Choice of tree species and nesting position in relation to mosquito avoidance in Sumatran orangutans (Pongo abelii)



Master Thesis

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Contents

Abstract4		
1) Introduction	5	
1.1 Nest site selection in primates	6	
1.1.1 Predator avoidance	7	
1.1.2 Thermoregulation	8	
1.1.3 Comfort	9	
1.1.4 Parasite avoidance	9	
1.2 Mosquito life-cycle and host seeking behaviour	11	
1.2.1 Life-cycle	11	
1.2.2 Host seeking behaviour	12	
1.3 Summary of previous studies	15	
1.4 Study objectives and hypotheses	17	
2) Material and Methods	21	
2.1 Study site	21	
2.2 Study species	22	
2.3 Data collection	23	
2.3.1 Weather data	23	
2.3.2 Mosquito data	24	
2.3.3 Nesting data	31	
2.3.4 Phenology data collection	35	
2.3.5 Statistical analyses	35	
3) Results	37	
3.1 Mosquito abundance in relation to water availability	37	
3.1.1 Measurements of rainfall and standing water		
3.1.2 Mosquito catches in relation to rainfall and standing water		
3.1.3 Mosquito high- and low season		
3.2 Mosquito trapping tests	41	
3.2.1 Results of repellency tests	41	
3.2.2 Structural properties of tested tree species	45	
3.2.3 Results of exposure tests		
3.2.4 Results of height tests	56	
3.2.5 Regression model for height tests		
3.3 Nest site selection		
3.3.1 Tree species preferences		
3.3.2 Nestina heiaht	61	
3.3.3 Exposure of nests	62	
3.3.4 Nest type	65	
3.3.5 Regression model for nesting height and for exposure	66	
3.3.6 Presence of pitcher plants	68	
3.3.7 Amount of standing water at the nesting site	70	
3.3.8 Presence of lianas.	71	

3 3	3.3.9 Influence of rainfall 3.3.10 Influence of mosquito high and low season	73 75
4) Dis	scussion	78
4.1	Mosquito trapping tests	
4	1.1.1 Mosquito-repelling properties of tree and liana species	
4	1.1.2 Mosquito abundance and exposure of nests	
4	1.3 Mosquito abundance and height of nests	
4	1.4 Mosquito abundance dependent on rainfall and standing water.	
4.2	Nesting behaviour	91
4	2.1 Relevance of nesting features to mosquito avoidance	
4	2.2 Alternative explanations	
4	2.3 Influence of rainfall and mosquito seasonality	
4.3	Conclusion	
5) Ac	knowledgements	103
6) Re	ferences	105
7) Ap	pendix	110
7.1	Growth of lianas on tree species	
7.2	Height of nest types	111
7.3	Raw data for repellency tests	
7.4	Raw data for the exposure test at J25	114
7.5	Data phenology plot	

Abstract

Recent studies of Bornean orangutans (*Pongo pygmaeus*) at Tuanan, Central Kalimantan, have reported that preferred nesting tree species of this population might have mosquito-repelling properties. The main objective of this study was to examine whether preferred tree species of a population of wild Sumatran orangutans (*Pongo abelii*) at Suaq Balimbing posses anti-mosquito properties as well. The hypothesis under investigation was that tree and liana species used for nesting differ in their ability to repel mosquitoes, based on the secondary compound properties of their leaves and bark.

Results of this study quite clearly show that the selection of certain tree species for nesting is not related to mosquito-repelling properties of preferred tree species. For none of the most popular tree species an indication of mosquito-repelling properties could be found. Instead nesting trees might be selected due to structural advantages. Repellecy tests for liana species in contrast found one liana species (Akar melinjo) to be mosquito-repelling. Further, investigation of nests revealed that orangutans include this liana species mostly during rainy nights, when mosquito density is higher.

Further nesting features like the height of a nest within the tree and exposure of a nest to wind are suggested to be related to avoidance of mosquitoes as well. Tests with mosquito traps yielded significantly fewer mosquitoes at low locations (5m) compared to higher ones (15, 20, 25m). Differences in nesting height of orangutans, however, were best predicted by the sex/age class of the nest builder, which suggest that nesting height is driven by the hierarchical position of individuals within the population. Positions of different exposure did not differ in the amount of mosquitoes present, thus exposure of nest very likely is not related to mosquito avoidance. In contrast, the enlarged area around the nesting site seemed to influence mosquito occurrence. More open areas with a less dense vegetation appeared to be avoided by mosquitoes as they offer less cover and probably are more windy.

The comparison of this study to tests carried out at Tuanan is only to a limited extent useful since test set-ups were fundamentally different. For nesting features, like nesting height or exposure, most differences between sites can probably be ascribed to differences in forest structure.

1) Introduction

Nest building with its basic features is shared by all four species of great apes and thus is believed to be an important step in hominoid evolution (Fruth and Hohmann, 1996). No other species within the order of primates show this behavior except for Prosimians – and they build nests that are used for longer periods of time, e.g. for breeding and keeping their young. In great apes in contrast nests are build anew every day and only used for resting or sleep. Despite a large variety in habitat types and differences in social organisation in the four great apes, nest building appears to be quite uniform among the species. This suggests that nest building behavior is a long standing trait for all the great apes rather than an independent development of each of them (Fruth and Hohmann, 1996). This leads to the question: for which purpose might a common ancestor have evolved this trait?

Some suggest that it is related to body size: since great apes are the largest of all primates, they might not be able to find comfortable locations where they can sleep in the sitting position in which most other primates sleep. They might have developed nest building as a measure to find appropriate and comfortable sites for resting and sleeping at night (Prasetyo et al. 2009). Another hypotheses is that nest building may have evolved as a byproduct of feeding habits (Fruth and Hohmann, 1996). To reach fruits on peripheral branches apes often are observed to bend and break these branches towards their body. Thereby they create a platform of broken branches at more proximate parts of the tree on which they can sit, which leaves their hands free to pick at the fruit. This "feeding nest" allows food consumption in a secure and comfortable place and may have been the prototype of sleeping nests.

Traditionally nest building has been treated separately from tool use. However, recent studies have demonstrated that nest building techniques vary within and between populations (van Schaik et al., 2003) which suggests that the trait varies culturally and therefore qualifies as a tool use. Certainly building a nest implies a modification of environment and thus illustrates the appearance and phylogenetic development of "constructivity" (Yerks and Yerks, 1929). For this reason, amongst others, Fruth and Hohmann (1996) value nest building as one of the crucial steps in hominin evolution. They further suggest that the ability of nest building facilitated the evolution of cognitive abilities within hominoids: because nests improve sleep by providing the potential for a more relaxed and comfortable sleeping

posture, great apes spend more time in REM sleep. This, in their opinion, accounted for an increase in learning abilities that evolved in apes compared to monkeys.

In summary it can be said, therefore, that nest building from a comparative point of view offers a great opportunity for gaining insights into the evolution of our hominin ancestors, because it is a shared, derived feature of all great apes.

1.1 Nest site selection in primates

Most primates spend about half of their lives at sleeping sites making this "inactive" half of primate life an important part of primate nature (Anderson, 1998). Assuming a life-span of 35 years and the construction of 1.5 nests per day, including day nests, a bonobo probably builds about 19.000 nests during its lifetime (Fruth and Hohmann, 1994). Yet nest building behavior has only recently been studied in more detail – mainly due to the fact that observations of primate behavior usually are focused on the times of the subjects' activity (Fruth and McGrew, 1998). Studies conducted so far reveal that many primate species are highly selective towards specific resting or sleeping sites (e.g. Fruth and Hohmann, 1994 ;Gibson 2005), especially chimpanzees, bonobos and orangutans which nearly exclusively nest arboreal.

Bonobos at a study site at Lomako in Zaire, for example, only use a small subset of available tree species for nest construction: 61% of the nests were build in five tree species (Fruth and Hohmann, 1994). Important for tree choice in this population were leaf size and flexibility and strength of the wood. Ancrenaz et al. (2003) reported that in an orangutan population in a disturbed forest in Sabah, Malaysia, only six tree genera accounted for 37% of all nesting sites – even though in total 89 different genera were used (of approximately 139 different tree genera available in this study area). Another study on Bornean orangutans revealed that animals of the respective population used one tree species (*Campnosperma coriaceum*) for 25% of all nest constructions (Gibson, 2005).

This selectivity for nest sites seems appropriate since at the sleeping site animals are in a state of decreased awareness over a long period of time which makes them more vulnerable to threats like predators and parasites. A well constructed nest in the correct position may minimize the risk of being detected by predators or being affected by parasites. Furthermore it can be advantageous in the context of thermoregulation and promote enhanced sleeping comfort. Identifying factors which influence nest site selection is a promising approach towards a better understanding of the functions of nests. This study focuses on the factor of parasite avoidance, particularly mosquitoes, by means of choosing certain tree species and nesting positions for the construction of a nest. There are, however, many factors which are thought to influence nest site selection, therefore the most important ones are presented below.

1.1.1 Predator avoidance

The most obvious factor determining nest site selection is the degree of safety a certain location provides, e.g. by reducing detectability to predators, enhancing the detection of an approaching predator and also by reducing accessibility for a predator. Guinea baboons (Papio papio) show a preference for tall, emergent trees as sleeping sites and often build their nests at some distance from the trunk (Bert et al., 1967). Fruth and Hohmann (1993) also explained the building of nests by baboons high in the canopy as an anti-predator measure. A study by Ancrenaz et al. (2003) revealed that orangutans in a disturbed forest choose the largest and tallest trees for night nests. In a study conducted on Sumatran orangutans, Sugardjito (1983) noticed that adolescent animals and females with infants select nests sites further away from fruiting trees and also higher in the canopy. He ascribed this to a greater vulnerability to predators as fruiting trees often attract predators. And another recent study by Rayadin et al. (2009) found that immature orangutans tend to make nests at higher sites than adults and in locations which are less easily accessible, like at the end of branches. Hamilton (1982) surveyed the literature on the use of different sleeping sites by free-ranging baboons (Papio sp.) and concluded that protection against predators was the major determining factor in site selection.

Orangutans, however, face a relatively low predation pressure: the only documented attacks occurred by pythons (*Python reticulates*) and the clouded leopard (*Neofelis nebulosa*) and were only directed at immature individuals (Rijksen, 1978). Those two predators are able to climb all trees, therefore a selection for high and large trees cannot be explained by predator avoidance. Also orangutans do not benefit from a better view to enhance detection of an approaching predator, because orangutans rather rely on camouflage and concealment for protection and are not alert on their nest at night. Therefore a high nest or a tall tree is not necessarily an advantage (Gibson, 2005). On Sumatra in some areas still Sumatran Tigers (*Panthera tigris sumatrae*) can be found, which is why Sumatran orangutans are believed to hardly ever travel and nest on the ground. This can, however, not explain the preference of certain tree species or differences in nesting positions between sex/age classes. In conclusion it is more likely that other factors determine the process of nest site selection in orangutans.

1.1.2 Thermoregulation

Exposure to wind and rain at night, especially during the inactive phase of sleep, may have crucial consequences for an animal. All animals exchange heat with their environment through radiation, convection and evaporation (Gates, 1980). Net rates of heat exchange depend on thermal characteristics of the environment, such as air temperature and wind velocity, as well as on thermal properties of the animal, like metabolic heat production, body mass and body shape (Patterson, 1986). Particularly small primates with a large surface to volume ratio suffer high energy loss from low temperature and wind currents. Therefore many small monkeys sleep in tree holes or tangled vegetation (Anderson, 2000). Yet, also larger primates adapt their sleeping and nesting behavior to environmental factors: A study on Guinea baboons (Papio papio) (Bert et al., 1975) showed that wind currents can influence sleeping patterns – animals of this population responded stronger to wind currents above a critical level (3 miles/h) than to low temperatures. Another study on baboons (Papio cynocephalus), which focused on the early morning hours when animals experienced changing thermal conditions in their sleeping trees, revealed that baboons respond to temperature, solar radiation and wind velocity (Stelzner and Hausfater, 1986). They changed body orientation in a way to reduce exposure to cold wind currents and to maximize solar radiation. Gorillas also alter their nesting behavior: if temperatures are higher they tend to sleep on bare ground but during times of more rainfall they build arboreal nests more often to stay dry and warm (Mehlman and Doran, 2002). Orangutans often respond to rainfall in the evening by building a roof above their nest and use blankets to protect themselves from wind (Berlowitz, 2008).

However, orangutans posses a rather thick and long pelage which reduces wind penetration and convective heat loss (Treager, 1965). Furthermore temperature in their tropical habitat hardly ever drops below 20°C. Thus nest site selection and nesting behavior should not be affected that severely by thermoregulatory needs. On the other hand mothers with small infants tend to sleep in more closed locations than flanges males which might protect them against wind and rain (Rayadin et al., 2009). This indicates that in orangutans some sex/age classes are possibly more vulnerable to heat loss and therefore could show a corresponding selection of microenvironments for nesting.

1.1.3 Comfort

Comfort is related to thermoregulation to some degree as it also includes protection from unpleasant weather influences. Yet, comfort also involves the selection of certain tree species as some might provide more comfortable nesting material or enable an easier nest construction. Bonobos choose trees for night nests depending on the quality of the wood such as its flexibility and strength (Fruth and Hohmann, 1994). Branches need to be flex-ible enough to be bent but rigid enough to be only partly broken and still support the weight of the animal. Disturbing insects, like ants, seem to play a role in nest site selection as well. Kloss gibbons (*Hylobates klossii*) avoid trees with certain epiphytes (*Myrmecodia tuberosa*) as they are often inhabited by ants. Generally root systems of epiphytes are frequently used by insects and therefore trees with such plants tend to be avoided (Anderson 2000). Other mammals may also be sources of disturbance at night and thereby affect nesting behavior: Gorillas, where they live sympatric with forest elephants, choose sleeping places which are less likely to be visited by the elephants (Tutin et al., 1995).

In orangutans Florez (2007) investigated whether some structural features of trees can account for the preference of some tree species and avoidance of others. It seems reasonable that orangutans choose certain tree species with big, soft leaves or architectural advantages like horizontal side branches over others without such characteristics. Therefore a careful comparison of leave texture and length, and the branching angle of the most used and avoided trees was carried out. However, neither a structural parameter nor a combination of them could explain the preference of some tree species. Thus, Florez (2007) concluded that, at least for this population at Tuanan, the architecture of a tree has only a modest influence on nest site selection and that other factors are probably more important.

1.1.4 Parasite avoidance

Parasites belong to the group of pathogens and include helminths, several protozoa, bacteria, fungi and viruses (Foitova et al., 2009) and are defined as organisms which depend on a host. All animals are affected by parasites (Nunn and Heymann, 2005) which exert a great selective pressure by either threatening an individual's life directly or by restricting its reproductive success/fitness (Hart, 1990). Thus diseases are an important ecological factor and play a crucial role in the evolution of primate behavior (Freeland, 1976). It can be assumed that animals adjust their behavior in a way to minimize the probability of acquiring new pathogens. Yet, reports of behavioral patterns leading to a decrease in parasitic infection are rare, probably because it is often difficult to relate a specific behavior to parasite avoidance (Foitova et al., 2009).

