests are considered to offer higher fruit production levels than those in Borneo, with strangler figs being of particular importance to orangutans in Sumatra as they offer a stable food source due to their year round fruiting unlike other seasonal and masting fruits (Windsor et al. 1989; Sugardjito et al. 1987; Wich et al. 2004; Wich et al. 2011). However, Sikundur differs from other Sumatran sites as it has one of the lowest fruiting scores and lowest densities of strangler figs of any Sumatran site (Wich et al. 2004a; Nowak & Singleton 2015, 2016). Sikundur's fruiting score is most comparable to that of Bornean field sites and is considerably lower than the published range of the Sumatran sites of Ketambe and Suaq Balimbing (Wich et al. 2004; Wich et al. 2011; Nowak & Singleton 2016). This extremely low average fruit availability outside of masting events is likely the reason for the lower density estimates for the site and why when masting events do occur that the population density increases so significantly as orangutans move into the area from areas where fruit availability may be lower to make the most of the high fruit availability (Buij et al. 2002; Kanamori et al. 2017).

Kanamori et al (2017) found that in Danum Valley in Borneo found that orangutans with wide and overlapping ranges gathered into these smaller core areas during periods of high fruit availability so that they could make the most of the localised high fruit availability. Similarly, in Ketambe in Sumatra Buij et al. (2002) found evidence supporting the seasonal movement of orangutans as they commuted between areas following the fruit peak as in Ketambe the seasonal fruit availability changed with altitude. Buij et al. (2002) found that periods of peak fruit availability differed with altitude and that increases in orangutan densities were highly correlated with those periods of peak fruit availability. Their surveys were conducted in areas that included altitudes of 250-500m, 500-1000m and 1000-1500m. Within the space of 20km travelling south-west from Sikundur the elevation increases from 50m to 1200m as there is a large mountain range to the west of Sikundur. This variation in altitude and therefore differences in peak fruit periods could explain from where the increased densities of orangutans have come from. A future research project could investigate the orangutan densities in these areas to the west of Sikundur and whether they also show different periods of peak fruit availability.

A study by Singleton & Van Schaik (2001) found that in the Sumatran peat swamp of Suaq Balimbing, minimum home range size for females was estimated at ~850ha and utilised a core area of ~500ha and occasionally made excursions to peripheral areas in search of favoured fruit and the longest recorded excursion coincided with a mast event. Fruit availability is generally more consistent and masting species are less common within peat swamps compared to forests and as such there is less pressure for orangutans to expend as much energy searching for fruit (Appanah 1993; Wich & Van Schaik 2000; Singleton & Van Schaik 2001; Marshall et al. 2009; Wich et al. 2011b) to find food, so there is the potential that the home ranges of orangutans in the lowland forests of Sikundur and Sei Betung are significantly larger than those in Sei Betung. This could be an interesting topic for future research.

Other events such as floods (Kanamori et al. 2017) and logging (MacKinnon 1971; Mackinnon 1974) have also been found to cause temporary increases in orangutan densities as orangutans move away from the disturbance to less disturbed forests. However, no such events occurred during the field research period of this study. Our results appear to further support the conclusions of Kanamori et al. (2017) and Buij et al. (2002) that in areas with generally low fruit availability such as dipterocarp forests, during periods of high fruit availability, such as during a mast event, orangutans from neighbouring areas and those with overlapping ranges will congregate into this smaller area to make the most of the increased fruit availability and then disperse once fruit availability drops which would give the more typical lower densities. These results suggest that within these lowland disturbed forests orangutan densities are likely to fluctuate significantly with supra-annual fluctuations in fruit availability and that to give reliable estimates of orangutan densities survey must either be conducted over larger areas to record those individuals moving through the peripheral areas. Alternatively, surveys could be conducted over a longer period of time to determine the size of the “resident” population whose home range is Sikundur and Sei compared to the “transient” or “visitor” population who are individuals from neighbouring areas who have followed the fruiting peak.

Multi-model inference indicated that the variables which most influence orangutan densities do not differ between Sikundur and Sei Betung and that the important biotic variables are the same, irrespective of the level of disturbance a site has experienced, similar to what was found in the previous chapters of this thesis. Nest and orangutan densities were most influenced by reduced distance to the edge of the forest This result was the opposite of what was expected with distance found to be negatively correlated with orangutan densities. This result is also in direct opposition to what was found by Marshall et al. 2006; Wich et al. 2012, though the distances from the edge of the forest they used were much greater than in our study. A possible explanation for why orangutans are using areas near to the forest edge more could be potentially be due to the edge effect, lack of hunting and the compression effect if habitat loss was more recent.

Through the opening up of the forest, edges provide an opportunity for new growth and for pioneer species to grow which are otherwise generally absent from the forest interior (Laurance et al. 2006, 2009; Broadbent et al. 2008; Berry et al. 2008; Goosem & Tucker 2013; Nguyen et al. 2014). Vegetation densities (Lovejoy et al. 1986; Williams-Linera 1990) and fruit production/availability are also found to be higher in forest edges (Restrepo et al. 1999) and the basal areas of trees within the edges are also larger than those of similar age in the interior (Williams-Linera 1990) with basal area being linked to greater nest stability (Cheyne et al. 2013). These factors suggest that these edges of the forest could provide both good food sources and safe, stable nesting sites for orangutans. Edges also potentially offer greater potential for thermoregulation as their more open habitat would allow for more wind and breezes that could help cool the animal. However, this increased wind could also lead to lower nest stability and potential for nest failure in strong winds. Our results in Chapter 2 and 3 found that orangutans appeared to take measures that minimised the impact of wind on the nest so that nest comfort and safety could be maximised. Further research is needed to identify the tree species occurring in these edge areas as well as observe orangutan behaviour within these areas to determine if they do have higher productivity and that as such orangutans are feeding more within these edge habitats.

Though hunting is known to influence orangutan densities and habitat selection for Bornean orangutans (Marshall et al. 2006) and Tapanuli orangutans in Batang Toru in Sumatra (Wich et al. 2012b), it is less understood for the Sumatran orangutans within the Leuser Ecosystem. It has been suggested though that due to the Islamic religious beliefs within this area hunting for orangutans may occur less with hunting for food very unlikely to occur. In contrast to in Batang Toru where hunting and consuming orangutans and other forest species has been a part of the culture for a long time (Rijksen & Meijard 1999; Davis et al. 2013). This lower level of hunting could be a reason why orangutans in this area do not avoid areas closer to the forest edges within these two sites that closely border plantations and agroforestry areas. In areas where active logging is occurring orangutan densities have been found to decline sharply, whilst in neighbouring areas which are less disturbed the densities increase as orangutans move to these areas (Husson et al. 2009). However, such behaviour has only been recorded in Borneo and in studies from Suaq and Ketambe in Sumatra orangutans; females in particular, appear to have more stable and fixed home ranges. Furthermore, no large scale logging was recorded in Sikundur in 2015 or just prior to the study, only small scale disturbances but is unlikely to significantly impacted orangutan densities across the site (Nowak & Singleton 2015). Though hunting may be lower there is still a significant potential for killings due to fear or in retribution for crop raiding as Sikundur and Sei Betung are both surrounded by oil palm plantations and fruit gardens planted by local villagers (Fig 4.20) (Meijaard et al. 2011; Campbell-Smith et al. 2012; Davis et al. 2013).

The forest edges also offer easier access to the nearby plantations and could also provide a reason for why the edges of the forest are so preferred as both Sikundur and Sei Betung are found on a “peninsula” of forest surrounded by a sea of oil palm plantations and local people’s “gardens” where they grow fruits such as oranges and jackfruit (Rijksen & Meijard 1999). Given Sikundur’s extremely low fruiting score outside of mast events ad extremely low density of strangler figs which are usually a fall-back food for orangutans in other Sumatran sites (Sugardjito et al. 1987; Wich et al. 2004a) , it could be assumed that orangutans within Sikundur and Sei Betung (by virtue of its close proximity to Sikundur and lower forest condition) are be utilising another food source as a fallback food during periods of low fruit production. This could potentially lead to orang-utans raiding the nearby plantations and fruit “gardens” as these offer a potential fall-back food, this would explain their preference for nest sites near to the forest edges but also presents a potential source of conflict with local villages due to the loss of economically important crops and fear of the animals (Freund et al. 2017; Wich et al. 2011). It is unknown how frequently if at all crop raiding occurs in the plantations surrounding Sikundur and Sei Betung. Crop raiding by orangutans is a serious issue that does occur at other sites in Sumatra such at Batu Serangan (Wich et al. 2011a; Campbell-Smith et al. 2011a, 2012) as well as on Borneo (Meijaard et al. 2011; Spehar & Rayadin 2017; Freund et al. 2017) where this already leads to significant numbers of orangutans being killed in retribution for damaging economically valuable crops (Wich et al. 2011a; Freund et al. 2017). Further research could both survey the plantations for possible orangutan use and visit local villages and plantations and conduct surveys with villagers to assess how often raiding may occur and how much of a threat orangutan are perceived as to their crops and therefore locals' attitudes to orangutans and killing them. Should orangutans be found to be frequently entering and raiding plantations and fruit gardens then this is a potentially significant source of conflict and measures would need to be taken to minimise conflict such as through education or use of deterrents.