Night nests are places where primates are very likely to come into contact with parasites as the resting animals are immobile and in a state of decreased awareness (Freeland, 1976). This might be one reason why great apes construct a fresh nest every night (McKinnon, 1974). Selection of an appropriate nest site might also reduce exposure to parasites: *Callitrichidea* sleeping in tree holes attract less mosquitoes and thereby minimize the risk of malaria infection (Nunn and Heymann, 2004).

Mobile vectors like mosquitoes are of great importance for the transmission of diseases. Bornean orangutans for example have been tested positive for a lot of mosquito-borne diseases like malaria (Wolfe et al., 2002), dengue fever, Japanese encephalitis and Zika (Wolfe et al., 2001). The study of Wolfe et al. (2002) showed that 11% of a sample of wild orangutans were infected with a protist causing malaria (*Plasmodium pitheci*) and in captive/semicaptive animals the prevalence even reached a percentage of 93,5. Lethal cases due to malaria in juvenile orangutans were diagnosed at the Sepilok Orangutan Rehabilitation Center in Sabah, Malaysia (Kuze et al., 2008). Several possible vector species are very abundant within the study area of Suaq as large parts of the forest are flooded most of the time, which provides an optimal breeding place for mosquitoes.

To summarize it can be stated that parasite avoidance, especially reduction of mosquito bites, may be of great importance for the fitness of orangutans, thus also during the selection of a nest site.

For this reason this study aims to investigate whether nest site selection is influenced by mosquito occurrence and whether animals show behaviours which might reduce mosquito exposure. For this purpose it is useful to have an understanding of reasons for fluctuations in mosquito densities and consider ways of protection against mosquitoes. Thus I will shortly outline some important facts about the mosquito life-cycle and host finding behaviour.

1.2 Mosquito life-cycle and host seeking behaviour

Mosquitoes belong to the family of Culicidae within the order of Diptera, the two-winged flies (Table 1). The family of Culicidae is divided into two subfamilies: Anophelinae and Culicinae. Nearly all species functioning as vectors belong to the subfamily of Culicinae and only few pathogens are transmitted by Anophelinae.

Table 1: The family of Culicidae and the most important diseases transmitted by each subfamily

Subfamily	Anophelinae	Culicinae	
Genus	3 genera (Anopheles, Bironella, Chagasia)	38 genera (Aedes, Culex, Mansonia, Coquillettidia,)	
Diseases	Malaria (Anopheles)	Yellow fever (Aedes) Dengue fever (Aedes) Japanese encephalitis (Culex)	

1.2.1 Life-cycle

Only female mosquitoes feed on blood as this provides them with the nutrients necessary for egg development. For the production of eggs they need a blood meal every second to fourth day. The eggs are laid either singly (*Aedes, Anopheles*) or in batches of several hundred, forming rafts (*Culex*). Depending on the species, 30-350 eggs are laid in each ovipositioning, normally on the surface of still or slow moving water. All *Anopheles*, most *Culex* and some *Mansonia* species place the eggs directly on the water surface while other *Mansonia* species place them under the surface of the leaves of aquatic plants. Particularly *Culicines* make use of natural container habitats such as tree holes, leaf axils and pitcher plants (Lehane, 1991).

In the tropics eggs hatch within three days. The following four larval stages can be completed within seven to ten days (Fig 1-1). After that there is a short pupal stage of two to three days which is attached to the water surface film or to aquatic vegetation (*Mansonia*, *Coquillettidia*) finally leading to the adult individual. Thus the development from egg to adult can be completed within twelve to sixteen days with three of the four life stages being aquatic. Under tropical field conditions male mosquitoes live for about seven to ten days while females survive notably longer, living up to a month. Mosquitoes may survive the dry season in tropical areas as eggs or aestivating adults but in most other areas they breed continuously throughout the dry season, albeit at greatly reduced rate (Lehane, 1991; Snow, 1990).



Fig. 1-1: Generalized mosquito life cycle (source: Purdue Entomology, Catherine A. Hill and John F. Mac-Donald, site authors; and S. Charlesworth, artist)

1.2.2 Host seeking behaviour

Female mosquitoes feed on a range of vertebrates from birds to mammals but each species typically has a narrow range of preferred hosts. Many mosquitoes feed in a particular place (e.g. canopy, forest floor) and each species usually has a characteristic peak biting time. Thus diurnal, nocturnal and crepuscular species can be differentiated.

Odour and visual cues are the most important factors involved in the orientation of mosquitoes to the host. Commonly mosquitoes are initially activated by host odour and then use odour plumes to track down the host from a distance. As they close on the host, visual information is used in the final stages of orientation (e.g. shape, movement, contrast and colour). Visual cues like colour information are widely used by diurnal species while mosquitoes active at night are particularly sensitive to intensity contrast, therefore the contrast between a target and the background.

Olfactory stimuli implicated in host location include carbon dioxide, lactic acid and acetone. Such cues may be more important for night-feeding species and also for the ones living in open habitats, since there the odour plume is likely to be much more continuous, thereby providing a relatively linear guide. Each mosquito species responds differently to such olfactory host stimuli, especially to combinations of odours; probably because a particular combination of host signals is a far better guide to the presence of a host than one stimulus alone (Lehane, 1991).

Male mosquitoes generally do not travel more than about 100m from the larval site. Females in contrast travel further to find blood meals and new larval sites to colonize. However, few actually fly more than one or two kilometres. A study about three *Mansonia* species by Grass et al. (1983) for example demonstrated a mean dispersal radius of 150-700m with maximum flight ranges between 1000 and 1700m. Dispersal was more pronounced in the forest than in open habitat which seemed to act as a barrier, suggesting that mosquitoes prefer to stay within or near the forest. This can be explained by the rather poor flying skills that are generally ascribed to most mosquito species (Bidlingmayer, 1967). Tall vegetation interferes with air movement so that the air within a forest is relatively still. This permits directed flight for delicate insects like mosquitoes which would be unable to perform these activities outside a shelter (Unwin and Corbet, 1991).

Wind currents further play a crucial role during host location as many mosquito species rely heavily on wind-generated host-odour plumes. They can influence mosquito foraging success in two ways: firstly, increased wind velocity leads to an enhanced dilution of host odours, thereby making it more difficult for mosquitoes to find the emitting source (Stimulus dilution model: Hoffmann and Miller, 2003). Secondly, already weak wind velocities (0,3 - 1,0m/s) are thought to reduce successful orientation because of weak flying capabilities of mosquitoes (Flight-limitation model: Grimstad and De Foliart, 1975). Thus wind currents offer a possible measure of protection against mosquitoes.

A much more direct approach of protection, which is often adopted by humans, is of course the application of mosquito-repelling substances, either synthetic ones like DEET (N,N-Diethyl-*meta*-toluamide) or by traditional usage like burning of plants (Palsson and Jaenson, 1999) or application of plant oils (Yarnell and Abascal, 2004). Studies on the efficiency of such substances as protection against mosquitoes are numerous and also in-

clude tests with live intact plants (Seyoum et al. 2002). This is especially important for the study of nesting preferences in orangutans as it offers an opportunity for how orangutans might be able to protect themselves from mosquitoes in their nests. Semi-field test in western Kenya with *Anopheles gambiae* for example revealed that live intact plants are actually able to repel mosquitoes: plants of the family of *Verbenaceae* and *Lamiaceae*, placed inside experimental huts, showed a significant repelling effect, reducing exposure to mosquitoes by 30-40% (Seyoum et al. 2002).

In nesting context the use of plants as a protection against ectoparasites like mosquitoes has so far only been investigated in birds. The European starling (*Sturnus vulgaris*), for example, selects certain plant species as nest material which contain high concentration of mono- and sesquiterpenes (Clark and Manson, 1988) and act as repellents against parasites and pathogenes (Gershenzon and Dudareva, 2007). Likewise, Corsican blue tits incorporate plant materials into nests containing aromatic secondary compounds that may repel parasites or mask chemical cues which ectoparasites use to find hosts (Lambrechts and Dos Santos, 2000). Similar mechanisms might be involved in orangutan nest building.

From this knowledge of mosquito host-seeking behaviour two possible mechanisms of protection viable for orangutan nest building can be derived:

- 1.) Orangutans can use tree species or genera for nesting which are unattractive for mosquitoes or mask their odour.
- 2.) Orangutans can choose nest sites which are exposed to a certain amount of wind currents these in turn might distract foraging mosquitoes.

1.3 Summary of previous studies

First experiments applying this framework were carried out by Florez (2007) on Borneo in Central Kalimantan (Tuanan). He identified several tree species which are selected more often for nest building than expected based on their frequency in the forest and placed mosquito traps in those tree species to investigate their repelling potential against mosquitoes. As a result he found that the traps put in one of the preferred nesting tree species (*Elaeocampus masterii*) contained significantly less mosquitoes than control traps. The genus *Elaeocampus* is includes some species with antiplasmodial activity, e.g. *E. kontumensis* (Nguyen-Pouplin et al. 2007) or *E. parvifolius*, which is used in Indonesia for the treatment of malaria infections. Thus, a preference for building nests in trees of this genus could indeed provide protection against mosquitoes and malaria infections.

Those experiments were repeated by Largo (2009) in the same study area, placing mosquito traps on wooden platforms of 2m height to test tree species in a more direct way. The most favoured tree for nesting during her study was *Campnosperma coriaceum* which also showed a significant effect in repelling mosquitoes. This species belongs to the family of *Anacardiaceae*, of which several species are known to have antimalarial (Asase et al., 2005) and anti-microbial features as well (Kozubek & Tyman, 1999).

Finally, Hermann (2010) tested several other tree species with platforms of a more relevant height (6m) and identified a third possibly repelling species (*Nephelium mangayi*). She furthermore could show that mosquito densities increase at higher places (10m). This is the height where orangutans normally build their nests, therefore she concluded that measurements of repellency should best be performed at this relevant heights.

A possible protection against mosquitoes by means of wind currents was first investigated by the study of Largo (2009) and later by Hermann (2010) as well. They did so by differentiating between two different nesting positions, exposed and unexposed. Orangutans can either nest in a more concealed location, e.g. near the main stem of a tree or at a position where nests are covered by overhanging branches (non-exposed) – or they can construct their nest in a more open position, e.g near the canopy where tree branches are smaller and cover by branches of neighbouring trees is sparse (exposed). In an exposed location the animal is likely to be stronger affected by wind currents. On the one hand this leads to a loss of body heat but on the other hand such currents might also reduce mosquito for-aging through the two mechanisms presented above: firstly, by diluting odour, making it

harder for mosquitoes to locate a host (Hoffmann and Miller, 2003) and secondly, by simply blowing mosquitoes away. In contrast, in a non-exposed nest the animal can restrict energy-loss by wind but on the other hand may suffer from more mosquito bites.

In those two studies (Largo, 2009, Hermann, 2010) wind speed and temperature in the two different nesting positions were not measured effectively. Nevertheless some interesting preliminary results were reported: Largo (2009) found distinct differences between sex/age classes in building a nest exposed or unexposed. Flanged males preferred to build exposed nests above the canopy where wind currents probably are stronger, whereas unflanged males and mother-infant pairs tended to sleep in unexposed nests below the canopy. This suggests that bigger flanges males are less vulnerable to heat loss through wind and therefore can afford to sleep in an open position with less mosquitoes around. However the sample size of thus study was only very moderate. Thus Hermann (2010) repeated the experiment, yielding similar results with a larger data set: flanged males built exposed nests more often than the other three sex/age classes (unflanged, mother-infant, female). Another recent study (Rayadin and Saitoh, 2009) has reported a similar finding with flanged males building significantly more nests in open locations compared to females with infants which prefer closed locations.

1.4 Study objectives and hypotheses

Based on those results of previous studies carried out at Tuanan in Central Kalimantan, the present study investigates the influence of mosquitoes on nest building in a population of wild orangutans at Suaq Balimbing in Sumatra. Since this is the first study about nesting behaviour at Suaq Balimbing and results from Tuanan provide several starting points, the objectives and hypotheses of the present study are manifold:

Primarily, the hypothesis about mosquito-repelling tree species is tested. To determine whether orangutans of this population prefer tree species with mosquito-repelling properties as well, tree species which are favoured for nesting were identified. These tree species then were examined for possible mosquito-repelling properties using a similar test setup as at Tuanan. Some changes, however, were made to better simulate the conditions of an orangutan in an actual nest. In contrast to studies at Tuanan mosquito traps were not placed on wooden platforms but actual orangutan nesting heights were used. Nesting heights at this site range between 5 to more than 25 meters (unpublished data), thus it was not possible to build platforms of that height. Instead the traps were put into the trees by placing them into wooden baskets which were attached to a nylon rope (see Fig.2-4). Furthermore, all tests using mosquito traps were run in the forest, not at the edge as at Tuanan (Largo 2009, Hermann 2010) to assure that mosquito density was comparable to locations of night nests of orangutans. At Suaq, so far it cannot be excluded that nesting preferences are related to structural properties of tree species. Therefore physical properties of several tree species at Suag were investigated and compared as well. Taken together, these considerations lead to hypothesis 1:

1.) Orangutans at Suaq prefer certain tree species for nesting over others.

- a) Orangutans prefer these tree species due to mosquito-repelling properties which are based on the secondary compound properties of leaves and/or bark of the trees.
- → The tree species mostly used and avoided should show differences in their ability to repel mosquitoes or to attract them. It should be possible to provide experimental evidence for this by catching significantly less mosquitoes in traps covered with branches and leaves of those trees orangutans prefer for nest building (compared to traps covered with branches and leaves of a control species).

- b) Orangutans prefer some tree species over others due to structural parameters.
- → Tree species which are chosen most for nesting should provide advantageous structural features, like wide branching angles or a large amount of foliage, compared to tree species which are used less.

Secondly, differences in nesting behaviour between sex/age classes and a possible connection to mosquito avoidance was investigated. To test the hypothesis about a trade-off between heat loss and exposure to mosquitoes (Hermann, 2010) a specific test set-up was developed. This way it was assessed whether wind speed and temperature at the nest are actually different for distinct locations of a nest, and if this affects mosquito occurrence (see exposure tests, page 28-29). Accordingly, hypothesis 2 is formulated:

- 2.) Nests in different positions (exposed vs. non-exposed) differ in mosquito numbers nearby the nest, based on the influence of wind gusts.
- → The two distinguished nesting positions should differ in the amount of mosquitoes that can be caught with traps in each position. If they differ significantly in their ability to provide protection against mosquitoes, then certain nesting positions can be considered as a measure of mosquito avoidance as well.