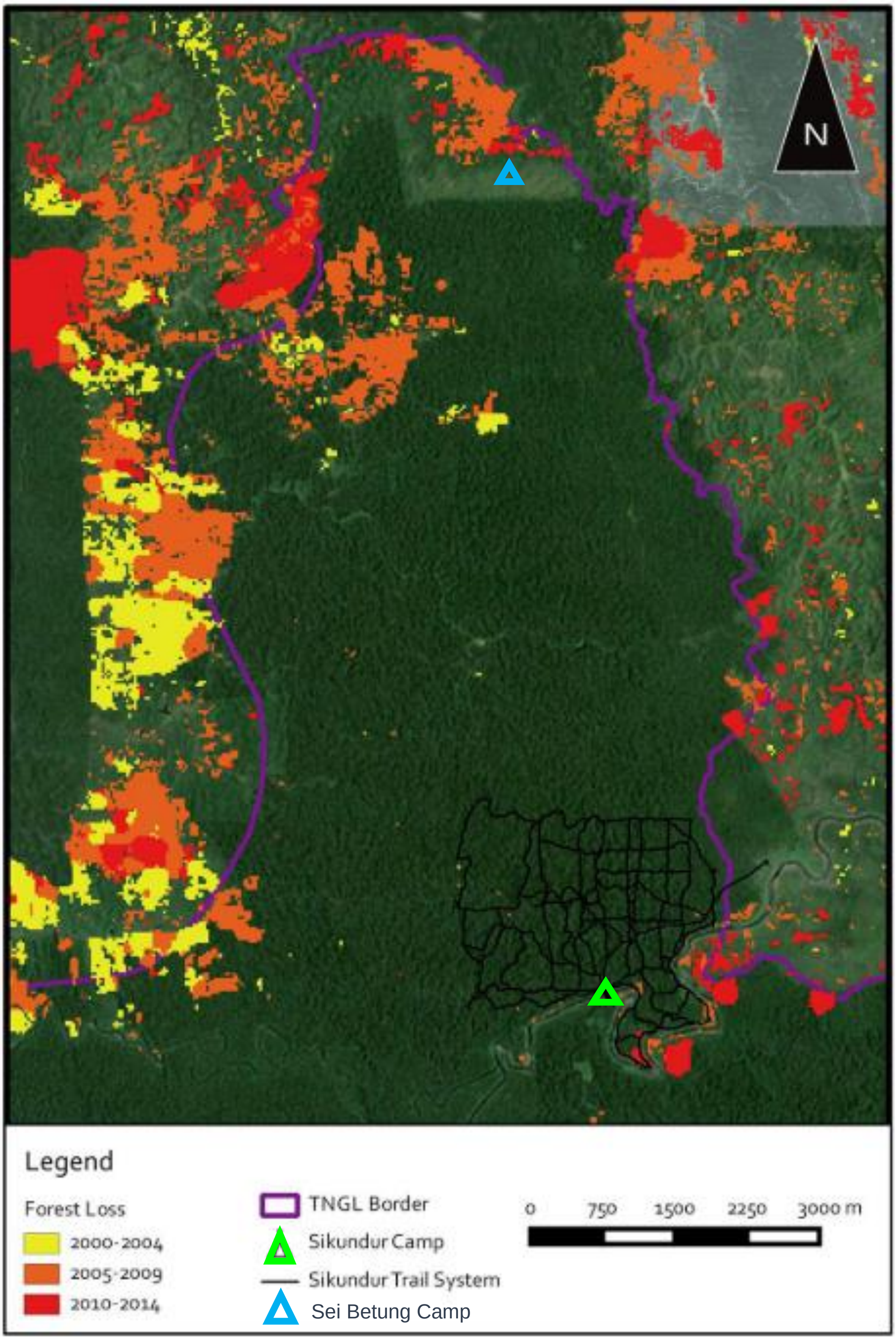

Figure 4-10 Map taken from Nowak & Singleton (2016) showing forest loss in the Sei Beutng area of Gunung Leuser National Park (TNGL) betweeen 2000-2014. Sikundur is in the south of the map and Sei Betung in the north.

The other variables which were found to be of importance for predicting nest densities reflected the forest structure and the quality of the forest and its level of recovery, these were canopy density, Morosita index, stem density and the Shannon-Wiener diversity index of tree heights. The models suggest that orangutans prefer habitats with greater canopy closure with fewer, more dispersed gaps and greater stem densities which would both allow for easier travel through the forest but also greater choice of nest sites (Ancrenaz et al. 2004a; van Noordwijk & van Schaik 2005; Manduell et al. 2011, 2012; Cheyne et al. 2013). A more heterogenous forest in terms of tree heights is both likely to be older and healthier as regrowth forest will tend to be of similar heights as it was cleared at the same time rather than the mixed ages you find in an intact forest where natural tree fall provides the opportunity for new trees to take their place and creating a natural heterogeneity of heights (Kaufmann et al. 2000; Okuda et al. 2003). The results from Sei Betung display such a trend, having a significantly lower rugosity (Shannon-Wiener H' tree height diversity) score when compared to Sikundur. Areas with a greater diversity of tree heights are also going to have a higher number of larger trees which are preferred for nesting by orangutans which again is what we found between Sikundur and Sei Betung (Ancrenaz et al. 2004a; Cheyne et al. 2013).

4.5 Conclusion

The results of this study have found that orangutan densities are significantly lower in reforestation areas compared to old naturally recovered selectively logged forests. The underlying soil type was found to have little impact upon the above ground forest structure and the orangutan densities within these land units. However, orangutan densities fluctuated significantly with season and year and appear to correlate with fluctuations fruit availability in Sikundur reported in (Nowak & Singleton 2016). Prior research by Buij et al. (2002) found that orangutans in Ketambe were travelling between sites following the peak fruit availability which changed timing with altitude. As there is a large mountain range within 20km of Sikundur there is potential that a similar altitudinal gradient of seasonal fruit availability exists there. Such changes in the timing of peak fruit could lead to similar seasonal movements of orangutans into Sikundur. This suggests that either surveys over wider areas or longer survey periods over a number of years are required in these forests to get accurate population estimates due to highly variable population densities due to seasonal movements. Distance to the edge of the forest was negatively correlated with orangutan densities which could be a product of increased fruit productivity due to the edge effect, lower hunting pressures in the area due to local religious beliefs and the proximity to oil palm and fruit plantations. The quality of the forest structure also had a significant influence on nest densities with areas with more heterogenous tree heights, denser canopies, fewer and more disperse gaps and higher stem densities preferred.

Given the increasing rate at which the world's forests are being lost and in particular in North Sumatra, which could lose >25% of its forest cover by 2030, leading to a possible to a loss of 25% of the Sumatran orangutan population it is vitally important to both protect what forests remain but also to try to increase forest lands within North Sumatra. Reforestation efforts and natural forest regeneration both play an important part in this and have been found to offer useful habitat to orangutans. The enrichment of less degraded areas surrounding intact forests provides the best method for both increasing orangutan habitat in both a cost-effective method as opposed to full replanting and quicker than natural regrowth to obtain similar forest structure properties. Further research is necessary to understand whether orangutans are using the nearby plantations and if so, how this is perceived by locals.

Chapter 5: General Discussion and Conclusions

This thesis adds to a growing body of work regarding orangutan nest ecology with the novelty of the direct comparison between sites which have experienced different levels of disturbance and the first in-depth research into orangutan nest ecology within the lowland dipterocarp forests of Sumatra and in an actively reforested site. This study also utilised novel methods such as canopy photography to quantify tree architecture and forest structure to determine what influences nest densities such as canopy quality and gap frequency through the use of canopy photographic methods to quantify canopy density and Morosita index (Goodenough & Goodenough 2012; Williams et al. 2013). The comparison between sites and differences in disturbance levels has allowed us to understand how trends in nest site selection, nest positions and nest densities are influenced by forest disturbance levels and selection preferences change with disturbance. The results provide support for the selectivity of orangutan nest site selection and nest building and further support the hypotheses that predator avoidance is the principal drivers for nest site selection and that nest stability, safety and protection from wind and rain are limiting factors that prevent nests being built in unsuitable branches. The patterns of selection for nest sites and responses to tree architecture determining nest height and position were found to be similar across sites and across levels of disturbance, but that the lower densities of quality nest sites and the increased openness in Sei Betung have led to nests being more clustered at that site. Furthermore, a significantly higher proportion of trees holding multiple nests than has been previously mentioned anywhere in the literature was also found in Sei Betung, suggesting that there is a significant pressure on quality nest trees in these more disturbed forests. The data for nest densities however appear to suggest that nest densities are not only influenced by the availability of preferred nest trees and the forest structure, but that other factors beyond forest structure may be significantly influencing the clustering of nest sites in Sei Betung such as fruit availability, edge effects and the opportunity of feeding in plantations. Further research is needed to truly determine what these other factors are and how they influence nest densities. Future research into the demographics behind nest positions and nest site selection could help to both build on prior research suggesting a link between age, body size and nest positions and if found to be true, nest positions could provide researchers and land managers with a simple way of determining the populations demographics. However, this study does conclusively show that forest structure significantly influences nest site selection, nest height, position and nest densities in Sumatran orangutans.