According to data from Tuanan sex/age classes which are more vulnerable to threats associated with mosquitoes show a more pronounced avoidance behaviour which is reflected by differences in nesting parameters (Hermann, 2010). For the investigation of nesting features of different sex/age classes at Suaq data on specific mosquito-related aspects of the nest were collected. Such mosquito-related aspects of the nest are:

a) Exposure of the nest

To gain further insights into exposure preferences of different sex/age classes, an exposure-index was developed, which considers cover of branches and leaves around the nest.

b) Presence of lianas

The presence and amount of lianas at the nest was examined, since Gibson (unpublished data) reported that orangutans of this population occasionally include lianas into their nests. On the one hand certain liana species can be beneficial for nesting because they

might increase stability of the nest or might be able to repel mosquitoes (see repellency tests, page 25-27). On the other hand liana species growing densely on the main stem of trees are often inhabited by a lot of insects, which can disturb the orangutan's sleep.

c) Standing water at the nest site

As already suggested by Florez (2007) the amount of water at the nest site might be an important factor influencing mosquito density at the nest. The water within the peat-swamp forest most likely provides the breeding places for nearly all mosquito species. Yet, as the number of water pools and amount of standing water differs within the research area, some locations offer better breeding places than others. And as mosquitoes generally do not travel very far from larval sites (Grass et al. ,1983), the amount of standing water within a certain area might correlate with mosquito numbers within the respective area. Therefore it was investigated whether orangutans prefer to nest in drier areas of the forest.

d) Amount of rainfall

Rainfall enhances mosquito flight activity and host seeking behaviour (Shaman et al., 2007). Therefore the amount of rainfall during the night of each respective nesting event was noted down as well to investigate whether orangutans change their nesting behaviour in case of rain, respectively adapt it to such conditions.

e) Presence of pitcher plants

The surrounding of each nest site was inspected for pitcher plants after initial surveys showed that some mosquito species use these plants for ovipositioning. Areas with a high density of these plants might thus be inhabited by more mosquitoes.

Hypothesis 3 accordingly is as follows:

3.) Nesting preferences of sex/age classes differ in terms of the properties listed above.

These differences reflect the vulnerability to mosquitoes of each respective sex/age class.

→ Some sex/age classes show stronger avoidance of mosquitoes than others, which is reflected by the position within the tree and location within the forest of the nest.
Adolescents and mothers with small infants might be more vulnerable to mosquitoes and therefore more often adopt mosquito avoidance strategies. Nests of these sex/age

classes consequently should be more exposed, have less water pools on the ground and be constructed more often using mosquito-repelling tree species.

Finally the amount of standing water within the forest and precipitation were recorded regularly during the entire study period. The development of mosquitoes is strongly bound to availability of water and mosquito foraging often correlates with rainfall: Rainfall a) increases near-surface humidity, thereby enhancing mosquito flight activity and host-seeking behaviour and b) can alter the abundance and type of aquatic habitats available to mosquitoes for the deposition of eggs (oviposition) and the subsequent development of the immature stages (Shaman et al., 2007). Within the peat swamp forest at Suaq large areas are constantly covered with water, especially within the floodplain of Lembang river. Thus, the research area is an ideal habitat for the development of mosquito larva. By analysing factors which influence mosquito occurrence, possible mosquito avoidance strategies can be derived.

The fourth hypotheses thus reads as follows:

- 4.) Mosquito density within the forest is determined by the amount of water pools available for oviposition.
- → Dependent on the developmental rate of mosquitoes, the amount of water pools within the forest influences mosquito occurrence of the following weeks: if more breeding places are available, mosquito numbers should increase after a certain time span.
- → Rainfall enhances mosquito flight activity, thus leads to higher mosquito densities during rainy nights.

2) Material and Methods

2.1 Study site

The field study was conducted at the Suaq Balimbing research station (N 03° 02' 87"; E 97° 25'01") in the Gunung Leuser National Park, Aceh Selatan, Indonesia. The study site is located at the Lembang river in the local district of Tapak Tuan (Fig. 2-1). The forest of the research area is classified as a peat swamp forest (van Schaik, 2004) and consists of a swamp area close to the river and a drier, slightly higher forest area closer to the hillside. The floodplain of the Lembang river is regularly flooded during the rain season which provides fresh nutrients for this area and results in a highly productive forest. This flooding and the absence of a distinct seasonality in fruit abundance make it an ideal orangutan habitat.



Fig 2-1: Location of the research area The camp is located within the province of Aceh (picture: courtesy of UNESCO office, Jakarta) **Inset:** Location map of the Gunung Leuser National Park in North Sumatra

The study area has a north-south and east-west trail system, which are small paths within the forest to facilitate access to the forest and orientation during follows (Fig. 2-2). At 50m intervals the paths are marked with coloured flags.



Fig. 2-2: The grid system of the study area The camp (red) is located at the south-western tip of the study area, at the Lembang river. The main path to enter the forest is trail U, which marks the very south of the study area.

2.2 Study species

Orangutans belong to the taxonomic family Pongidae, which is subdivided into two distinct species: *Pongo pygmaeus*, which is found in Borneo and *Pongo abelii* in Sumatra (Goossens et al. 2009). Orangutans are distinctive among great apes as they are highly sexually dimorphic and truly arboreal.

This study focuses on the nesting behaviour of the Sumatran orangutan *Pongo abelii*, which today is only found in a small number of dry lowland and hill forests, and peatswamp and freshwater forests. In Sumatra only six of these forest patches support at least 250 individuals, which is the proposed minimal viable population size (Husson et al., 2009).

Animals recognized during the study were divided into four sex/age classes: adolescent, mother/infant pair (adult female with infant), unflanged (sub-adult) and flanged (adult) male. All four adolescents encountered were females, between nine and fifteen years old. Five mother/infant pairs were observed during the study and several unflanged males, who often could not be further identified. The dominant flanged male within the research area during the study time (Eddy) was encountered quite frequently; other flanged males were hardly observed.

2.3 Data collection

During the study three different sets of data were collected:

- a) Mosquito data
- b) Nesting data
- c) Weather data

To investigate hypotheses 1 and 2 mosquitoes were actively caught using mosquito traps (BG-Sentinel Trap®). A specified set of nesting data was collected for 84 night nests to explore hypothesis 3 and weather data was used to check hypothesis 4.

2.3.1 Weather data

The amount of precipitation and standing water within the forest were recorded regularly during the entire study period.

1.) Rainfall

The amount of rainfall was recorded at the camp using a pluviometer. The pluviometer was emptied each morning and evening so that rainfall at night and during the day could be differentiated. It rained mostly at night, only during periods of strong rainfall, rain also occurred during the day.

2.) Standing water

The amount of standing water was measured at five locations along tail U, where most mosquito experiments were run (see Fig. 2-8). The water level was recorded in centimetres with the aid of wooden stakes which were knocked into the ground (see Fig. 2-3, right). Measurements were taken daily, in the morning and in the evening. Data collection at all five locations started in September 2010.



Fig. 2-3: Measurement of standing water Wooden stake used for measurement at U 630 (left) Floodplain of Lembang river – most of the area is constantly flooded (right).

2.3.2 Mosquito data

All mosquito sampling was done using mosquito traps (BG-Sentinel Trap®). These traps consist of a cylindric plastic body which contains an electrical fan, a catching bag and a lure (Fig.2-4).



Fig. 2-4: The BG-Sentinel Trap® (www.bg-sentinel.com)

The top is covered with a white gauze which possesses a round vent in the middle. The fan inside the trap creates an air-circulation: by sucking in air through the vent in the middle (yellow arrows) which then exits the trap through the outer gaze (red arrows). The ascending currents of the trap are similar to convection currents produced by a human host. Due to the lure the currents also releases a combination of non-toxic substances that are found on human skin: ammonia, lactic acid, and fatty acids. This way the trap attracts mosquitoes and draws approaching mosquitoes into the catch bag inside. Besides these

olfactory and thermal cues the trap also works with visible cues for mosquitoes such as the black/white contrast.

To keep the fan running, each trap needs a power source of a 12V motorcycle battery, otherwise mosquitoes are able to escape out of the catching bag. The traps were ran overnight, from 6 p.m. to 6 a.m. to collect mosquitoes during the usual resting time of orangutans in their nests. Each morning the mosquitoes of all traps were collected and killed by hanging the catching bags for ten minutes into a closed plastic bag with chloroform at its bottom. After that the mosquitoes were dried, counted and presorted for later identification at Fakultas Matematika dan Ilmu Pengetahuan Alam at Universitas Syiah Kuala, Banda Aceh. The identification, however, was not successful and therefore no results about mosquito species within the research area could be obtained.

Altogether eight mosquito traps were located at different locations in the forest (see Fig. 2-8) for three test set-ups, which were:

1.) Repellency Tests:

Testing tree and liana species for possible mosquito repelling effects.

2.) Exposure Tests:

Comparing mosquito densities in open and closed positions/locations.

3.) Height Tests:

Measuring mosquito densities at different heights within the forest.

Test set-up 1: Repellency tests

For this tests two mosquito traps were raised to a height of about 15m, which is the mean nesting height of orangutans at this site (based on the data from 2007-2009 by Andrea Permana).

The design of this test was as follows: One trap always served as a control and was covered with plastic leaves (Fig. 2-5, top). The plastic leaves should rule out that mosquitoes, which are able perceive information about form and contrasts, choose a trap due to shape differences. The other trap was covered each night with a defined amount of fresh branches and leaves of a tree or liana species. Both traps were placed in the same

tree, at the same height with at least five meters distance between one another (Fig. 2-5, bottom). Furthermore the exposure of both traps was as similar as possible to ensure that only the applied branches and leaves on top of the traps account for differences in mosquito catches between the traps.



Fig. 2-5: Test set-up of repellency tests Control trap (top, left) covered with plastic leaves and an example of a test trap (top, right) for the tree species Ubar. Bottom: Position of the traps within the tree – both traps are situated at the same height and in a similar microclimatic environment (exposure to wind and rain etc.)

After the traps were installed in the trees, they were first tested for several nights without any leaves or branches. Mosquito catches showed that the traps worked equally well, yet the positions (left or right of the trunk) differed significantly in the amount of mosquitoes caught (Wilcoxon-Test: Z= -2,137, df= 11, p< 0,033). Therefore the position of test and control trap was changed every night, to rule out that any positional factors might account for differences between the traps. During those nights without any leaves or branches the two positions of the traps were also compared in terms of wind gusts, temperature and humidity using two devices of the SKYWATCH (**R**) GEOS N°11. For these parameters no considerable differences could be detected.

After those preliminary tests tree or liana species were applied on the test trap. Due to some technical difficulties (failure of battery chargers and fans) eventually only four tree species and two liana species were tested, to ensure a sufficient amount of data for statistical analysis. The species were selected based on nesting data from a PhD project conducted at Suaq Balimbing between 2007 and 2009. Comparing the choice of tree species for night nests with the actual availability of these tree species within the forest (based on a phenology plot) provides a preference-index for nesting trees. Two highly preferred nesting trees (Ubar, Puin), one neutral tree species (Meranti batu) and one avoided species (Rengas) were chosen for this study (Table 2). Furthermore two liana species (Akar melinjo, Akar kekait) were tested - those are frequently included into night nests by several individuals in the research area and thus might have parasite repelling properties as well. Tree and liana species were tested randomly and over all months of the study period to exclude any seasonal influences.

Table 2: Overview for the tree and liana species which were tested. The last column shows whether tree species were preferred, avoided or used accordingly to the availability within the forest (neutral). Lianas were hypothesized to be repelling as well.

Local name	Scientific name	Family	Hypothesis nesting -> mosquitoes
Ubar	Horsfieldia polyspherulla	Myristicaceae	Preferred -> repelling
Puin	Sandoricum beccarianum	Meliaceae	Preferred -> repelling
Meranti batu	Shorea teysmanniana	Dipterocarpacreae	Neutral -> Control
Rengas	Gluta renghas	Anacardiaceae	Avoided -> attracting
Akar melinjo	Rourea minor	Connaraceae	Inclusion -> repelling
Akar kekait	Uncaria glabrata	Rubiaceae	Inclusion -> repelling

The repellency tests were conducted simultaneously at two locations on trail U, at U850 and U1000 (see Fig.2-8). Data collection at both locations started in August 2010 and lasted until February 2011.

Alternatively to mosquito-repelling properties a basic analysis of structural properties for the four main nesting tree species was carried out as well. Therefore branches of each tree species were examined on leaf quantity, branching angle and resilience and leaves were compared in size. Further, for each tree species a profile was compiled, focusing on tree stability, fruiting and major advantages/disadvantages for nest building.

Test set-up 2: Exposure tests

During this test set-up the effect of the nesting position within a tree on mosquito abundance at the nest was investigated.

Thus, for this test two traps were raised into different positions of the same tree but at the same height. The only difference between the positions of the traps was the cover by nearby branches and leaves: one trap was installed in a position where cover by branches of the tree or neighbouring trees was sparse (exposed position). The other trap was raised into a more concealed location where cover by surrounding branches was more pronounced (unexposed position). The same exposure-index which was used to acquire exposure of night nests (see page 33) revealed an exposure of 0,6 for the exposed trap and a value of 0,25 for the unexposed trap. Thus the two positions differed distinctly in exposure and still were within the range of a usual orangutan night nest.





Fig. 2-6: Test set-up for exposure tests Left: The two traps at J25, with the unexposed trap on the left side and the exposed trap on the right side. Right: The SKYWATCH-device was attached to the bottom of the wooden basket.

As this test focused on positional effects only, no branches or leaves were directly applied on the mosquito traps. Instead, climatic parameters (wind gusts, temperature and humidity) were measured in both positions using the measurement device SKYWATCH ® GEOS N°11. This device automatically measures climatic parameters on a selectable interval. Data can later be transferred to a computer and is displayed in a graph on a time scale (see Results, page 54). Two devices were available, both were calibrated for two nights before used for measurements. This way it should have been possible to measure climatic parameters in both positions during the same night and later relate them to mosquito catches in the respective position. For this test set-up it was hypothesized that less mosquitoes will be caught in the exposed position due to less vegetational cover and more or stronger wind gusts. For the unexposed position instead it was assumed that more mosquitoes will be caught and less or weaker wind gusts will be detected. However, one SKY-WATCH-device broke down during the first trials and thus had to be send back for repair. For that reason it was not possible to collect climatic data for both positions at the same night, but always only for one position.

These tests were carried out from December 2010 – January 2011 at the location J25 (see Fig. 2-8). However, at this location vegetation was rather dense and hardly any wind gusts could be recorded. Therefore the tests were moved to another location (U1100) by the end of the study period. At this location the vegetation of the forest was more open and more wind gusts could be detected.

Test set-up 3: Height tests

These tests were conducted to investigate mosquito abundance at different heights of the vegetation within the forest. Mosquito numbers at specific heights will be related to respective nesting heights of certain sex/age classes or during a certain season in terms of mosquito avoidance.

Mosquito traps were also run without any application of leaves or branches, only some black plastic cover was used during most of the heavy rainfall period to protect the batteries of the traps (Fig. 2-7). After some preliminary tests the heights of 5,15, 20 and 25m were chosen for further investigation of mosquito densities. This range of heights covers the height of the majority of night nests build by the focal animals within the research area.