5.1 The influence of forest structure on nest tree selection

The research chapters of this thesis sought to test a number of hypotheses. In the first research chapter; Chapter 3, the principal aims were to investigate the influence forest structure has upon nest tree selection in particular tree architecture and tree species and whether the patterns of selection were shared across sites with having experienced differing levels of human disturbance. Nest site selection and preferences were found not to differ significantly across sites showing that regardless of disturbance levels the important tree architecture factors remain the same. Methods used in this chapter were chosen as they offered a direct test of nest site selection by comparing nest tree selection with both trees within the immediate vicinity of the nest tree (5m radius) along with trees randomly sampled throughout each site to provide a test of selection ratios (use/availability) as was noted in Prasetyo et al. (2009) to be a concern with previous studies. Those studies which did test selection ratios Cheyne et al. (2013) & Ancrenaz et al. (2004a) both utilised vegetation data from phenology plots to test against nest trees, these plots were set in a limited number of areas and could potentially mispresent what the true availability of tree species and architecture types may be available within the forest. By using transects and also measuring the trees within the immediate vicinity of the nest tree we are able to give a true value of the availability of each tree type within the environment and what was available to the orangutan when it decided to rest and build a nest.

The differences in the comparisons between nests and non-nest trees and nests and those within 5m radius were very similar and model averaging for both showed the significant influence crown size and crown shape have upon nest site selection. For both sites, orangutans showed significant preferences for larger than average trees in terms of crown size, tree height and crown area and significant preferences for cone and upside down-cone shaped crowns, whilst significantly avoiding extremely large trees and those with bent-over crown and elongated-spheroid crown shapes. This preference for "larger than average" trees but avoidance of extremely large trees lends weight to Cheyne et al's (2013) findings that orangutans prefer to nest within the upper canopy but avoid more exposed positions that extremely large trees would provide and that more stable trees are preferred for nest sites. This both contrasts with both the findings of Ancrenaz et al. (2004a) that within disturbed sites that orangutans select for the tallest trees available but also those of Prasetyo et al. (2012) where orangutans were nesting in quite small trees compared to the surrounding ones. This could be due to site differences such as average wind speeds and predation pressures as Ancrenaz et al. (2004) stated that the preference for extremely large trees in their site is likely a response to disturbance and frequent tree fall in heavy winds. Similarly, orangutans in Prasetyo et al. (2012) study may be in a site with either frequent strong wind or rain, thus by nesting in smaller trees below the canopy they are able to find more shelter from overhead canopy. For our site however, model averaging found that DBH was negatively associated with the probability of a tree holding a nest. Such an association suggests that although the majority of tree architecture parameters orangutans select for are associated with stability, predator avoidance is likely the primary driver for nest site selection, however further testing is required to prove this. A potential avenue of study could use a model similar to that in the study by Lameira et al. (2013) but rather than investigating alarm calls we record changes in nest site selection as a response to the placement of predator models in a site.

Unexpectedly, a large proportion of nest trees in Sei Betung were found to contain multiple nests, analysis of the data found that the number of multiple nest trees was significantly higher in Sei Betung (40%) than Sikundur (11.1%) and indeed much higher than has been reported from any other field site (Singleton 2000; Ancrenaz et al. 2004a; Prasetyo et al. 2009, 2012; Kanamori et al. 2017). Furthermore, the trees holding multiple nests in Sikundur were found to be significantly taller than single nest trees and in Sei Betung these multiple-nest trees had significantly larger crowns than those of single nest trees in terms of volume, size and area. Modelling found that there was a significant link between trees holding multiple nests and lower crown connectivity as well as larger crown size, DBH and crown area. This link between multiple nests, low connectivity and tree structure attributes which are associated with increased stability suggest that in these more open habitats, preferred nest trees that are large and strong are rare and as such reuse is required do to the limited number of potential nest sites compared to forests such as Sikundur. When these results are paired with those from Chapter 4 that trees with larger crown areas are preferred for Position 2 nests there does appear to be more support for the predator avoidance hypothesis. Position 2 nests are one of the most difficult for predators to access due to the limited pathways to the nests (Rayadin & Saitoh 2009; Stewart & Pruetz 2013) and by being nearer to the end of the branch vibrations from the movement of the predator are likely to be more noticeable and give the nesting individual more time to escape (Anderson 1984, 2000; Fan & Jiang 2008; Teichroeb et al. 2012). Furthermore, when comparing the proportions of nest positions used in single nest and multiple nest trees a greater proportion of nests in multiple nest trees were found to be built in Position 2- on the end of branches. These results further support the hypothesis that predator avoidance is the primary driver of nest site selection for orangutans in Sei Betung, with selection for trees with greater stabilising properties allowing for higher and safer nest positions to be built.

These results also further support the findings of Ancrenaz et al. (2004a) that in more disturbed or open areas where large trees are sparser, orangutans will reuse those few large tree significantly more than in areas where large trees are common, suggesting that this lack of ideal nesting sites places an added pressure upon orangutans to find good, stable nest trees and that there may be competition over these ideal nest trees. Prior studies have found that although orangutans travel through and forage in plantations and heavily disturbed areas, they still rely upon more natural forests for sleeping, resting and feeding (Spehar & Rayadin 2017). This reliance on more natural forests may be due to a lack of quality nest sites, this lack of quality nest sites could constrain the recolonization of orangutans in this area and movement to new areas and lead to the clustering of orangutans in areas where preferred nest sites are available. Nests were found to be clustered significantly more in Sei Betung than Sikundur which suggests that not only are there few ideal nest sites within Sei Betung as evidenced by the high incidence of multiple nests trees but also the clustering shows that these nest trees are poorly spread through the forest. Therefore, there is a need for further replanting to encourage the wider use of the site by orangutans. To promote the recolonization of sites by orangutans there should be a focus on planting of preferred nest tree species which have the preferred architecture for nest building along with planting more preferred food species and filling in gaps with fast growing trees to ensure high canopy densities to facilitate easier movement through the site. These planting focuses could also be used in habitat corridors to better facilitate the movement of orangutans between habitat areas and avoid the need for travelling through plantations. Our results showed that orangutan highly utilised pioneer species in Sei Betung as nest sites so a focus should be placed on planting these species when conducting reforestation projects. We also identified a number of other species that orangutans' favour as nest sites which have significant value as timber but also have high potential value for medicine and drug discovery (Wang et al. 2004; Fern 2019). Such beneficial uses could offer a way to support the conservation of orangutans and their habitats for the gathering of such valuable forest products.

5.2 How forest structure influences nest height and nest position

In chapter 4, we sought to understand how forest structure and tree architecture influenced nest height and nest position to determine whether these could be linked most strongly to either the nest stability and comfort hypothesis, improved thermoregulation or predator avoidance. Forest condition had also been hypothesised as having an influence upon nest position with Prasetyo et al. (2009) suggesting that an increased preference for tree tied (position 4) nests in Tuanan and Sabangau could be a result of the significant disturbance both of these sites have previously experienced or that it could be due to species or geographic differences. The two sites of Sei Betung and Sikundur offered the perfect opportunity to test the disturbance hypothesis as a leading driver for a greater proportion of tree tied nests.

The results of this chapter further supported the hypothesis that predator avoidance was the principal driver of nest height and nest positions with forest structure and stability and comfort being constraining factors which limited the potential height and placements of nests. Nests were found to be built within the upper canopy, following the findings of Cheyne et al. (2013). However, in less connected areas nest heights and the height of the nest trees were lower than the surrounding canopy. This is most likely a likely a response to the increased exposure of the nest to side winds and rain due to the more open forest structure, future research could assess the effect crown shape and openness has upon wind speed, wind sway and rain experienced within a nest. Nest heights were found to be significantly influenced by tree height as expected and greater crown area which is likely due to the increased stability the greater crown area provides (Nicoll & Ray 1996; Soethe et al. 2006). Crown size, however, is negatively associated with nest height; however, this could be due to the relative position of the nest within the crown. Trees with deep crowns also tend to be tall, by nesting lower within the crown of these tall trees the orangutans could be trying to keep the nest within the level of the upper canopy of the surrounding trees rather than the more exposed position at the top of the crown of these large trees with deep crowns. Crown shape was found to have a significant influence upon nest height with nests being built higher within more structurally stable crown shapes such as spheroid and cone shaped crowns whilst nests in bent-over trees were significantly lower than all others, most likely due to their inherent instability. Further research could assess the structural properties of crown shapes both in the strength of branches as well as the amount the tree sways in the wind. These results suggest that stability and comfort may be a constraining factor upon nest height with nests being selectively built within the upper canopy which increases the distance from ground predators and more layers of foliage to obscure the nest from predators (Sugardjito 1983) but not nesting above the surrounding canopy layer so as not to be exposed to wind, rain and sunlight.

Nest position unlike nest height can provide a clearer insight into whether anti-predation is a driver of nest position selection and by comparing between the two sites with varying levels of human disturbance. Should comfort and stability have been the principle driver of the selection of nest positions and nest height, a greater proportion of the highly stable Position 1 nests built against the main stem should be found. However, in Sikundur, Position 1, 2 and 3 nests were found to be built in roughly similar proportions with a range of 3.3% dividing them, whilst in Sei Betung Position 2 and Position 3 nests were found twice as often as Position 1 nests. This preference for more precarious nest positions in Sei Betung where mean tree heights, canopy density and connectivity are all lower further suggests that predator avoidance is driving the selection for nest sites in Sei Betung and is responsible for why Position 1 nests are not as common as would be expected if comfort was the main driver instead. Position 4 nests were also significantly rarer in Sei Betung than Sikundur accounting for only 2.2% of all nests in Sei Betung whereas in Sikundur they accounted for 10.5% of all nests which is a greater proportion than has been recorded at any other Sumatran field site or Kinabatangan in Borneo (Prasetyo et al. 2009). Potentially the availability of the smaller, more flexible trees needed to build Position 4 nests is lower in sites such as Ketambe and Kinabatangan due to the higher average tree heights in those sites when compared to Sikundur (Ancrenaz et al. 2004a; Prasetyo et al. 2009; Manduell et al. 2012). The relative rarity of Position 4 nests in Sei Betung compared to Sikundur also provides evidence against the hypothesis that this nest position has arisen due to a paucity of large tree and instead lends further weight to the argument that this is likely due to species differences between Bornean and Sumatran orangutans and geographic differences between the populations (Prasetyo et al. 2009).

Using PCA analysis, the differences in tree architecture between the four nest positions was visualised and found that Position 4 nests were the most distinct of all nest positions, whilst the other three nest positions were more similar to each other. The principal variables found to most significantly influence nest position through model averaging were crown size, crown area and overhead canopy. Position 4 nests were as expected built in the smallest trees and had the lowest nest heights so would offer the least benefits in terms of predator avoidance and stability, though smaller more flexible trees are needed to be able to build this nest position. Conversely, Position 2 nests were found to be built in the largest trees, in particular those with very large crowns in terms of size, area and volume. These larger crowns both provide added stability to the tree by the larger number of branches helping to reduce harmonic sway (James et al. 2006) but also providing greater supply of building materials for nest sites and the greater likelihood of the large branches needed to nest further from the main stem (Horn 1971; Rayadin & Saitoh 2009; van Casteren et al. 2012, 2013; Samson & Shumaker 2013; Stewart & Pruetz 2013; Hernandez-Aguilar et al. 2013; Samson & Hunt 2014). Position 3 nests were as expected found to have the least overhead canopy, but were built within shorter trees which meant that although they were at the top of the crown they still remained in the upper level of the surrounding canopy, thereby ensuring potential escape routes and cover from overhead canopy. Though Position 1 nests appear to be the position offering the least protection from predators by being built against the main stem and lower in the crown, they were still built at a similar height as Position 2 and Position 3 nests. Position 1 nests were found to be built in the tallest trees and by having a higher first branch height access by predators is limited, thereby ensuring that the nest does provide some anti-predatory adaptation. When combined with the results from Chapter 3 it appears that nest site selection is driven by predator avoidance with orangutans preferentially selecting trees which will allow them to build the highest and safest nest but being constrained by comfort and stability which prevents nesting above the canopy or building nests in positions unsuited to the tree architecture.

Research by by Rayadin & Saitoh (2009) found that that immature and female orangutans tended to nest in more precarious positions such as Position 2 and Position 3 nests whilst large males nested lower in the tree in more stable positions. Smaller, immature orangutans are more susceptible to predation (Rijksen 1978b; Rayadin & Saitoh 2009; Kanamori et al. 2012) so would need to use more precarious nest positions to reduce the increased predation risk. Large flanged males however are extremely unlikely to be predated upon (Rayadin & Saitoh 2009; Mohamad et al. 2015) but due to their large body size require more stable nest positions, thus Position 1 nests are most likely to be built by these larger individuals. It could be suggested due to this separation in nesting habitat that studies into nest positions could potentially provide information about the demographics of the population and be used when developing new conservation strategies for populations. Further research from behavioural follows and observing nest building would be needed to determine whether this is true. It does pose the possibility that in Sei Betung that either there is a smaller proportion of males in this site or that they are being forced to nest in more precarious nest positions due to the dearth in tall trees preferred for Position 1 nests. The presence of tigers in Sikundur provides further support for the conclusion that a preference for higher nests may be a form of predator avoidance and that due to the paucity of tall trees in Sei Betung those individuals which normally build Position 1 nests must then build nests in more precarious positions to protect themselves from possible predation. Building in these more precarious positions however makes the nest itself less safe as it is more likely to experience sway due to the increased weight in the wind and potential failure during strong winds or a storm. The need for larger animals to use more precarious nest positions or suitable nest trees within more heavily disturbed areas could both lead to fewer large males being present in these habitats as they move towards less disturbed areas. Spehar & Rayadin (2017) found that though orangutans were travelling and feeding in plantations they were nesting more frequently within the patches of natural forest suggesting that the lack of quality nest trees was influencing the ability of orangutans to survive fully within that disturbed habitat.

The building of Position 4 nests is most likely linked to forest structure and a response to a paucity of large trees in a habitat where large ground predators are absent. Position 4 nests are the most commonly built nest position in both Tuanan and Sabangau where mean tree heights are very low, as in Sei Betung. However, though both sites are highly disturbed and have low average tree heights the canopy closure and connectivity are most likely significantly higher in Tuanan and Sabangau compared to Sei Betung, as Sei Betung was previous clear felled in many parts and still has numerous large, open areas (Husson et al. 2009; Marshall et al. 2009; Prasetyo et al. 2009). As Position 4 nests require at least 2 trees in close proximity to bend and weave either the tops or branches together to form the nest, the opportunities to build such a nest are lower in a more open site such as Sei Betung. Therefore, we would add that Position 4 nests are built in sites where there is a paucity of large trees but where stem densities and connectivity scores are high.

5.3 Influence of forest structure on nest densities

In chapter 5 we sought to understand how Sikundur and Sei Betung differed in terms of forest structure and how those differences in forest structure influenced orangutan densities. Sikundur and Sei Betung were found to differ in almost every measure except crown size and crown area which is likely due to the greater light availability in Sei Betung because of its more open structure allowing for trees to grow wider as they make the most of the available light and shade out potential competition (Yoda 1974; Hartshorn 1978; Alvarez-Buylla & Martinez-Ramos 1992; Ackerly 1996; Clark et al. 1996; Clark & Clark 2000; Sterck & Bongers 2001). The forest in Sikundur was significantly taller, denser, with fewer and smaller gaps, and more rugose than that in Sei Betung, as such the orangutan densities in Sikundur were also far higher than Sei Betung. Along with higher orangutan densities, the orangutan nests were more dispersed in Sikundur as opposed to Sei Betung where 82.2% of all nests were found on 2 adjacent transects, reflecting what was also found by Wich et al. (2016) in Sei Betung. This significant clustering lends further weight to the observations of Ancrenaz et al. (2004b) and those of our study in Chapter 3 in that in severely disturbed areas or those in which preferred nesting trees are rare then orangutans will tend to both reuse preferred nest trees to a greater extent and cluster within and around these preferred nest trees forming “villages”. This places a greater pressure upon these trees and could lead to competition for nest sites and an increase in negative social interactions (Delgado & Van Schaik 2000).

When Sikundur was broken down into land units based upon its underlying soil types as defined by Laumonier et al. (2010), the differences in forest structure were less significant, though the Alluvial landunit was the most distinct, showing a greater number of significant differences between it and the other two land units than was found comparing the Plains versus the Hills. Though the no significant differences in orangutan densities were found between the land units in Sikundur, the differences were still visibly large, with the Alluvial land unit having the lowest orangutan density whilst the highest densities were to be found in the Plains. This was possibly due to either the differences in human disturbance rates within each land unit due to accessibility, differing forest structure and rates fruit productivity in each; due to both past selective logging levels and the underlying soil type (van Schaik & Mirmanto 1985; Johns 1988; Clark & Clark 2000; DeWalt & Chave 2004; Paoli et al. 2006; Paoli & Curran 2007). The Alluvial land unit was typified by lower stem density, canopy density and rugosity than the other land units which is likely due to either increased levels of past disturbance or as van Schaik & Mirmanto (1985) found that there are lower biomass levels in alluvial soils and shorter life-spans for trees suggesting a greater rate of turnover which could lead to more frequent gap formation and fewer large trees preferred for nesting. These results however only suggest that these areas are not preferred for nesting but may still be used for foraging, further study from follow data is needed to determine whether these areas are less utilised than others.