In this test set-up two mosquito traps were attached to one rope, with a defined distance between both traps. This way it was possible to reliably install both traps at designated heights. One trap continuously was run at a height of 15m, the second one at 5, 20 or 25m respectively.



Fig. 2-7: Test set-up for height tests Measurements at 5m and 15m; the black plastic cover on top of the wooden baskets protected the batteries of the traps from heavy rainfall.

Data collection for this test lasted from August 2010 until January 2011 and was conducted at the location U900, halfway between the two locations of the repellency tests (see Fig. 2-8). Measurements at different heights were balanced across months as well as possible, yet some of the data for the height of 20m was gathered during a period of a particularly high mosquito density within the forest.





2.3.3 Nesting data

Nesting data was collected based on a data sheet specifically designed to investigate mosquito-related features of the nest.

The data sheet also included standard parameters like sex/age class of the nest builder, nest type, nesting height, height of the nesting tree and identification of the species of the nesting tree. Yet, all this data was also useful to analyse possible mosquito avoidance strategies of orangutans. As specifically mosquito-related features exposure of the nest, the presence and amount of lianas at nesting height, amount of standing water and presence of pitcher plants at the nesting site and finally the rainfall during the night of the nesting event were added (see study objectives and hypotheses, page 18-19).

It follows a short description of definitions and the exact procedure of data collection for each feature:

At the end of each follow day the position of the focals night nest was marked with coloured tape and the location was recorded via GPS to further find the focal animal the

subsequent day. Within at least five days I went to inspect the nest together with an assistant to ensure that all nesting parameters still were in original condition.

Nesting data of all 84 nests was collected by myself and an assistant trained by me to ensure consistency of measurements and eliminate bias. Several photos of each nest were taken for further analysis in camp.

1.) Nest type

The nest type distinguishes five general nesting positions within the tree (Fig. 2-9). Type 0 nests are ground nests, not build inside a tree. Type 1 nests are build close to the main stem at a primary branching point. Type 2 nests are found at secondary branching points, further away from the main stem. Type 3 nests are build on top of a tree and a type 4 nest indicates the use of two or more trees for a nest.

This feature was examined for a first time by myself and the assistant at the actual nesting site and later on finally determined by means of photos together with other assistants in camp.



Fig. 2-9: Schematic sketch of the five nest types Usually each nest can be assigned to one of these five categories (Source: <u>http://www.aim.uzh.ch/orangutannetwork.html</u>). Ground nests are not found at Suaq Balimbing.

2.) Nesting height/ height of nesting tree

Heights were determined using a clinometer. This device measures the degree at which an observer, standing in straight succession to the nest is looking at the nest. After also measuring the distance of the observer to the nest, the height of the nest can be calculated using the law of tangents.

3.) Species of the nesting tree

The identification of the nesting tree was also done preliminarily by myself and an assistant at the nesting site and and later on finally determined by means of photos together with other assistants in camp. The choice of tree species was particularly important for the investigation of possible repellency effects.

4.) Exposure of the nest

The exposure of each nest was investigated based on a specially developed exposure-index. This index considers the presence of cover by branches or clusters of leaves at a distance of two and five meters around the nest.

Standing below the nest, for all four cardinal directions it was recorded whether any cover was present at two and five meters from the nest – horizontal and diagonal, within a degree of 45° (see Fig. 2-10). The same was done for two and five meters above and below the nest.



Fig. 2-10: Investigating exposure of a nest by means of the exposure-index Left: The red arrows indicate how data for 2m (small arrow) and 5m (big arrow) around the nest were collected. Right: Example of an exposed nest (top) and a rather unexposed nest (bottom)

Presence of branches or leaves was coded with a 1, absence with a 0. For the assignment of a 1 it was already sufficient if only one branch was present at the respective location. In cases where such branches were isolated or did not offer any real cover a 0 was ascribed to the location instead. For each cardinal direction four values were created – two horizontal and two diagonal ones (two and five meters respectively). Together with four values for above and below in total 20 values describe the surrounding of the nest. Dividing the sum of all values by 20 then results in an index between 0 and 1, with 0= no cover at all and 1= completely hidden. Yet, as the index is titled "exposure-index" results were converted by subtracting the value of each nest from 1. Therefore in the end a value of 0 indicates a very unexposed nest and a value of 1 an extremely exposed nest.

This data was collected by myself with occasional consultation of the assistant. Whenever possible I verified the measurements by rechecking all values from a different point of view. This index is much more impartial than simple assignment of just two categories (exposed or unexposed) based on the impression of an observer walking around the nest, which was used at Tuanan (Hermann, 2010).

5) Amount of standing water at the nesting site

The amount of standing water around the nest was measured similar to the exposure: For all four cardinal directions and also the intermediate directions (north-east, north-west, south-east and south-west) the presence or absence of standing water at a distance of two, five and ten meters from the nest was recorded. This yielded 24 values for each nest and by deviation also leads to an index between 0 and 1, with 0= no water at all to 1= maximum amount of water. The presence of standing water was defined as at least 2cm of standing water above the ground, which was assumed to be the minimum depth for mosquito larva to successfully develop.

6.) Presence of lianas

Each nest was checked for presence of lianas at nesting height and integration of lianas into the nest. In most cases lianas climbed the nesting tree itself, only sometimes lianas of surrounding trees had to be taken into account. The amount of lianas was rated on a scale of 0-3 (0= no lianas; 1= 1-5 lianas; 2= 6-10 lianas; 3= more than 10 lianas) and the species was identified (possible in most cases).

7.) Presence of pitcher plants

The surrounding of each nest site was inspected for pitcher plants. It was noted whether pitcher plants were present or absent in a radius of five and ten meters.





Fig. 2-11 The two species of pitcher plants which were found within the research area belong to the genus Nepenthes Left: *Nepenthes ampullaria*, right: probably *Nepenthes mirabilis* (pictures taken by myself)

2.3.4 Phenology data collection

The phenology plot is based on tree abundance along three transects of the research area. For each transect 500 trees close to the trail with a DBH of at least 10cm were tagged, which results in 1500 trees in total. The species of all trees were identified and the height of all trees was measured. Regularly all trees are checked for fruit abundance, new leaves and flowers. These data provide information about fruit availability for orangutans and give an approximation for the abundance of each tree species within the forest, which is necessary to calculate species preferences for nesting. Tree species composition of the three transects can be found in the appendix (table 7-4).

2.3.5 Statistical analyses

The statistical analyses were conducted using SPSS Statistics 19.0. All probability levels are two-tailed and the alpha level was set at p = 0.05.

For repellency tests a Wilcoxon signed rank test was applied since most data sets did not show normal distribution and were rather small. The data for exposure tests were normally distributed, as determined by a Kolmogorov-Smirnov test, and thus analysed by using a paired T-test. Generally, non-parametric test were used in cases when data-sets were too small to conclusively determine whether data is normally distributed.

For the comparison to rainfall and standing water data the numbers of mosquitoes were all log-transformed to achieve normal distribution of the data.

For the comparison of rainfall and exposure of nests (3.3.9) nights without rainfall were considered with a value of 0,1 to enable log-transformation.

To test the influence of several variables, multiple linear regressions were carried out (section 3.2.4 and 3.3.4).
3) Results

3.1 Mosquito abundance in relation to water availability

3.1.1 Measurements of rainfall and standing water

Rainfall and the amount of water within the forest were recorded to investigate the impact of water availability on mosquito abundance.

The amount of rainfall varied greatly within the study period (Fig. 3-1). During the months of September – November it rained quite frequently, whereas in December and January hardly any rainfall occurred. Generally there were some days and nights of heavy rainfall, followed by one or two weeks without rain. Only in November rainfall was more frequent with several nights of regular rain and some of strong rain. In December, in contrast, there was nearly no rain at all.



Fig. 3-1: Rainfall (mm) and standing water within the forest (cm) for the months of September 2010 to February 2011

The amount of standing water within the forest changed accordingly to rain. After nights of heavy rainfall the water level abruptly increased and then slowly decreased again. On one occasion of extremely strong rainfall for two days in a row in early October the river

overflowed and flooded parts of the forest close by. This led to an extremely high water level at some measuring locations, resulting in a total value of 60cm of standing water within the forest. In November the water level was constantly high due to frequent rain. In December the water level then gradually decreased, reaching the lowest possible level by the beginning of January.

3.1.2 Mosquito catches in relation to rainfall and standing water

Results of water availability next were compared to the amount of mosquitoes that were caught with the traps.

The mean number of mosquitoes per trap (Fig. 3-2) was calculated based on catching results of repellency tests and height tests. Catching results of exposure tests were not included as during these tests generally less mosquitoes were caught.

The amount of mosquitoes caught during the study period showed a distinct trend. At the beginning of the study period a lot of mosquitoes were present: in September on average more then 100 mosquitoes were caught in each trap (mean \pm SD: 117,8 \pm 70,27). After that mosquito density gradually declined: in October (mean \pm SD: 50,13 \pm 15,15) and November (\pm SD: 64,93 \pm 47,52) there were about 60 mosquitoes per trap, in December on average 38,87 \pm 19,7 mosquitoes and in January only 25,43 \pm 14,13 mosquitoes per trap.







Fig 3-3 The comparison of weekly means of rainfall and mosquito catches

Figure 3-3 illustrates the record of mosquito abundance compared to rainfall. Here, weekly means were calculated for a better illustration. The figure displays that mosquito density declined right after mosquito tests started in August 2010. Rainfall and standing water measurements in contrast showed several ascents and descents over the study period. Hence mosquito density declined for other reasons than just water availability.

Despite this discrepancy mosquito abundance, rainfall and standing water data were tested for correlation.

Using results of dry and rainy nights and according mosquito means of the same nights revealed no significant correlation (r= 0,165, n= 72, P= 0,166). Periods of rainy nights of course influenced mosquito abundance of following dry nights, which led to diverging values for dry nights. Therefore the test was repeated with values of rainy nights only: here, the correlation between rainfall and mosquito values was stronger and statistically significant (r= 0,394, n= 35, P= 0,026). Thus, with increasing rainfall at night mosquito numbers increased as well.

Standing water provides breeding places for mosquitoes and therefore should correlate with mosquito density as well. Mosquito larva need a certain span to develop, thus an increase of water within the forest might lead to higher mosquito densities only after an appropriate timespan. Therefore mosquito catches were compared to standing water measurements of the week before. Correlation, however, was not significant (r= 0,146, n= 41, P= 0,362), therefore the test was repeated with a shift of two weeks. This test yielded a

positive correlation which was statistically significant (r= 0,357, n= 49, P= 0,012). This shift however is rather critical as neither the data record for mosquito density nor the one of standing water was continuous.

3.1.3 Mosquito high- and low season

Mosquito catches declined from mid-September onwards, therefore a division into two different mosquito seasons like at Tuanan seemed to be useful (Largo 2009, Hermann 2010).

As over the study period mosquito numbers decreased quite independently of rainfall and standing water, mosquito catching results, rather than weather data (Largo 2009, Hermann 2010) were used to define the seasons. Furthermore, since mosquito density at all times was higher than at Tuanan, seasons were not labeled "mosquito season" and "non-mosquito season" like at Tuanan (Largo 2009, Hermann 2010). Instead the terms mosquito high and low season are applied. During high season (Sep. - Dec. 2010) weekly means of mosquito catches always were above 50 mosquitoes per trap. At the beginning of December 2010 weekly means then dropped below 50 mosquitoes per trap and never increased again; thus December 2010 to March 2011 were labeled as low season (Fig. 3-4).

A Mann-U-Whitney test revealed that numbers of mosquito catches differed significantly between high and low season (U= 148, P= 0,001).



Fig. 3-4: Visualisation of the division into a mosquito high (blue) and low season (grey)

3.2 Mosquito trapping tests

Mosquito data was obtained using mosquito traps at five different locations within the study area. Between August 2010 and February 2011 about 25'175 mosquitoes were collected in total. The identification of mosquito species at Universitas Syiah Kuala, Banda Aceh did not produce any meaningful results as mosquitoes could only be identified on family level. Possible differences in species composition of catching results could therefore not be examined. The presorting based on phenotypical characteristics, however, revealed a large diversity of mosquito species within the research area.

3.2.1 Results of repellency tests

The test for repellency examined four nesting tree species for their potential to repel mosquitoes. Catching results of traps covered with plastic leaves (control trap) were compared to results of traps covered with real leaves (test trap). According to their preference as nesting trees it was presumed that Ubar and Puin are mosquito-repelling. Meranti batu served as a control since this tree species was used in proportion to its availability within the forest. Rengas was chosen less often for nesting than expected based on its frequency within the forest and therefore might be mosquito-attracting.

Figure 3-5 illustrates how large differences in mosquito catches between test and control trap were for each species. Values below zero indicate a possible repelling tree species with less mosquitoes caught inside the test trap. Only for one tree species, Rengas, a negative mean value could be determined – for all other tree species normally more mosquitoes were caught inside the test trap (all catching results can be found in the appendix in table 7.1.and 7.2).

For statistical analysis catching results of test and control trap of each night were compared using a Wilcoxon signed-rank test. The difference between test and control trap for Rengas was statistically not significant (Z= -0,626, P= 0,531). For the other three tree species, in contrast, most of the times more mosquitoes were caught with the test trap, which led to statistically significant differences between test and control traps (Ubar: Z= -2,53, P= 0,011; Puin: Z= -2,22, P= 0,026; Meranti batu: Z= -2,20, P= 0,028).



Fig. 3-5: Mean difference in mosquito catches between test and control trap for each tree species Error bars: ± 1 SD

Based on the assumption that mosquito-repelling tree species are identified by lower mosquito numbers inside the test trap, these results suggest that Ubar, Puin and Meranti batu might even be mosquito-attracting compared to plastic leaves. This is contradictory to their preference as nesting trees and the presumed mosquito-repelling properties. However, it could be possible that plastic leaves did not act as a neutral control but for some reason were avoided by mosquitoes.

To eliminate the possibility that plastic leaves affected catching results of the control trap, the results were reanalyzed with a corrected data-set. This data-set is based on catching results with bare traps: as the effect of plastic leaves became apparent, mosquito traps without any leaves were tested parallel to traps with plastic leaves for one week. This way it should be checked whether plastic leaves significantly repel mosquitoes. Results however were inconclusive: at U850 (see Fig. 2-8) plastic leaves had a strong effect on mosquito catches (Z= -2,366, P= 0,018) but at U1000 no influence could be found (Z= -1,014, P= 0,310). Therefore tests after that were continued with plastic leaves again. The comparison of bare traps and traps with plastic leaves after all could be used to calculate a corrected data-set (Fig. 3-6). It should be mentioned, however, that the data with bare traps originated from only one week and thus the conversion of data is just a rough approximation.



Fig. 3-6: Corrected data with bare traps as control Variation in catching results increased since data for control traps were multiplied by a calculated factor (based on catching results with bare traps: U850: factor 2,78; U1000: factor 0,73)

According to this data Rengas was significantly mosquito-repelling (Z= -2,07, P= 0,039). The other tree species were more or less neutral in terms of mosquito attraction/repellency (Ubar: Z= -1,09, P= 0,278; Puin: Z= -1,29, P= 0,196; Meranti batu: Z= -0,86, P= 0,388).

The results of nesting tree preferences in contrast showed that Rengas is a tree species which was used less than would be expected, compared to its abundance in the forest. And tree species which were preferred for nesting (Ubar and Puin) did not repel mosquitoes at all. This result is contrary to the hypothesis that orangutans prefer mosquito-repelling tree species for nesting.

After all these four tree species differed significantly in the way they attracted or repelled mosquitoes: comparing differences of test and control traps over all tree species revealed significant differences between the species (Kruskal Wallis H-Test: H(3)= 10,438, P= 0,015) with a mean rank of 19,44 for Rengas, 30,16 for Ubar, 29,42 for Puin and 39,75 for Meranti batu. Thus, especially Rengas and Meranti batu differed in their potential to repel mosquitoes whereas Ubar and Puin were quite similar.

Altogether repellency tests of tree species were not very meaningful, also as the influence of plastic leaves on mosquito catches could not be defined unequivocally.

Results for liana species revealed a species with repelling effect: for both liana species generally less mosquitoes were caught inside the test trap (Fig. 3-7), but only for Akar melinjo the difference between test and control trap was statistically significant (Wilcoxon: Z= -2,511, P= 0,012). For Akar kekait the difference was not significant (Z= -0,561, P= 0,575) since sample size was smaller because tests for this liana species were started a bit later. Statistical tests for lianas were repeated with a corrected dataset as well. The result, however, did not change: the difference between test and control trap for Akar melinjo was significant (Z= -1,962, P= 0,050) and not significant for Akar kekait (Z= -1,120, P= 0,263).



Fig. 3-7: Mean difference in mosquito catches between test and control trap for liana species top: Illustration of original data obtained with plastic leaves as control. bottom: Corrected result with bare traps as control

Results of liana tests thus were more in line with expectations: one liana species which is preferred for integration into nests, showed a mosquito-repelling effect (Akar melinjo).

3.2.2 Structural properties of tested tree species

Alternatively to possible mosquito-repelling properties a basic analysis of structural properties for the four main nesting tree species was carried out as well. A comparison should reveal, whether orangutans at Suaq prefer some tree species for nesting because of structural advantages offered by such tree species. Therefore branches of each tree species were examined on leaf quantity, branching angle and resilience and leaves were compared in size. The collected results are shown in Table 3-1.

Ubar seems to have fewer leaves per branch than the other tree species as branches are very straight with a regular foliation. This however is compensated by the large number of branches per tree in comparison to the other tree species. Furthermore branches of Ubar branch off very straightly from the main stem, nearly at an angle of 90 degrees (Fig. 3-9).

Branches of Puin divide into several smaller branches, forming a larger surface at the tip of each branch and thus carry more leaves. The leaves in contrast to the other tree species are rather round and soft. The branching angle is not as advantageous as for Ubar and also the stability of branches is a little lower.

Table 3-1: Comparison of leaves and branches of the four test species Amount of leaves: number of leaves on a young branch of 1m, Length and diameter were calculated by measuring 20 small, medium and large leaves; branching angle was estimated, resilience was determined by attaching weight to branches of a fixed length and diameter

Tree species	Leaves			Branches	
	Amount	Length	Diameter	Branching angle	Resilience
Ubar	57 (± 12)	17,6	7,4	90°	13kg
Puin	119 (± 32)	14,2	8,6	45-60°	11kg
Meranti batu	107 (± 41)	16,5	7,3	60-90°	13kg
Rengas	165 (± 58)	20,3	5,7	60-90°	18kg

Meranti batu has a similar amount of leaves per branch and leaves are rather longish. The large main branches are quite horizontal.

Rengas has most leaves per branch as a lot of leaves form clusters at the distal end of branches. The leaves are long and rather thin and the branches are characterized by a high resilience. Most branches during the test could not be broken but only bend extremely.



Fig. 3-8: Leaves of Puin, Rengas, Meranti batu and Ubar compared (from the left to the right) Leaves do not differ notably in size; Leaves of Puin are rather round and leaves of Rengas and Ubar are a little rougher than the ones of Meranti batu and Puin

By way of illustration for each tree species a photo of a typical tree and branch, a representative nest within each tree species and the stem are shown below:

<u>a) Ubar</u>

The tree species Ubar (*Horsfieldia polyspherulla*) is characterized by a lot of very long and rather thin branches which grow in a very straighter manner from the main stem. Foliation is very regular all over the branch. The amount of leaves however can vary strongly between trees of this species: some have a lot of branches with many healthy leaves whereas other trees only have few branches with few leaves. The roots are stilted which for trees in a swamp environment very likely is a more stable root system than just straight rooted trunks. Fruits are produced seasonal and are among the ones orangutans feed on. The greatest advantage of this tree species probably are the horizontal branches which enable an easy construction of a stable nest and might explain the strong preference for such trees.



Fig. 3-9: Photos for Ubar: Typical branch (top, left) and nest within Ubar (top, right) and the root (bottom, left) bottom, right: a nest within a tree with many branches can be very concealed

<u>b) Puin</u>

Trees of the species Puin (*Sandoricum beccarianum*) are often large, emergent trees with a smooth bark. The branches can grow in a rather sharp angle from the main stem, especially closer to the top of the tree. Nevertheless most nests in this tree species were built around the top of the tree (see photo top right), rather than on the large, more horizontal branches below. Leaves are concentrated at the distal end of branches, where branches split up into several smaller ones. Always three leaves are found at the very tip of each young branch. The trunk is straight rooted. Fruits are produced seasonal as well and trees are visited very often during fruiting. A preference for this tree species might be connected to the large, soft leaves at the tip of branches which allow a very comfortable nest.



Fig. 3-10: Photos for Puin: Typical branch (top, left) and nest within Puin (top, right) bottom: the branching angle at the top of trees is rather sharp (left), below larger branches are more horizontal (right)

<u>c) Meranti batu</u>



Fig. 3-11: Photos for Meranti batu: Typical branch (top, left) and tree of this species (top, right) bottom: the buttressed root (left) and a representative nest, constructed on top of one of the large branches (right)

Large trees of the species Meranti batu (*Shorea teysmanniana*) usually only have a few, very large main branches which are quite horizontal. At the distal end branches divide into a lot of small branches which carry all the leaves, so that clusters of leaves are formed. Often all leaves of such clusters were used to construct a nest, which left very few surrounding cover by the tree. This species is characterized by buttressed roots, which should provide more stability. Meranti batu does not provide any visible fruits.

The species was used more or less accordingly to its availability within the forest, mostly by adolescents. The main advantage for this tree species is the possibility for a nest on a large branch with a lot of leaves due to leaf-clusters.

<u>c) Rengas</u>



Fig. 3-12: Photos for Rengas: Typical branch (top, left) and root of this species (top, right) bottom: a nest within a small Rengas tree, built by a flanged male (left) and a representative tree (right)

Rengas (*Gluta renghas*) structurally is quite similar to Meranti batu: the main branches are quite large and horizontal and leaves are concentrated in clusters at the distal end of each branch. The concentration of leaves for Rengas is even more distinct as a lot of leaves grow at the end of each branch. Also branches compared to the other tree species are rather short and of irregular growth. The root of the trunk is straight. Fruits of this species are not eaten by orangutans, sometimes they however feed on larvas inside the fruits. The most distinguishable feature of this tree species however is the acrid sap inside the branches and trunk which can cause severe burns for humans. This characteristic probably also explains why orangutans rather avoid this tree species for nesting. The sap

issues from branches when they are broken and, despite their pelage, might harm orangutans as well.

3.2.3 Results of exposure tests

For the exposure tests positional effects of nests on mosquito abundance were investigated. Therefore, two traps were raised into positions of different vegetational cover within the same tree. Then mosquito catches of the exposed and the unexposed trap of each night were compared. Figure 3-13 shows the mean number of mosquitoes which were caught in each position: there was no significant difference in the amount of mosquitoes between the two positions (paired T-test: t(20)=-0.946, P= 0.356). Also, when nights with only few mosquitoes (less than ten mosquitoes in each trap) and nights of slight differences (smaller than five mosquitoes) were excluded, the result was still not significant. The catching results of all nights can be found in the appendix in table 7.3.





Originally it was planned to compare the amount of wind between the exposed and unexposed position as well so that mosquito catching results could be related to wind measurements of respective nights. However, one SKYWATCH-device broke down and it was not possible to collect climatic data for both positions at the same night, but always only for one position. Wind gusts within the testing area (J25) were very sparse, thus no difference between the exposed and unexposed position could be found and exposure tests were moved to another, more open location (see methods exposure tests, page 29). It was expected that differences in mosquito numbers between exposed and unexposed positions are larger if more wind is present. Wind measurements confirmed that wind gusts at the new location (U1100, see Fig. 2-8) were a lot more numerous and also stronger:

The mean wind speed for each location was calculated based on the wind speed of all single wind gusts. A comparison shows that wind gusts at the exposed, more open location were stronger than at the location with more dense vegetation (unexposed) – by day and by night (Fig. 3-14). The mean wind speed by day at the exposed location was 3,92 km/h (SD 2,03 km/h), while at the unexposed location wind speed reached only a mean value of 2,48 km/h (SD 1,11 km/h). At night the difference between locations was about the same. A statistical analysis of this values was not possible because at the unexposed location only one wind gust was detected at night.



Fig. 3-14: Comparison of mean wind speed at the exposed (blue) and unexposed (purple) location within the forest

Comparing the number of wind gusts revealed an even larger contrast: at the exposed location 284 wind gusts were measured, within four nights (mean amount per night: 71). At the unexposed location only one wind gust was recorded within six nights (mean amount per night: 0,166). This contrast is illustrated best by characteristic plots of microclimatic measurements of each location.

At the unexposed location with a dense vegetation (J25) only few wind gusts were recorded, usually by day, and none at night (between 6 pm and 6 am) as it is shown in Figure 3-15. Further, wind speed of most wind gusts were in a range of 1 - 3km/h.

For the exposed location at U1100 instead a lot of wind gusts were recorded, during the day as well as at night (Fig. 3-16) and many gusts reached a wind speed of 3 - 4km/h.



Fig. 3-15: Record of wind gusts (red), temperature (green) and humidity (blue) at the unexposed location (J25) on December 8th -9th.



Fig. 3-16: Record of wind gusts (red), temperature (green) and humidity (blue) at the exposed location (U1100) on February 3th -4th.

Altogether these measurements suggest that the density of vegetation in a certain area of the forest strongly influences the number and intensity of wind gusts.

Due to this large difference in the number and intensity of wind gusts between the two locations in the forest, mean mosquito numbers of the two different locations, J25 and U1100, rather than positions within the tree were compared (Figure 3-17). This way a connection between the density of vegetation, wind gusts and mosquito abundance should be investigated.





As presented in Fig. 3-17 there was a clear difference in the number of mosquitoes that were caught at the respective locations in the forest.

The comparison between the two locations, however, was strongly influenced by seasonal effects: Data collection at the open location took place at the very end of the study period in January and early February 2011 and by then mosquito abundance had already declined a lot. The difference in catching results between the locations thus can not only be ascribed to density of vegetation or wind gusts but also reflects the decrease of mosquito density by the end of the study period. Also, a statistical evaluation of these data-sets was not possible due to the small number of repetitions in the open location.

To examine the connection between the density of vegetation and wind gusts on mosquito abundance, simultaneous measurements at both locations are necessary to exclude seasonal influences in mosquito numbers.

3.2.4 Results of height tests

The traps at different heights should reveal whether the construction of nests at certain heights is advantageous to avoid mosquitoes.

Overall, there was a statistically significant difference in the number of mosquitoes that were caught at different heights (Kruskal Wallis H-Test: H(3)= 19,61, P< 0,001).



Fig. 3-18: Boxplot for the number of mosquitoes caught at the heights of 5, 15, 20, and 25m Errorbars: ± 1 SD

At 5m (n=17) on average 29 (SD 21) mosquitoes were caught, at 15m (n=46) on average 78 (SD 51) mosquitoes. At 20m (n=15) the mean number of mosquitoes was 94 (SD 61) and at 25m (n=16) on average 85 (SD 84) mosquitoes were found.

One mosquito trap was always run at 15m height while another one was either positioned at 5, 20 or 25m. Therefore results at 15m were compared to catches at 5, 20 or 25m of the respective nights using a Wilcoxon signed-rank test. The analysis revealed that mosquito abundance at 15m only differed significantly from the one at 5m (Z= -3,351, P= 0,001). Differences between 15m and 20m (Z= -0,502, P= 0,615) and 15m and 25m(Z= -1,319, P= 0,187) were not significant.

The high mosquito number at 20m partly can be ascribed to a seasonal effect: tests at 20m were mainly run at the beginning of the study period when mosquito density was still

very high. Also, catching results at different heights might be affected differently by the amount of rainfall.

3.2.5 Regression model for height tests

To further disentangle influences of height, rainfall and season, a multiple regression with these variables was carried out.

The analysis revealed that the height of traps accounted for only 10,8% of variance in mosquito catches. Adding rainfall measurements to the model led to an increase of another 10% to 19,7%. Thus mosquito abundance is determined by height and rainfall to about the same extend. Seasonality hardly influences mosquito numbers for this test as addition of this variable only led to an increase of 2,5%. Altogether height, rain and seasonality therefore explain only 22,3% of variance in mosquito catches. This result suggests that variation in mosquito density at the test location was mainly determined by other factors.

Table 3-2: Results of the multiple regression including the complete data set of all heights * p < 0.05; ** p < 0.01; ***p < 0.001;

	Model 1	Model 2	Model 3
n	85	85	85
Variance explained (r ²)	0,108*	0,197***	0,223***
Standardized ß coefficient			
Height trap	0,329*	0,378***	0,361***
Rainfall	-	0,301*	0,278*
Season	-	-	-0,163

Table 3-2 shows that the height of traps still was the most important determinant for differences in mosquito numbers. As the tests above revealed, this was, however, mainly due to large differences between mosquito catches at 5m and the other three heights. Therefore, the multiple regression was repeated once again without the data from 5m. As shown in table 3-3, the influence of height on mosquito numbers then no longer is significant. Instead the influence of rainfall on variance in mosquito numbers increases.

Γable 3-3: Results of the multiple regression without the data from 5m	* p< 0,05	; ** p<0,01	; ***p<0,001
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	Model 1
n	69
Variance explained (r ²)	0,170*
Standardized ß coefficient	
Height trap	0,096
Rainfall	0,355***
Season	-0,181

3.3 Nest site selection

The data for nest site selection contains 84 nests which were constructed between August 2010 and February 2011. Nests built by adolescent individuals contributed the major amount, with 32 nests. All four adolescents encountered were females, between nine and fifteen years old. Mother/infant pairs added 20 nests to the total nest number. Five mother/infant pairs were observed during the study with two pairs contributing most of the data for this sex/age class. Nest data from unflanged males (17 nests) comes from several different individuals who often were not further identified. The sex/age class of flanged males contributed the smallest share with only 15 nests. Most nesting data for flanged males originate from the male who was dominant within the research area during the study time (Eddy); other flanged males only contribute a few nests as there were hardly any other adult males observed.