Our analysis found that the most significant predictors of orangutan densities were canopy density, Morosita index, canopy rugosity/diversity of tree heights, stem density and distance to the edge of the forest. Orangutan densities were found to be associated with areas with greater canopy densities, stem densities and canopy rugosity and lower Morosita indices and somewhat surprisingly, were positively associated with reduced distance from the edge of the forest. These variables are more positively associated with forest health and recovery levels and facilitate greater ease of movement for orangutans to travel through the canopy (van Noordwijk & van Schaik 2005; Manduell et al. 2011, 2012; Davies et al. 2017) and well as providing a greater proportion of preferred nest sites based on the results in chapters 3 and 4 as well as the studies by Cheyne et al. (2013) and Ancrenaz et al. (2004b). A recent study by Davies et al. (2017) found that orangutan travel paths were influenced by forest structure and that orangutans were more likely to move in the direction of increased canopy closure, tall trees and more uniform heights whilst avoiding gaps and moving towards large emergent. Those results suggest a preference for areas where forest structure provides easier pathways and does agree with our study in the preference for more closed canopies and avoidance of gaps, however, our study has found that for nesting, more rugose tree heights are preferred and emergent trees were highly avoided as nest trees. As orangutans must travel to and from nests and there is a need for ease of access via arboreal routes. Generally, more homogenous tree heights are a sign of prior disturbance as trees would have been removed at a similar time and so grow at similar rates, however homogenous tree heights also offer a more direct path and less need to expend energy ascending and descending to travel laterally. Yet, we see orangutans in our study preferring to nest in areas with greater tree height heterogeneity as these differences in tree height are what allows for the orangutans to nest within the upper canopy but not needing to always nest at the tops of crowns or in less stable, peripheral positions. When combining these results, it suggests that although some areas may not be preferable for nesting, they still may be used for travel and foraging, a future research project could try to combine these aspects to determine which parts of the forest are most heavily utilised for nesting and foraging and which are least used or of least value to orangutans to better inform management decisions.

These important variables were used in a PCA analysis to visualise the differences between the transects in Sei Betung where nests were present and those without in an attempt to understand what may be the cause of the significant clustering of the nests there. However, the PCA analysis found that both completely overlapped and that no particular variable most defined those nests other than a lack of extreme values. The age and previous disturbance levels across Sei Betung were suggested to be a potential explanatory factor as prior research by Wich et al. (2016) also found significant clustering of nests in the same locations which unlike much of the site had only received enrichment planting as it was not completely clear felled unlike the rest of the site.

The significant preference for nesting nearer to the forest edge suggests a number of points, firstly: as a number of villages border both sites it suggests that hunting is less of an issue or pressure upon orangutans within these sites as previous research has shown orangutan densities to be lower near to settlements know to hunt orangutans (Marshall et al. 2006; Wich et al. 2012b). Secondly, this preference for areas near to the edge of the forest could suggest and that these areas are more productive or hold trees with more preferable architecture for nesting due to the actions of selective logging and relative younger age of the trees in these edges. It is also possible that by being near to the edge of the forest the orangutans have greater access to and are able to forage within the nearby plantations and fruit garden planted by local villages, supplementing their diet with these more consistent food sources when fruit availability is low (Rijksen & Meijard 1999; Ancrenaz et al. 2015). Normally strangler figs are a common fall-back food for orangutans during periods of low fruit availability (Wich et al. 2004a), but Sikundur and Sei Betung have extremely low densities of figs, so another food source must be used during these periods presenting the possibility of a need for crop raiding (Sugardjito et al. 1987; Wich et al. 2004a). If crop raiding is occurring and is a primary driver in the preference for nesting nearer to the forest edge then this could lead to a conservation dilemma as crop-foraging is significant source of conflict between orangutans and local villages in other parts of Sumatra and Borneo, where already significant numbers of orangutans are killed in retribution for crop damage or perceived threat (Meijaard et al. 2011; Wich et al. 2011a; Campbell-Smith et al. 2011a, 2012; Spehar & Rayadin 2017; Freund et al. 2017). However, whilst orangutans have been found to range and nest within oil palm plantations and feed upon the mature fruits (Campbell-Smith et al. 2010, 2012; Ancrenaz et al. 2015), oil plantations are not a preferred habitat though due to the difficulty of travelling within the plantations and low diversity of food outside of oil palm fruits. When the fruit of oil palms are not ripe or in low abundance these plantations may form more of a barrier to orangutan movement rather than a new feeding opportunity (Campbell-Smith et al. 2011a). Further research is needed to understand to incidences of crop-raiding within the nearby plantations and to determine whether the orangutans are utilising the oil palm or only fruit plantations.

Orangutan densities in Sikundur were found to differ significantly between sampling seasons in 2015 and 2016. The differences in population densities and nest ages showed a correlation with a prior mast event in mid-2014 (Nowak & Singleton 2016) following which the population densities decreased. A similar pattern of increasing orangutan densities with high fruit periods and masting events has been recorded in Borneo in the Danum Valley as orangutans with wide and overlapping ranges gathered into this smaller area to make the most of the high fruit availability during those periods (Kanamori et al. 2017). Prior research in Sikundur by Knop et al. (2004) found no significant correlation between fruit availability and orangutan densities. However, Kanamori et al. (2017) suggest that it is possible that the research period of Knop et al. (2004) may have been to short to detect any significant correlation or that they may not have experienced any periods of major fluctuations in fruit availability or mast period during their study. Another previous study in Sumatra by Buij et al. (2002) however did detect a positive correlation between fruit availability and orangutan densities. In their study they found that orangutans were commuting between three areas following the fruit peak as the seasonal fruit availability in their study site in Ketambe changed with altitude. Our results further support the conclusion made by Kanamori et al. (2017) that in areas of low fruit availability such as dipterocarp forests orangutans will seek the fruit and when there is a large peak of supra-annual fruit availability in an area or neighbourhood then orangutans will commute to and congregate within this area. Other events such as a floods (Kanamori et al. 2017) and logging (MacKinnon 1971; Mackinnon 1974) have also been found to cause temporary increases in orangutan densities as orangutans travel away from the disturbance, however no such disturbances were known to have occurred during the field research of this study. These significant fluctuations in orangutan densities associated with supra-annual fruit availability and disturbances presents another consideration when estimating orangutan densities for an area and suggests that longer periods of study are needed within dipterocarp forests to accurately estimate orangutan densities. Furthermore, when estimating the size of area necessary for the conservation of orangutans within these habitats the large scale movements of orangutans following these peak fruiting event must be considered as this travel is needed to ensure adequate food supply throughout the year; especially during the periods of low fruit which follow these peaks (Kanamori et al. 2017).

5.4 Key findings and conclusions

The key findings of this study provide further insight into orangutan nesting and show how complex a behaviour nest building is and that not only are orangutans highly selective upon nest trees but they are also adept at utilising a tree’s structure to provide a safe, stable and comfortable nest. The use of nest positions and nest heights are in a fine balance between forest structure, nest site availability, the need for stable and safe nest sites and predator avoidance. If one changes or is removed it alters the balance such as the removal of taller trees and creation of gaps in areas with tigers either forces larger animals to leave the area or utilise more precarious nest positions and reuse the fewer preferred nest sites more frequently. Conservation and land managers must consider this when allowing for selective logging to occur within a site to further minimise the impact on orangutans and when reforesting a site potentially focusing on creating areas of denser forest first should be a priority over less densely replanting a larger area. Areas which have been illegally logged or selectively logged could be supplementary planted, as in the western side of Sei Betung, using native species and prioritising pioneer species such as those belonging to the genus Macaranga which are able to offer useful nest sites within a short period of years (Fern 2019).   Companies planning selective logging must try to minimise the damage caused to the canopy when felling trees (Pereira et al. 2002; Okuda et al. 2003) and try to minimise creation of large gaps which would make travel harder (Davies et al. 2017). Following extraction, roads which are no longer used should be closed or controlled with carriers at major access points to prevent the influx of poachers and illegal loggers into the area (Morgan & Sanz 2007).

Within these reforested and disturbed sites orangutans have been found to cluster within smaller areas which must hold either preferred forest structure for nesting and travel or may hold an important food source. In the recovered site of Sikundur orangutan densities were found to fluctuate in correlation with the supra-annual peaks of fruit availability during periods such as mast events. These fluctuations in orangutan numbers suggests that both longer periods of time are needed to accurately assess the population densities of dipterocarp forests such as Sikundur but also that larger areas may need to be protected when developing conservation strategies for these populations due to their large ranging throughout these habitats in search of fruit peaks. The preference for nesting nearer to the edge of the forest in both Sikundur and Sei Betung may also suggest that orangutans at these sites are ranging into and foraging within the neighbouring plantations and that in periods where fruit availability is low within the forest these crops may provide an important fall-back food source due to the low densities of figs which are the normal fall-back food for orangutans (Wich et al. 2004a). Determining whether orangutans are ranging into and crop-raiding within plantations and locals fruit “gardens” is important in order to mitigate and reduce any potential conflicts arising from these behaviours and to ensure that the local farmers do not resort to retaliatory killings in response to losses from crop-raiding orangutans (Campbell-Smith et al. 2010, 2012; Meijaard et al. 2011; Davis et al. 2013).