3.3.1 Tree species preferences

Comparing the distribution of tree species based on the phenology plot to the actual choice of nesting trees for night nests shows that Ubar and Puin were used much more than actually available (Fig. 3-19). Merati batu was also chosen more than available, yet not as clearly preferred as Ubar and Puin. Rengas in contrast was used considerably less than based on the phenology plot.



Fig. 3-19: The four most popular nesting trees in terms of abundance within the forest (grey) and usage as nesting tree (blue)

To determine whether the abundance of each tree species differed significantly from the frequency of usage as a nesting tree a chi-square test was applied. Results show that Ubar (X² (1)= 48,66 ; p< 0,001) and Puin (X² (1)= 18,97 ; p< 0,001) were significantly more often chosen for night nests than expected by their abundance within the forest. Together these two tree species make up 41% of all nesting trees, but only 11% of all trees. The difference for Meranti batu did not reach a significant level (X² (1)= 3,23). Rengas in contrast was avoided significantly (X² (1)= 6,67 ; p< 0,01). This species accounts for only 11% of all nesting events can be found in the appendix in table 7.5, together with the frequency of tree species within the phenology plot (table 7.4).

At Tuanan tree preferences for nesting were pronounced to a similar extent, yet not as strongly as at Suaq. There, the three most popular tree species for nesting make up only 20% of all night nests (Hermann, 2010).

Figure 3-20 illustrates that there were notable differences in tree preferences between the four sex-age classes. While adolescents and mother/infant pairs mainly used the three tree species Ubar, Puin and Meranti batu, flanged and unflanged males mostly used other tree species. Sample sizes, however, are too small to determine whether these differences between sex/age classes are statistically significant.





It should be noted that more nests of adolescents were examined and thus their preferences contribute more to the overall tree preferences (Fig. 3-19). Adolescents for example preferred Ubar over all other tree species, therefore the preference for Ubar in Fig. 3-19 is very distinct. If instead more nests built by flanged males, which do not prefer Ubar to such an extend, had been investigated, preference for Ubar in Fig. 3-19 would be less distinct.

At Tuanan tree preferences were more consistent over different sex/age classes. There the tree species chosen most overall (M. blawau) contributed to the majority of night nests in all sex/age classes (Largo, 2009).

3.3.2 Nesting height

The mean \pm SD nesting height for night nests at Suaq was at 15,8m \pm 4,97m. Besides distinct differences in tree preference, individuals of different sex/age classes also had different preferences in nesting height (Fig. 3-21). Adolescent individuals, with a mean \pm SD nesting height of 20m \pm 3,16m, built the highest nests. Mother/infant pairs also preferred rather elevated nesting positions, reaching a mean \pm SD height of 17m \pm 2,98m. Males instead chose to nest a lot lower: unflanged males at a mean \pm SD height of 11m \pm 3,14m and flanged males always nested at about 10m (SD 1,33m). A One-way ANOVA revealed that these differences in nesting height over all four sex/age classes are significant (F(3, 77) =82,581, p< 0,001). A Scheffe post-hoc then showed that all sex-age classes but flanged and unflanged males difference significantly in nesting height.





3.3.3 Exposure of nests

The exposure of nests was of critical importance to test the assumption that some sex/age classes are more vulnerable to mosquitoes than others – which is suggested by the results from Tuanan (Hermann, 2010; Largo, 2009).

The exposure-index (see methods) assigned a value between 0-1 to each nest and thus allowed to compare the variance between data-sets of different sex/age classes using a one-way ANOVA. The test was not significant at a level of 0,05 (F(3, 79) = 2,671, P= 0,053) but showed a trend. A Scheffe post-hoc test revealed that only adolescents differ from the other three groups (see Fig. 3-22). Comparing the data set of adolescents to a combined data set of the other three classes thus led to a significant result (Mann-U Whitney: U= 512,5; P= 0,004).





For a better illustration the exposure-values of all nests were subdivided into four classes. Then it was calculated how many nests fall into each category within the different sex/age classes (Fig. 3-23). The illustration shows that adolescents built notably more exposed nests, with an index above 0,5 - most of the nest lie within a range of 0,5 - 0,7 (blue). For all other sex/age classes unexposed nests prevailed. Mother/infant pairs, unflanged and flanged males mostly built night nests of an exposure of 0,3 - 0,5 (yellow). Mother/infant pairs showed the highest percentage of nests with an index below 0,3 (grey) which are very unexposed, thus very concealed nests. Still, the amount of unexposed

nests (<0,5) was lower than in flanged and unflanged males. Unflanged males also built a lot of very exposed nests (black), yet the amount of rather unexposed nest (yellow) prevails. Flanged males showed a distribution which is very similar to mother/infant pairs.



Fig. 3-23: Proportion of nests assigned to each of four kinds of exposure Division into nests which are build very exposed (black), rather exposed (blue), rather unexposed (yellow) and very unexposed (grey) for each sex/age class.

Altogether the results of the exposure-index demonstrate that adolescents built significantly more exposed nests than the other sex-age classes. This is a completely different finding than the one derived from the data at Tuanan, where flanged males built exposed nests more often than other sex/age classes.

As a next step exposure of nests was examined in relation to nesting height because cover of a nest is often determined by its height within a tree. Nests of high exposure (index 1 - 0,7) indeed were build highest (19m, SD 5,67m). Nests which were categorized as rather exposed (index 0,7 - 0,5) were constructed at a mean height of 17m (SD 4,39m). Rather unexposed nests (index 0,5 - 0,3) on average were build two meters lower (15m, SD 4,98m) and very concealed nests (index < 0,3) lowest, at about 14m (SD 4,84m).

There was a statistically significant difference in height between the four classes of exposure as determined by a one-way ANOVA (F(3, 80)= 2,856, P= 0,042). A Scheffe post-hoc test, however, did not reveal any significant difference between two of the respective classes (Fig. 3-24).



Fig. 3-24: Nesting height in relation to exposure A comparison of the mean nesting height for nests of the four categories of exposure

Finally the relationship between height measurements and exposure was investigated. A positive correlation, which was statistically significant (r= 0,299, n=84, P=0,006) was found. Thus, with increasing nesting height, nests were more exposed and lower nests were less exposed.

Based on this interaction between nesting height and exposure, high exposure of adolescents night nests partly can be attributed to the actual height of the nest itself. Flanged and unflanged males in contrast chose to to nest notably lower which seems to be accompanied by more cover. This interaction is also important for a comparison of nesting preferences of different sex/age classes: mother/infant pairs, for example, built significantly higher nests than flanged and unflanged males, yet these classes do not differ significantly in exposure. This suggests that mother/infant pairs have a preference for rather concealed nests, despite their tendency to nest quite high. For single sex/age classes correlation between nesting height and exposure was not significant, probably because nests within each sex/age class are quite similar in height and exposure.

The selection of the nesting tree's species also influences how much cover for the nest is available, since tree species differ in the amount of foliage and branches. Therefore preferred and avoided tree species for night nests were compared in terms of exposure as well (Fig. 3-25).

Differences in exposure between the four tree species turned out to be statistically

significant (One-way ANOVA (F(3, 46)= 4,501; P= 0,008). A Scheffe post-hoc test revealed that only the data-sets of Ubar and Meranti batu differ significantly, thus explaining most of the variance between tree species.

Ubar usually offers quite a lot of cover as trees of this species have a lot of branches with consistent foliage (see page 47). Trees of the species Meranti batu, in contrast, are characterized by only few large branches with clustered leaves. Nests in such trees consequently have less surrounding cover.





These differences are interesting in relation to tree species preferences. As presented in figure 3-20 adolescents mostly chose the tree species Ubar for the construction of night nests. The analysis of exposure revealed that Ubar on average offers a lot of cover, yet nests of adolescents are on average the most exposed nests (Fig. 3-22). Thus, it seems as if adolescents pick trees of the species Ubar with reduced foliage and cover.

3.3.4 Nest type

To describe the location of a nest within the tree, nests are categorized into different nest types. The construction of certain nest types is connected to stability and safety of the nest and therefore reveals additional information on nesting preferences of sex/age classes.

Figure 3-26 shows the total amount of nests constructed of each type for the different sex/age classes. Adolescents clearly preferred type 1 nest (53%) and also built a lot of

type 2 nests (31%). Mothers with infants show a similar preference: type 1 nest account for 50% of their nests and type 2 nests for 35%. These nest types are build close to the main stem. Unflanged males constructed mostly type 2 (53%) and type 4 nests (35%). For flanged males finally type 4 nests prevailed (60%), which are characterized by usage of multiple trees.



Fig. 3-26: Nest type preferences of the four sex/age classes. n= number of nests

3.3.5 Regression model for nesting height and for exposure

To gain further insight into the relation between the parameters examined so far, a multiple regression was carried out.

Two independent analyses were carried out in order to understand which parameters determine nesting height (dependent variable in analysis one) and exposure (dependent variable in analysis two) the most. The independent variables were sex/age class, tree species and nest type as predictors.

Nesting height was best predicted by the sex/age class of the nest builder: tree species, exposure and nest type together explained only 25,5% of the variance in nesting height (model 1), while adding sex/age class to the model led to an increase of more than 40% to 69,5% (model 2). Running the analysis with sex/age class as the first variable revealed that this parameter alone explained already 66,5% of variance. Overall the independent variables predicted nesting height very well (Table 3-4).

Table 3-4: Results of the multiple regression for nesting height as dependent variable * p < 0,05 ;

** p<0,01 ; ***p<0,001

	Model 1	Model 2
n	76	76
Variance explained (r ²)	0,255***	0,695***
Standardized ß coefficient		
Nest type	-0,133	0,068
Exposure	-0,235*	-0,126
Tree species	-0,342*	-0,145
sex/age class	-	-0,757***

The variance in exposure of nests could only poorly be explained by the measured parameters. Sex/age class, tree species and nest type did not account for more than 5,2% of variance (model 1). The addition of nesting height (model 2) only led to an increase of about 6% to 11,6% in total. Therefore rainfall was included into the analysis (model 3) as it was assumed that rain might induce orangutans to build nests of different cover. The inclusion of rainfall, however, did not influence the result strongly: altogether just 14,1% of variation in exposure could be explained by all parameters (Table 3-5).

An explanation for this result might be, that exposure also varied a lot within classifications (e.g. sex/age class), on an individual level. Nest built by one mother/infant pair (Friska & Fredy), for example, for some nesting events were very exposed (index: 0,75), while other nests were very concealed (index: 0,2). It seems as if exposure of the nest is adjusted very flexibly to the prevailing nesting area and conditions by all orangutans.

Table 3-5: Results of the multiple regression for exposure as dependent variable * p < 0.05; ** p < 0.01; ***p < 0.001

	Model 1	Model 2	Model 3
n	76	76	76
Variance explained (r ²)	0,052	0,064	0,055
Standardized ß coefficient			
Tree species	-0,044	0,027	0,014
Nest type	-0,140	-0,163	-0,166
Sex/age class	-0,102	0,265	0,279
Nesting height	-	0,465*	0,444*
Rainfall	-	-	0,160

3.3.6 Presence of pitcher plants

The presence of pitcher plants may be related to higher densities of mosquitoes as the water inside of pitchers can be used by mosquitoes for oviposition, even in dry areas. Therefore it was investigated whether orangutans adjust their nesting behaviour to the presence of such plants.

Nests of all sex/age classes more often were built in surroundings without pitcher plants. During 69% of all nesting events no pitcher plants were present. Especially for nests of flanged males rarely pitcher plants were found at the nest site (absent in 85% of nests). In most parts of the research area pitcher plants, however, were not very common. Usually they occurred in patches, then at high density, but there were no large, continuous areas in which the plant was present at similar densities. Thus, this result does not necessarily suggest avoidance of pitcher plants.

At nest sites were pitcher plants are present they might influence orangutan nesting behaviour. Higher nests are assumed to be more exposed to wind and thus might offer better protection against mosquitoes. Orangutans should therefore construct nests at higher locations or more exposed if pitcher plants are present in the nesting area.

Figure 3-27 (top) illustrates, however, that nesting height was not influenced by the presence of pitcher plants. Statistical analysis using the Mann U-Whitney test showed that there was no significant difference in nesting height for any of the groups (adolescent: U= 88,5; P= 0,944; mother/infant: U= 29; P= 0,775; unflanged: U= 20,5; P= 0,161; flanged: U= 10,5; P= 0,791). Only for mother/infant pairs there seemed to be a weak tendency: they on average nested three meters lower if pitcher plants were present.

Exposure of nests was hardly adjusted to the presence of pitcher plants either. As shown in Figure 3-27 (bottom) only mother/infant pairs and unflanged males showed some variation in exposure: Mother/infant pairs created slightly more exposed nests if pitcher plants were present, which is consistent with the assumption that more exposed nests offer a better protection against mosquitoes. Nests of unflanged males in contrast were less exposed if pitcher plants were present. However, none of the differences was statistically significant (adolescent: U= 63; P= 0,208; mother/infant: U= 15,5; P= 0,095; unflanged: U= 26; P= 0,417; flanged: U= 9,5; P= 0,659).



Fig. 3-27: Variation in nesting height (top) and exposure (bottom) in relation to the presence of pitcher plants

3.3.7 Amount of standing water at the nesting site

The amount of standing water was a parameter which was especially chosen to investigate mosquito related features of the nest. Water pools provide breeding places for mosquitoes, therefore wetter areas should be characterized by a higher mosquito density and should be avoided by orangutans for nesting.





There was a statistically significant difference in the amount of standing water at the nest site between sex/age classes as determined by a one-way ANOVA (F(3, 77)=5,872; P= 0,001). A Scheffe post-hoc test revealed that flanged males nested in places with significantly more standing water than mother/infant pairs (p<0,006) and adolescents (p<0,021). This result is consistent with the hypothesis that flanged males are less vulnerable to the threats associated with mosquito bites than younger individuals like adolescents and infants.

As the amount of standing water at nests and the general amount of standing water within the forest showed a similar seasonal variation, both data sets were tested for correlation. The correlation was positive and statistically significant (r= 0,440, n= 66, P=0,01), which means that the amount of standing water at nests is mostly explained by the amount of standing water within the forest during that time.

An analysis of nesting height revealed that nests were build at lower locations in case of more standing water. Yet, as it was flanged males who generally built the lowest nests, this result probably reflects sex/age class preferences rather than preferences connected to the amount of standing water.

3.3.8 Presence of lianas

Each nest was checked for presence and inclusion of lianas to further investigate the influence of two possible mosquito-repelling liana species (Akar melinjo, Akar kekait). Another liana species (Akar pakis) is associated with disturbing insects like ants (see below).