5.5 Conservation Implications

The results from this study suggest that there is still much to learn about orangutans and how forest structure influences their behaviour and ecology and their responses to changes in forest structure whether anthropogenic or natural in origin. Our results suggest that further emphasis must be placed on retaining patches of relatively undisturbed forest structure by limiting the removal of large trees from habitats and limiting the size of gaps created by selective logging but less focus is needed to be placed on preserving very tall emergent for the conservation of orangutans as they are less useful for nesting but still have uses to other species, in particular gibbons who favour them as their sleep sites (Anderson 2000). Where reforestation action is ongoing and planned to further support orangutan conservation the focus should be on the planting of preferred nest species, fruiting species and pioneer species. Planting should also be focused on ensuring areas are more densely planted to ensure a quicker return of a dense canopy and fewer gaps rather than sparse planting over a larger area which has less use for orangutans both for nesting and for travel (Davies et al. 2017). Similarly, when planning corridors, a focus must be placed on ensuring the presence of suitable nest trees as well as retaining good canopy connectivity to better facilitate travel through the corridor. When planning the conservation of spaces for orangutans within dipterocarp forests a longer period must be used to assess the population density as the densities are liable to fluctuate with the supra-annual changes in fruit peaks and mast events. Follows are required to understand the wider area used by the population as well as the core area most used by the orangutans within this area. Orangutans may be ranging into neighbouring plantations, assessing the frequency of crop-raiding events, the extent of damage caused and developing mitigation plans for locals affected by these losses is vital to ensure conflict is kept to a minimum and retaliatory killing are avoided.

5.6 Future Research

A number of avenues of potential further research were mentioned within the discussion which are surmised here. Preferences for certain tree species were noted within both sites, however data for the availability of these species were unavailable for Sikundur. It would be of interest to obtain these and test whether certain tree species were used more frequently than available but also assess whether orangutan nests are more frequently built in areas of greater diversity or higher concentrations of particular fruit species. The nest tree species were known and a number of these were species known to be food species but whether these were fruiting or not was not recorded and was an oversight as this would be useful in helping to understand why some of these species were preferred as nest sites over others. Building upon this, testing the mosquito repellent properties of proffered nest trees would also be valuable not only to understanding this aspect of nesting but also potentially discovering a new source of natural insect repellents. A future research project could look into the health and cortisol levels of orangutans in Sikundur and Sei Betung by taking hair samples from nests. This could help us to understand whether the need for frequent nest reuse and in suboptimal nest tees has an effect upon the health of the animals. Furthermore, the hair samples could also be used for identifying the sex of the nest builder to test the hypothesis that nest positions have a sex and age basis and could be used as a simple proxy for population demographics.

In relation to nest height and nest position further research at other sites is required to determine whether the absence of large trees is responsible for the increased proportion of precarious nest positions in Sei Betung compared to Sikundur. Future studies could be conducted at other sites which are undisturbed and those which have been heavily logged as opposed to reforested as they may show different forest structures and could provide information to how forest structure changes after the removal of trees as opposed to being replanted. Data from orangutan follows where the individuals age class and sex are known could help to shed light into how sex and body size differences reflect nest position. These data could also allow us to know whether nest positions represent the demographic makeup of the population and could be used to quickly assess the population health and demographics. Testing using a model of a tiger or tiger scat within field sites could be used to determine whether orangutans alter their nest site selection and positions if a predator is known to be in the area. This would require only recording fresh nests following the placement of the model.

A long-term monitoring of orangutan densities and the building of new nests along with the fluctuations in fruit availability could help to both determine the size of the orangutan population within the core area and the larger transient population which follow the fruit peaks from neighbouring areas. Further long-term research would also allow us to determine whether orangutan densities in Sikundur are truly influenced by fruit availability by also conducting surveys further out from Sikundur. Surveys to the west along the altitudinal gradient could allow us to test whether there is such a seasonal change in fruit availability occurring and whether this is responsible for the changes in orangutan densities. Further understanding of the tree species present in the areas where orangutans cluster and observations of behaviour in those areas could help us to understand what leads orangutans to nest in such high densities within those areas. Surveys of the surrounding plantations for nests and orangutans and surveys of local farmers and plantation workers on the frequency of crop raiding events would allow conservation agencies to assess the threat conflict and retaliatory killings pose to orangutans in these populations and develop mitigation plans to ensure their conservation.

5.7 Final remarks

Our study has helped to further display the complex nature and behaviours of orangutans and that nest site selection, nest height and nest position are all part of a complex balance of comfort, stability and predator avoidance in relation to the forest structure and tree architecture. Changes in forest structure can have profound impacts upon orangutan densities with orangutans clustering within the areas of preferred nest sites and fluctuations in fruit availability leading to the movements of orangutans into and out of the site.

Like the drivers of orangutan nest site selection, positions and height, conservation is also a balance of protecting habitats and species but also supporting locals and governments to be able to coexist with biodiversity and sustainably use their lands whilst preventing the overexploitation of these lands and the species that call them home. There is still much to learn about orangutans but the more we learn the better we will be able understand how our actions may affect them and develop better conservation management strategies that will allow us to coexist and live together for future generations.

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Appendix I Supplementary materials for Chapter 3

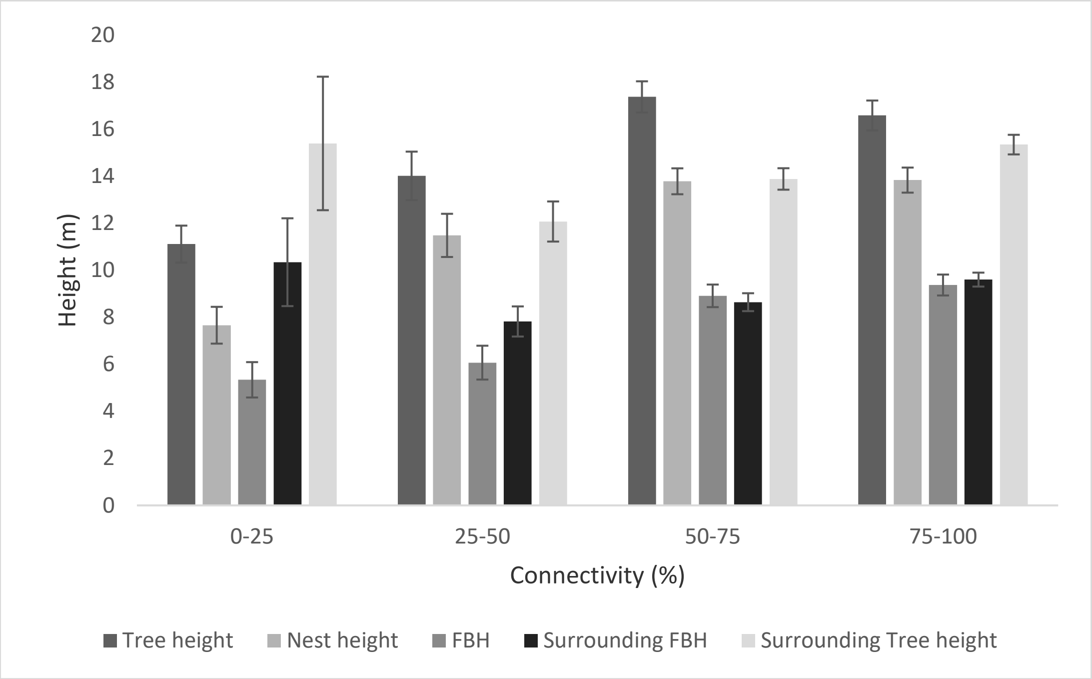

Figure S7 Nest height, tree height and first bole heights of nest trees based on crown connectivity

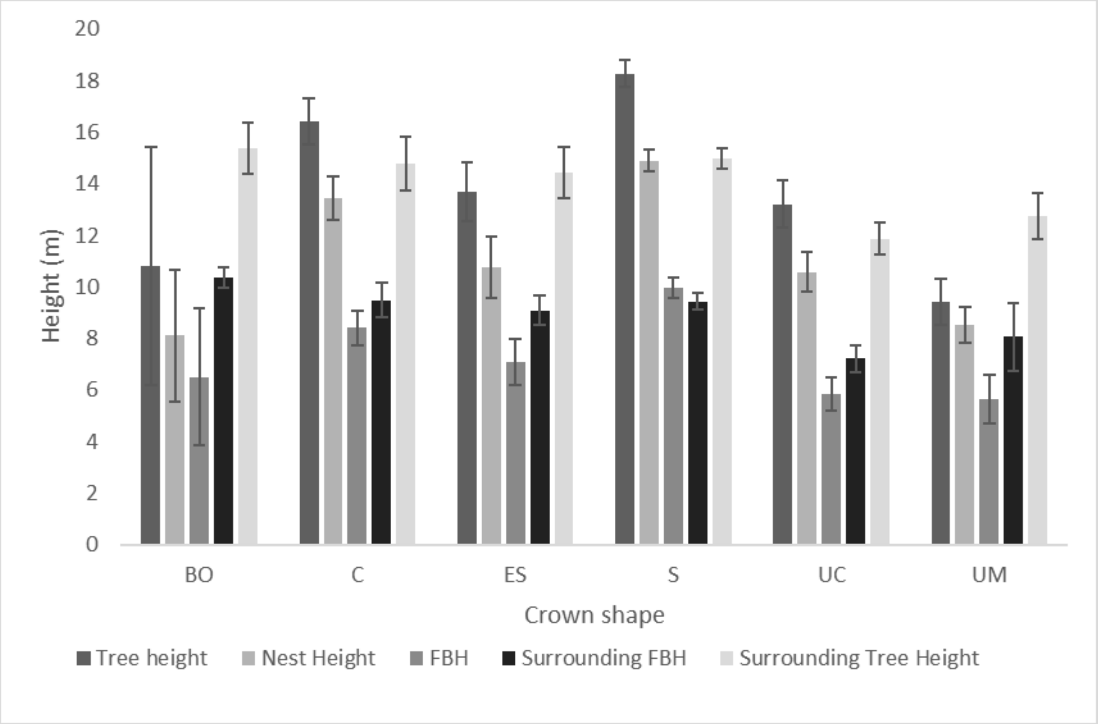

Figure S8 Nest height, tree height and first bole height of nest trees based on crown shape

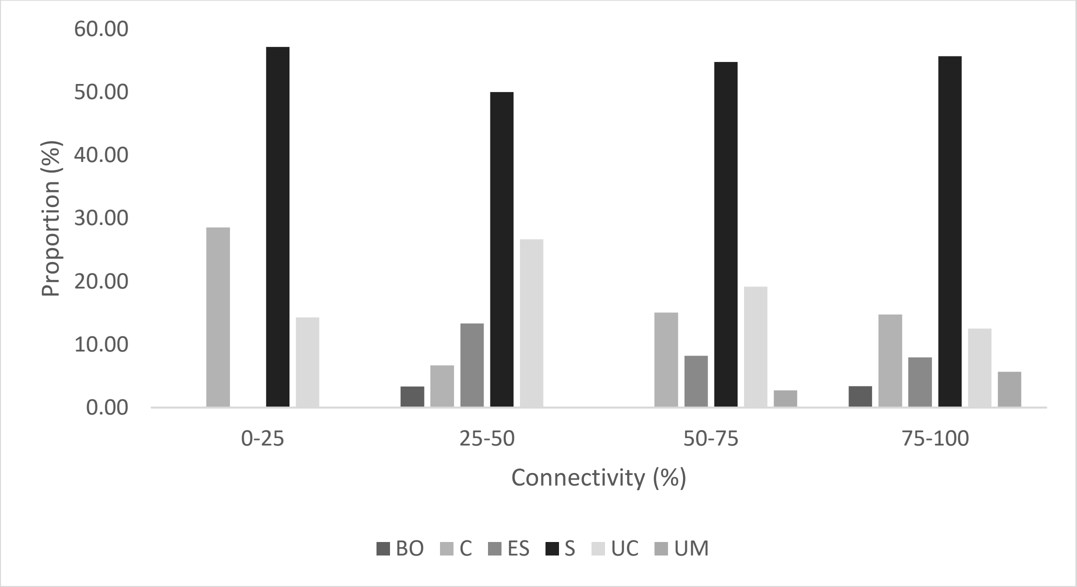

Figure S9 The proportion of nests built in trees of each crown shape in trees with differing crown connectivity

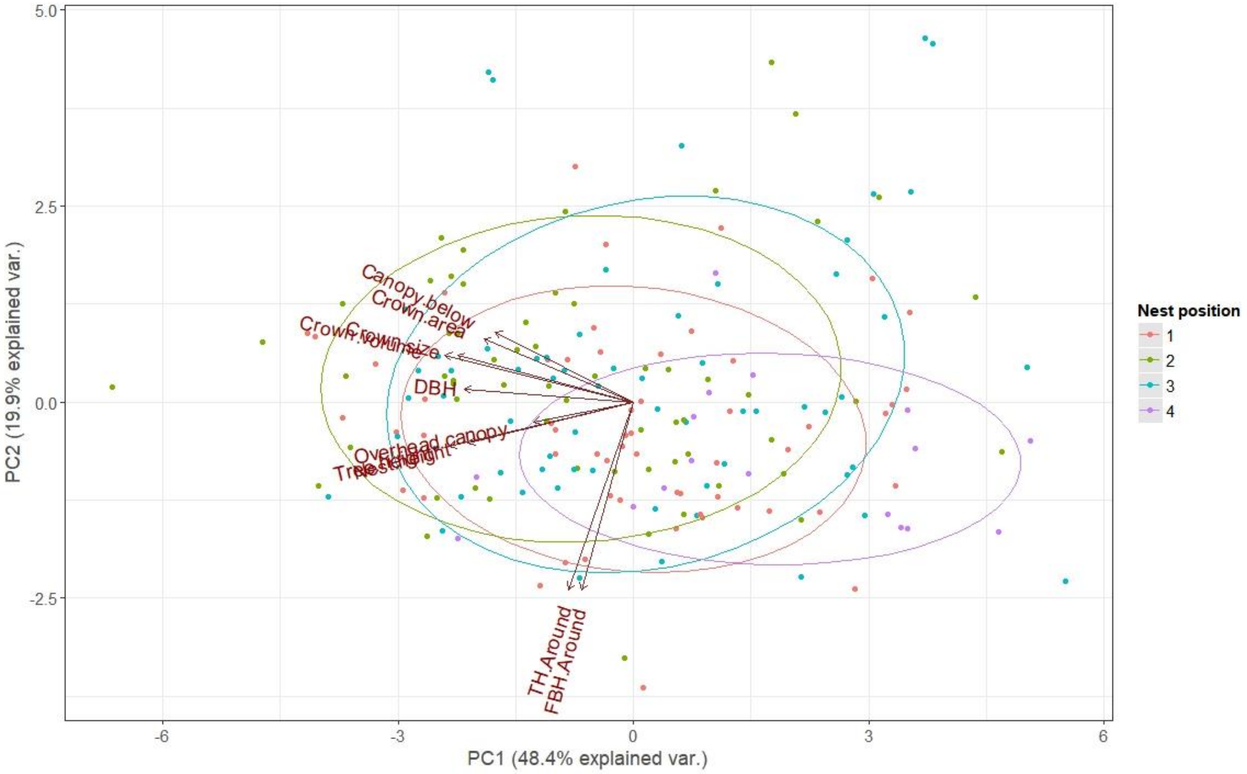

Figure S11 PCA biplot of the interaction of PC1 and PC2 for nest positions. Crown size and crown volume show considerable overlap as do Tree height, Nest height and Overhead canopy suggesting that in the interaction between these principal components they have similar influence.