The presence and amount of lianas at nesting height was noted for each nest and relevant liana species were identified. Overall lianas were present in 39% of all nests and absent in 61%.



Fig. 3-29: Amount of lianas present at nesting height for different sex/age classes class 1= 1-5 lianas; class 2= 6-10 lianas; class 3= more than 10 lianas

Figure 3-29 illustrates that mostly flanged males nested in locations where lianas were present, adolescents in contrast rather avoided lianas: For nests of flanged males lianas were present at nesting height in 53% of nests, while for adolescents lianas were present in only 28% of nests. Also, the amount of lianas present around nests of flanged males was larger (class 3, red) than for other sex/age classes. Especially mother/infant pairs tend to avoid large amount of lianas – for their nests lianas were present in 37%, but always only very few (class1 or 2). Sample size for nests with lianas was, however, too small to test whether these differences are statistically significant.



Fig 3-30: Percentage of nests with lianas associated with insects (top) and possible mosquitorepelling properties (bottom). (n= number of nests)

For further analysis of the data set possible influences of the different liana species were included. One liana species, Akar pakis, for example is associated with insects like ants. Quite often it can be observed that orangutans, especially males, search for (edible) insects in large clusters of this liana species. Adolescents and mother/infant pairs tended to avoid nesting trees vegetated by Akar pakis, whereas flanged and unflanged males built about one third of their nests in trees where this liana species is present (Fig. 3-30, top). Two other liana species might have mosquito-repelling properties (see methods,

repellency tests). The selection of this two liana species differed between sex/age classes as well. It was differentiated between nests which were built close to clusters of lianas or where lianas were present at nesting height and cases in which the nest-builder had actively included lianas during the nest building process. It was mostly adolescents who chose to nest close to the liana species Akar melinjo and Akar kekait or even included
these lianas into their nests (Fig.3-30, bottom). In four out of ten cases in which potentially repelling liana species were found in or around the nest, nests were constructed by adolescents. Further, of all nesting events investigated, lianas were actively included into the nest only eight times – six times of it by adolescents. All other sex/age classes hardly ever showed inclusion of liana species into their nests.

As mosquito abundance during rainy nights is positively correlated to the amount of rainfall (see 3.1.2), inclusion of mosquito repelling liana species would be of special use during rainy nights. A comparison of nesting events during rainy nights and dry nights showed that in nearly all cases lianas were included during nights of rainfall: In 38 cases of rainy nights lianas were used seven times, while during 42 dry nights lianas were included only once (Fig. 3-31). However, as inclusion was very rare the difference between conditions showed only a trend (Fisher's exact test: p<0,058).



Fig. 3-31: Inclusion of lianas into the nest in rainy and dry nights

3.3.9 Influence of rainfall

Rainfall might influence orangutans' nesting behavior and preferences, as rainy nights generally are characterized by a lower mean temperature and rainfall influences mosquito foraging (Shaman et al., 2007). Therefore, the relationship between nesting height, exposure and tree preferences during dry and rainy nights was investigated.

Nesting height is not significantly influenced by rainfall: the mean \pm SD nesting height of dry and rainy nights was about the same (dry: 15,91m \pm 4,28; rainy: 15,54m \pm 5,75). Also the correlation between the amount of rainfall and nesting height was statistically not significant (r= 0,048; n= 77; P<0,68).

Exposure, in contrast, turned out to be influenced by rainfall: the mean exposure of nests built in dry nights was 0,47 (SD: 0,16), while in rainy nights exposure reached a value of 0,55 (SD: 0,18). A Mann U-Whitney test revealed that this difference was nearly significant (U= 534,5; P= 0,06).

Testing the amount of rainfall and exposure for correlation (Fig. 3-32), resulted in a significant, positive correlation (r= 0,257; n= 77; P<0,024). Thus orangutans built their nests in a more exposed manner during rainy nights.



Fig. 3-32: Correlation between the amount of rainfall at night and exposure of corresponding nests

Comparing tree species selection during dry and rainy using the chi-square test nights did not reveal any statistically significant differences (Fig. 3-33). However, sample sizes were quite small after dividing the data set into nights with or without rain and different tree species.

As illustrated in Figure 3-33 there seem to be at least some trends for tree species selection: Ubar was chosen less for night nests in rainy nights while Meranti batu was clearly preferred during rainy nights. This selection must however not necessarily imply mosquito repelling properties of such tree species but might also be ascribed to certain structural features of trees or liana species occurring on a tree which are beneficial during rain.



Fig. 3-33: The usage of tree species during rainy and dry nights

3.3.10 Influence of mosquito high and low season

To investigate whether orangutans adjust their nesting behaviour to changes in mosquito abundance, tree species selection, nesting height and exposure of nests during mosquito high and low season were compared .

Possible mosquito repelling tree species (see repellency tests) should be chosen more often during times of high mosquito density, while mosquito attracting tree species should rather be used when mosquito density is low. Figure 3-34 shows that only one tree species seems to be selected based on mosquito abundance: Meranti batu was used significantly more often during the mosquito low season ($X^2(1)=4,08$; p< 0,043). Results of repellency tests (see 3.2.1) indeed revealed that Meranti batu, compared to the other three tree species, attracts significantly more mosquitoes. Thus orangutans might use Meranti batu more often during times of low mosquito abundance because of its mosquito-attracting properties.

Results of tree preferences during high and low season are, however, also dependent on the individuals who contributed to each season – because certain sex/age classes showed distinct tree preferences (see Fig. 3-20). Meranti batu was mostly used by adolescents; therefore if adolescents contributed more nests during the low season, this might explain

the large number of nests in Meranti batu during the low season. The contribution of adolescents to nests of high and low season, however, is about the same (high season: 19 nests, low season: 13 nests). A bias due to sex/age class contribution hence can be excluded.



Fig. 3-34: Tree species selection during mosquito high and low season. During mosquito high season Meranti batu was selected only 2 times, during low season in contrast 10 times

Following, nesting heights during mosquito high and low season were compared. In line with results from Tuanan (Hermann, 2010) it was presumed that orangutans construct nests at higher sites during the mosquito high season.

The comparison of nesting heights (Fig. 3-35), however, revealed that overall there was no statistically significant difference between the two seasons (Mann U-Whitney: U= 844,5; P= 0,902). Mean \pm SD nesting height during the high season was 15,7m \pm 4,5 and during low season 15,8m \pm 5,4. Mother/infant pairs, contrary to the assumption, even chose to nest significantly higher during the mosquito low season (U= 17; P= 0,050).

Orangutans, however, also did not adjust their nesting height to other influences which were assumed to increase mosquito numbers, e.g. rainfall (see 3.3.8) or the presence of pitcher plants (see Fig. 3-27). This suggests that variation in nesting height of orangutans probably can not be ascribed to mosquito avoidance.





Finally, exposure of nests during high and low mosquito season was compared. It was expected that orangutans build more exposed nests during the high mosquito season as it was assumed that a higher exposure to wind offers a better protection against mosquitoes (Herman, 2010).

However, the opposite was observed: overall, nests during the mosquito low season were significantly more exposed than during the high season (Mann U-Whitney: U= 547,5; P= 0,01). Mean \pm SD exposure of nests during the high season was 0,46 \pm 0,18 and during low season 0,56 \pm 0,15. The comparison for single sex/age classes (Fig. 3-36) showed that it was mother/infant pairs (U= 9,0; P= 0,008) and unflanged males (U= 9,5; P=0,010) who constructed significantly more exposed nests during the low mosquito season. Sample sizes for single sex/age classes, however, are rather small after dividing data-sets into mosquito high and low season. Also, nests of the high and low season were built by different individuals, so that it cannot be excluded that differences between the two seasons simply reflect individual preferences.

4) Discussion

The main goal of this study was to gain insights into nesting preferences of a population of wild Sumatran orangutans at Suaq Balimbing.

Referring to similar studies carried out at Tuanan in Central Kalimantan (Florez, 2007; Largo, 2009; Hermann, 2010) it was investigated whether a preference for certain tree species for nesting can be related to possible mosquito-repelling properties of leaves and bark of these tree species (hypothesis 1).

Further, specifically designed tests with mosquito traps were carried out to explore whether differences in nesting height and exposure can actually influence mosquito numbers at the nest site (hypothesis 2). According to data from Tuanan such nesting features might be related to mosquito avoidance as well (Hermann, 2010).

Therefore, several mosquito-related features of night nests were investigated for the population at Suaq. Sex/age classes which are more vulnerable to threats associated with mosquitoes might show a more pronounced avoidance behaviour which is reflected by differences in nesting parameters (hypothesis 3).

Finally, the influence of rainfall and availability of breeding places on mosquito abundance was investigated. Rainfall can enhance mosquito flight activity and over a long period leads to more possibilities for oviposition, thereby increasing mosquito density (hypothesis 4).

4.1 Mosquito trapping tests

4.1.1 Mosquito-repelling properties of tree and liana species

Results of the repellency tests quite clearly indicate that preferred nesting trees at Suaq are not mosquito-repelling. For all of the four tested tree species in most cases more mosquitoes were caught inside the test trap with real leaves compared to a control. There was a crucial problem with control traps as the plastic leaves for some reason did not act as a neutral control but were seemingly avoided by mosquitoes. Yet, still after calculating an alternative result by adjusting catches of control traps to ones without plastic leaves, results were not notably different. After adjusting, only Rengas then showed a mosquito-repelling

effect but that effect can nearly completely be ascribed to catching results of the last two nights, when mosquito abundance had already declined drastically (see appendix, table 7.1). However, Rengas was found to be used less than available for nesting by orangutans. So in conclusion tree choice for nesting in this population, at least for species tested, quite likely is not based on any mosquito-related properties of tree species.

Instead preferences for certain tree species and avoidance of others might be explained by cultural transmission. Tree preferences differ a lot between the various orangutan research sites, even though in many areas similar or even the same tree species are available. Some tree species are used frequently in some populations while other populations hardly ever choose these tree species for nesting. The tree species Campnosperma coriaceum for example is present at Tuanan and at Suaq as well. At Tuanan this species is one of the most preferred tree species for night nests, whereas at Suag this species is almost never chosen. At Suaq C. coriaceum is a bit less common, but still the difference in usage is striking. Such observations suggest that preferences are passed on by cultural transmission, e.g. as infants learned from their mothers which tree species are most suitable for nest building. These preferences are then probably mainly based on structural properties of trees, like the presence of vertical branches, flexibility and solidity of branches and the amount and size of leaves – as such parameters determine how easily a secure and stable nest can be constructed. It would also be guite simple to test this hypothesis: long-term data on nesting preferences of a population should reveal whether infants, after becoming independent, prefer the same tree species as their mothers. If they do so, this would clearly hint at a transfer of knowledge about nesting trees.

Despite the negative result for tree species some important improvements compared to tests at Tuanan were made for the test set-up.

First, tests were not carried out on platforms but instead mosquito traps were raised into trees to the mean nesting height of orangutans. Second, mosquito traps were positioned deeper in the forest, in an area where orangutans regularly were encountered and also freshly constructed nests were found. Also a larger amount of branches and leaves than at Tuanan was used to prepare the basket and the mosquito trap inside the basket, so that the product in the end considerably resembled a (rather exposed) orangutans' nest. This way the test set-up is much better comparable to the conditions an orangutan is subjected to at night in a nest.

Another advantage of the study at Suaq was that mosquito numbers were much larger. In total about 25.000 mosquitoes were caught over a period of six months. At Tuanan in contrast, during the study of Hermann (2010) only 3.000 mosquitoes were captured during a similar period. For the repellency tests the mean number of mosquitoes caught per trap ranged between more than 100 (in September 2010) and 25 (in January 2011). At Tuanan, in contrast, on average not more than 10 mosquitoes were caught per trap (Hermann, 2010). High numbers of mosquitoes improve statistical power to identify differences in mosquito attraction between tree species – if such effects are present. Low mosquito numbers always were a huge problem at Tuanan as consequently only small differences between test and control trap were found. This made tests prone to stochastic differences in mosquito abundance and led to less convincing results.

A possible disadvantage of the test set-up in the forest on the other hand was that catching results of traps could not definitely be ascribed to the applied branches and leaves. Within the forest there were a lot of factors which could not be controlled and might have influenced mosquito abundance and foraging. The availability of mosquito prey or suitable breeding places, for example, can change very quickly and might contribute to the amount of mosquitoes which are present within a certain microhabitat. Often mosquito catches of subsequent nights with very similar climatic conditions and weather varied greatly which suggests that there are a lot of unknown factors which act upon mosquito numbers. The potentially repelling effect of plastic leaves complicated the variation in catching results even more.

To fully exclude the existence of mosquito repelling substances in tree species at Suaq it might therefore be useful to test tree species more directly. For example in an approach where mosquitoes are forced more directly to choose between different leave samples under controlled conditions. If for any tree species a significant repelling effect can be found this tree species could afterwards still be tested in a set-up within the forest.

Testing of mosquito repellents, whether in the laboratory or in the field, usually is performed using biological assays, corresponding to standard methods of the World Health Organization (WHO) or the American Society of Testing and Materials (ASTM). According to these testing guide lines a certain area of a human test subjects' skin, usually the forearm, is treated with an ethanolic solution of the repellent and then exposed to mosquitoes – either to caged ones in case of laboratory tests or to natural mosquito populations in case of field tests. Alcohol should be used as a negative control and DEET as a positive control. Then the number of mosquito bites within a certain period is recorded (Barnard et al., 2007). As orangutans can only protect themselves with leaves and branches of tree and liana species such standard methods of course cannot be applied in this manner. Instead a modified device of the "repellometer", introduced by Dogan et al. (1999) could be used.



Schematic design of the repellometer.

Fig. 4-1: Schematic design of the repellometer by Dogan et al. (1999) Mosquitoes are introduced into the median chamber and have the option of moving into a proximal chamber toward the stimulus, of moving away into a distal chamber, or of remaining in the median chamber.

This device was designed to discriminate between inhibition and repellency of mosquitoes and basically allows mosquitoes to either move away or towards the stimulus (Fig. 4-1). Tree and liana species might be tested in a similar way, either by testing one species at a time or by comparing each species to a control. Repellency could be determined by either counting mosquitoes in the respective chambers or, when adding a human test subject, by counting mosquito bites.

For the justification and conduction of further experiments it also remains to be clarified to what extend wild orangutans actually suffer from mosquito-borne diseases. If the selective advantage of mosquito-avoiding behaviour is only small such behaviour spreads slower and is maintained in only few cases. Further studies which investigate parasite load of wild orangutan populations are necessary to conclude if orangutans really benefit from mosquito avoidance.

A more detailed observation of sleeping behaviour might help understanding the necessity of avoiding parasites during nesting as well. In wild animals such observations usually are not possible as nests are build too high and shortly before sunset. Instead captive animals could be observed: Do captive orangutans for example adjust their sleeping behaviour to the presence of mosquitoes as well, maybe by sleeping in a posture which protects hair-less parts of the body? It seems plausible that orangutans hide sensitive parts of their body, like the face and hands, from mosquito stings when other parts are protected by their pelage. Such behaviour might be are more direct response to the presence of mosquitoes and probably is effective as well.