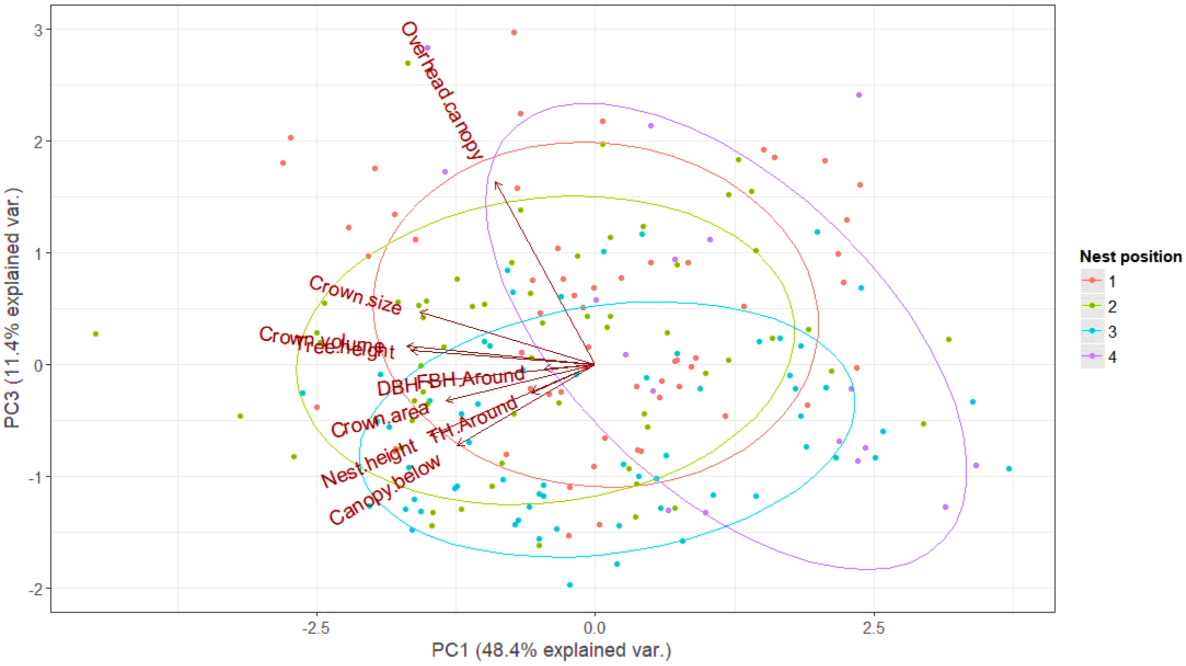

Figure S12 PCA biplot for the interaction of PC1 and PC3 for nest position

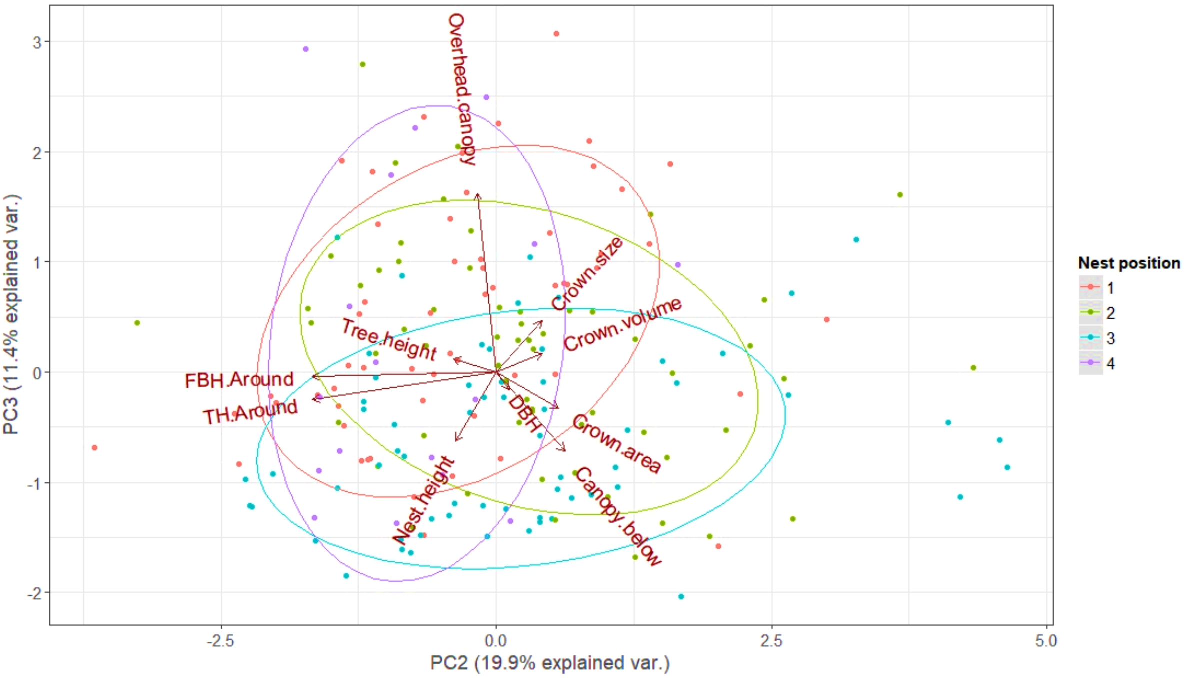

Figure S13 PCA biplot of the interaction of PC2 and PC3 for nest position

Appendix II Supplementary materials for Chapter 4

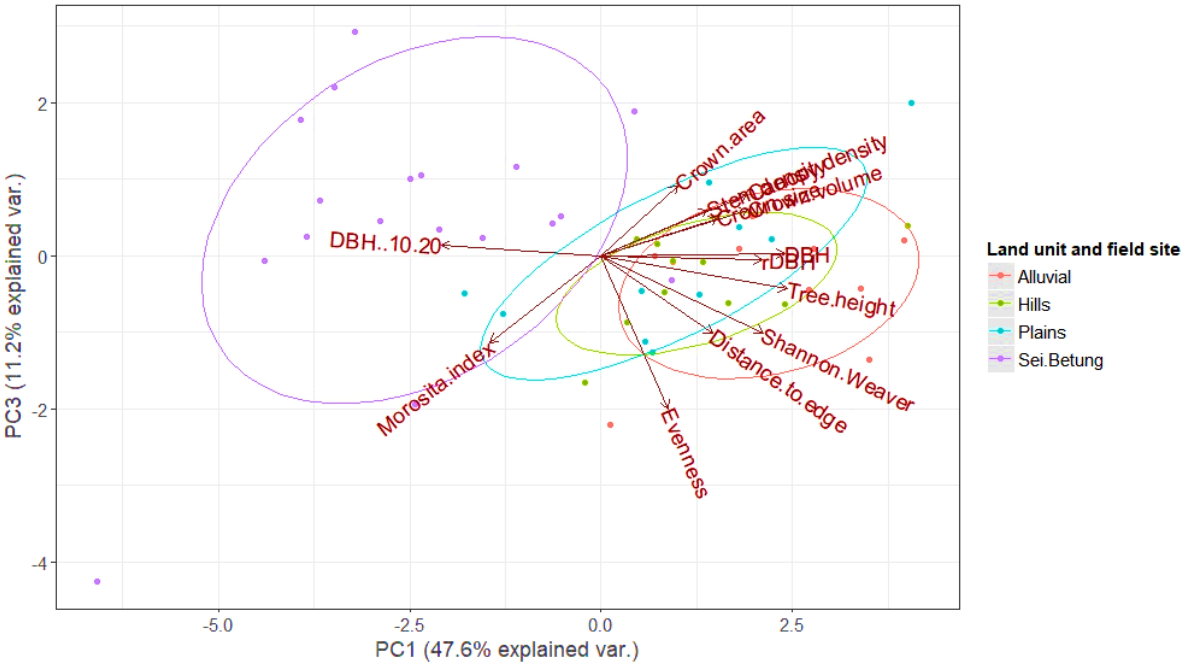

Figure S14 PCA plot of PC1 and PC3 for the differences in landunit and field site influencing nest densities

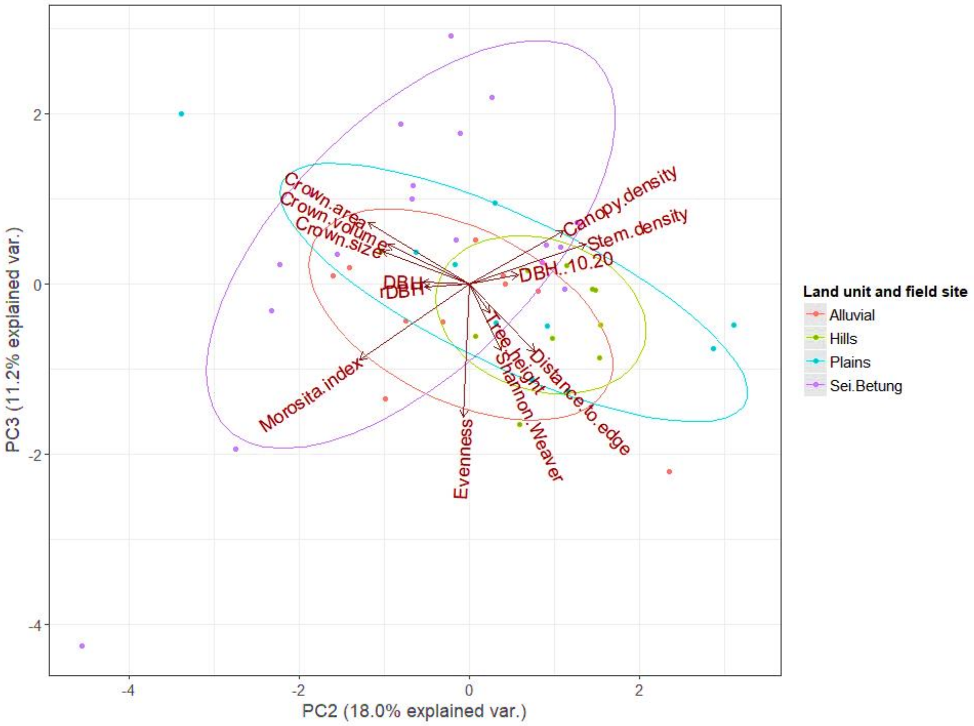

Figure S15PCA plot of PC2 and PC3 for the differences in landunit and field site influencing nest densities

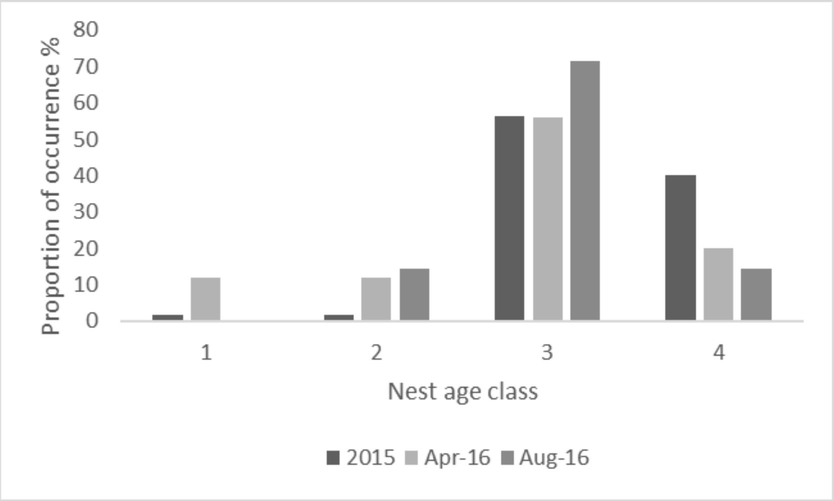

Figure S16 Proportion of occurrence of nest age class distribution in Sikundur across three sampling periods in 2015/2016

Nest age classes: 1- fresh leaves, still green, 2- mix of green and brown leaves, 3- all leaves turned brown, some holes forming, 4- all leaves gone, nest falling apart