For the test of liana species results were much more stable and distinct. Here a significant difference between test and control traps was found for Akar melinjo. Also for Akar kekait altogether notably fewer mosquitoes were caught within the test traps, even though the result was not significant in the end. This results shows that the test set-up actually is useful to identify leaves which are less attractive for mosquitoes. Test conditions for tree and liana species were exactly the same and also the amount of applied leaves was comparable. Different results for tree and liana species therefore can not be ascribed to variations of the set-up.

The repelling effect of Akar melinjo surely is the most interesting finding of this study. Especially in regard to inclusion of liana species into nests: Akar melinjo and Akar kekait were nearly exclusively included in nights of rainfall, when very likely more mosquitoes are around (see 3.2.1). This is a very promising observation and deserves further investigation.

For tree species it is suggested that secondary compounds of branches or bark might be responsible for repelling mosquitoes which possibly are released when orangutans bend and break branches during nest building. Lianas, in contrast, are more woven into the nest or nests were just build on top or beside a large cluster of the liana. This suggests that compounds on the surface of lianas are most likely already sufficient to influence mosquito foraging. It may also be possible that rain is necessary to dissolve certain substances on the surface of leaves before they develop an effect on mosquitoes. The tests with liana species however were carried out during dry and rainy nights and the repelling effect was found during dry nights as well.

A literature survey for the two liana species revealed that Akar melinjo (botanical name: *Rourea minor*) contains some weak antimalarial compounds. Samples made from stems of this liana species showed a weak in-vitro activity against *Plasmodium falciparum* (Zhen-

Dan He et al., 2006) and in Vietnam and Laos a decoction of plant parts of this liana is used to treat dengue fever (Bouamanivong, 1999). The medicinal effect of Akar melinjo against *Plasmodium falciparum* however does not explain its repelling effect on mosquitoes – instead it hints at self-medication in orangutans. This is supported by several studies which attribute antimicrobial and anti-inflammatory activity to other liana species of the family Connaracea to which *Rourea minor* belongs (Akindele et al., 2007). A screening of plants from Riau Province, Sumatra reported that a mixture of leaves and stem parts of *Rourea mimosoides* showed antimicrobial activity (Grosvenor et al., 1995).

Regarding the effect of lianas I suggest to be cautious labelling them as "mosquito-repelling" as this term implies a very strong effect and an active process in which mosquitoes are chased away. Instead it is more acceptable that orangutans use lianas to conceal their presence, respectively their smell, from mosquitoes, which is a rather passive process. A mechanism for this "masking" was recently discovered by Turner et. al (2011) who describe how a certain chemical (2,3-butanedione) makes it harder for mosquitoes to detect their prey by disturbing special CO_2 detecting neurons. If a similar mechanism works for liana species this is a conceivable explanation for why fewer mosquitoes were found in traps covered with lianas.

In summary, hypothesis 1a can be rejected for tree species at Suaq, for the liana species tested, however, the hypothesis is supported by the data.

The investigation of structural parameters was only done on a very basic level and therefore could not be analyzed in more detail. The main difference between the two preferred tree species (Ubar and Puin) compared to the neutral (Meranti batu) and rather avoided one (Rengas) was the number, diameter and growth of the main branches of these tree species. While trees of the species Ubar and Puin always have many, rather thin branches, Meranti batu and Rengas are characterized by few, large main branches. Also, the clustering of foliage is more pronounced for Meranti batu and Rengas. Thus, orangutans at Suaq might prefer regular foliage and growth of branches over large branches with leaf clusters. Rengas, however, most likely is chosen less often compared to its availability in the forest, due to the acrid sap inside the branches.

More extensive and detailed data collection on structural parameters of nesting trees at Suaq is needed to conclude whether orangutans prefer some tree species over others because of structural advantages (hypothesis 1b).

4.1.2 Mosquito abundance and exposure of nests

Exposure tests could only be conducted to a limited extend as originally planned since one SKYWATCH-device broke down. Nevertheless, some interesting new findings were achieved as for the first time mosquito numbers at different positions within a tree were measured. It was assumed that more exposed nests, simulated by a trap in an open location within the tree, are a better protection against mosquitoes than an unexposed nest. At the beginning of exposure tests it seemed as if there were indeed less mosquitoes in a rather exposed position within the tree (see appendix, table 7.3). This effect however vanished as the test proceeded so that in the end the number of mosquitoes in both positions overall was nearly the same (see Fig 3-13).

The result of this test implies that the exposure of the trap is not related to the amount of mosquitoes that was caught. This means that the exposure of a nest does not influence the number of foraging mosquitoes at the nest. It seems that in contrast the extended surrounding determines mosquito occurrence, namely by the amount of vegetational cover and the presence of wind gusts: As the test in a quite open location within the forest showed, considerably less mosquitoes are present in such areas. This result however could not exclusively be ascribed to the density of vegetation because tests at the open location were carried out when generally fewer mosquitoes were caught (February 2011). Simultaneous measurements at both, open and dense, locations are necessary to exclude that other influences (like seasonal influences, in this case) are responsible for differences in mosquito numbers.

Yet, also during initial mosquito trapping tests it was my impression that the density of vegetation in a certain area of the forest strongly influences mosquito abundance: one location (U1250, see Fig. 2-7) for example had to be abandoned as always insufficient mosquitoes were caught there to gain useful results. And this location seemed to offer less vegetational cover as well; tree density was lower and mainly large trees without a mediumheight canopy were predominant.

A possible explanation for this difference in mosquito occurrence might be provided by wind measurements: the comparison between the location of dense vegetation (J25) and a rather open location (U1100) showed that the amount of wind gusts as well as velocity of these gusts is higher at the open location within the forest. Mosquitoes need sufficient vegetation for directed flight as they generally are characterized by rather poor flying skills (Bidlingmayer, 1967). Less vegetation and consequently more air movement interfere with

mosquito foraging, possibly also due to enhanced dilution of host odours (Stimulus dilution model: Hoffmann and Miller, 2003).

For nesting behaviour this results suggest that orangutans should proceed to rather open areas with less dense vegetation in order to avoid mosquitoes. If that was the case there should be clusters of nests in certain areas of the forest, especially during times of high mosquito density.



Fig. 4-2 Spatial distribution of nesting events during the study period. GPS-data for 56 nests is presented

As illustrated in Fig. 4-2 such clusters might actually exist at Suaq. Two possible clusters could be identified based on GPS-data: one quite distinct cluster (cluster 1) and another another rather dispersed cluster south of trail U (cluster 2). That orangutans preferred to nest in the area of cluster 1 already became apparent during the study period as nesting sites were quite close to another. Two adolescents and three unflanged males built their nests there, within an area of only 200m². Nesting events were independent of each other and four out of five nests were constructed during October and November, thus during the mosquito high-season. And indeed this area was characterized by a rather sparse tree density with predominantly large or medium-sized trees and without a dense understorey. Nesting there consequently might serve as a measure to avoid high mosquito density. Cluster 2 is rather dispersed (400m²) but it was situated in an area where late exposure tests were carried out (U1100) – thus within an area which was actually selected for its low tree density and where measurements showed that quite a lot of wind gusts occur. This

strongly suggests that in this area less foraging mosquitoes might be around as well. Nest builders of this cluster came from all sex/age classes (3x adolescent, 1x mother/infant, 2x unflanged, 1x flanged).

Sample size of available GPS-data for this project however was quite small (56 nests), thus more data is necessary to ensure that such clusters are stable. For Tuanan no such clusters could be found (Florez 2007), yet this might be due to a rather homogeneous forest structure at this site. One must also consider that travelling for orangutans is quite costly so that they are restricted in searching for a suitable nesting site. These costs probably strongly influence where orangutans finally build their nests: sometimes it might simply be too costly to travel a long distance for a better nesting site. Further, nesting in a certain area might also be influenced by a range of other factors, like availability of food. To decide whether this is of importance for the selection of nest sites, one could determine the distance of each nest to the last feeding tree in the evening and the first feeding tree in the morning, respectively, like it was already done by Gibson (2005).

For most of the nests at Suaq it was recorded whether the nesting area in a radius of 100-200m was rather open or dense, however only as a subjective impression without any measured parameters. According to this data most nests were situated in rather open areas, implying that orangutans in general prefer such areas for nesting. Collection of more detailed data for this parameter however would be difficult because an assessment for the tree population within a radius of 100-200m around the nest has to be generated.

A connection between nesting in rather open areas and mosquito avoidance was already suggested by Florez (2007). He argued that several initial studies on orangutan behaviour mistook such exposed nests as good look-outs to detect approaching predators which seems unlikely since orangutans are largely unalert whilst inside the nest. Instead, Florez pointed out, nesting in a thermoregulatory disadvantageous area might be accompanied by a decrease in mosquito numbers due to the influence of wind on mosquito flight and for-aging behaviour. As a recent reference he cites Gibson's work from Sabangau (2005) who found that orangutans of that population preferred nesting sites of low canopy health and poorly interconnected trees. Results of the conducted exposure tests at Suaq support this idea and provide a foundation for further investigations.

Based on this results hypothesis 2 has to be rejected: whether a nest is build at a rather exposed or unexposed position within the tree does not influences mosquito occurrence at

the nest. If, however, instead of the immediate exposure of a nest the extended surrounding is compared in a similar manner, one might find differences in mosquito numbers.

4.1.3 Mosquito abundance and height of nests

Height tests of mosquito abundance were conducted to resolve whether variation in nesting height by orangutans might be connected to mosquito avoidance.

The results showed that distinct heights differ in the amount of mosquitoes - especially at lower positions (5m) significantly fewer mosquitoes were present. Mosquito numbers at 15-25m yet did not differ significantly. Therefore, it can be assumed that higher nests are not necessarily a better protection against mosquitoes, which was proposed in previous studies (Largo, 2009 ; Hermann, 2010).

An increase of mosquito abundance towards higher locations was found at Tuanan as well. There, heights of 2-10m were compared and most mosquitoes were caught at 10m. The trapping tests at different heights therefore show that at Suaq and at Tuanan mosquitoes also occur at high sites, seemingly even in higher numbers. For orangutans this means that mosquito numbers might even increase at higher nest sites.

Height, however, is only one of many factors which determine mosquito abundance. It is possible that nests at higher places are exposed to more wind, which is very likely accompanied by a decrease in mosquito numbers. This should however not uniformly be assumed for all nests which are build some meters higher: if a nest is constructed in the middle of a tree, a difference of a few meters in height probably does not notably influence the number of mosquitoes at the nest. An increase of mean nesting height during mosquito high season should therefore not necessarily be interpreted as an attempt to avoid mosquitoes (Hermann, 2010).

The location of mosquito traps within the forest seemed to be much more influential than their height. Despite great differences in height, during some nights nearly the exact same number of mosquitoes was caught in traps at different locations. An example: during the night of September 21th 2010 75 mosquitoes were caught at a height of 2m at one location while 70 mosquitoes were found at a height of 20m and 86 mosquitoes at 15m height at the location of height tests (U 900). This is in line with results of exposure tests which also

suggest that the location within the forest and associated differences in the density of vegetation are crucial for mosquito abundance of a certain area.

It should be possible to distinguish between the influence of height and other factors by running mosquito traps parallel at the same height in different locations. Other possible influential factors like the density of vegetation, amount of wind gusts and standing water etc. should be recorded for each location, so that the data-sets can be compared for all these factors as well.

There was a lot of variation in mosquito catches of traps in subsequent nights – even if climatic conditions were stable. For example during a dry week in December mosquito catches at 15m varied between 25-100 individuals, without any detectable pattern. Thus, there seem to be a lot of unknown factors influencing mosquito presence. Consequently, this will make it very difficult for orangutans to predict under which conditions and where mosquito numbers are high or low and search nest sites accordingly.

4.1.4 Mosquito abundance dependent on rainfall and standing water

Results of the weather record showed surprisingly low conformity with mosquito numbers. Considering the whole study period, neither rainfall nor the amount of standing water within the forest turned out to be good predictors of mosquito abundance. There seem to be a lot of further factors involved which all have to be suitable to result in a high mosquito density.

This obviously was the case at the beginning of the study period: during the summer months before the study started it had been very dry, as indicated by the extremely low water level of the river. Then in August and September 2010 there were some nights of heavy rainfall followed by a couple of dry days. This seemed to be the optimal conditions for mosquitoes, since numbers increased steadily and reached a peak by the end of September. Then, at the beginning of October 2010 it rained heavily for several days which caused a flooding of parts of the forest. Mosquito numbers immediately decreased drastically, which confirms that the water level within the forest is of crucial importance for mosquito survival. A possible reason for this at Suaq is rather exceptional: a lot of pools of constant standing water are inhabited by a species of small fish which, among others, feeds on mosquito larva. Water pools containing these fish always are completely free of mosquito larva. Yet, water pools usually are isolated from each other which restricts the access of fish. When the forest was flooded, isolated water pools converged, allowing the fish to freely move within the forest and feed on mosquito larva which before were not approachable. This possibly led to a rapid decrease in mosquito larva. The loss of larva may explain why the number of adults decreased some time after the flood but not why the number of adult foraging mosquitoes decreased immediately. Nevertheless, these fish, in combination with rainfall, could play an important role in the ecology of mosquitoes at this particular research site.

Later on, the water level within the forest decreased (October) and increased (November) again due to variations in rainfall. Mosquito abundance, however, did not change accordingly to the water level within the forest but decreased steadily. In December 2010 and January 2011 it was extremely dry which was also reflected by very sparse mosquito catches. The constantly high water level in November 2010 thus did not lead to a shifted increase of mosquito density, maybe it again promoted the distribution of fish. Afterwards it probably was too dry as the water level in the forest nearly reached the lowest possible level at all measuring points by the beginning of January 2011. During the last weeks of the study period mosquito numbers did not increase any more even though weather conditions for mosquito proliferation improved a lot by mid-January. This indicates that besides rainfall, water level and fish there are other factors which restrict mosquito proliferation.

Overall, there seemed to be a distinct seasonal trend: large numbers of mosquitoes developed shortly after the end of the dry season followed by a steady decrease. It would be very interesting to know if this is a general pattern or whether the pattern could change in case of another distribution of rainfall, for example if the forest was not flooded.

Besides this long term effects of weather parameters, it was observed that the number of foraging mosquitoes could change very quickly, dependent on rainfall at night: mosquito numbers were correlated with the amount of rainfall of respective nights (see 3.1.2). It did not take approximately two weeks for mosquitoes to develop after a period of increased rainfall, like it was the case at Tuanan (Hermann, 2010). Instead it seemed as if mosquitoes waited during dry nights and then started foraging immediately after rainfall. This led to large differences in foraging mosquitoes between nights and suggests that orangutans have to decide how much of mosquito protection is necessary anew every evening.

The positive correlation between mosquito numbers and the amount of standing water which was found after a two-weeks shift has to be treated with care. Neither data for

mosquito numbers within the forest nor data for standing water was continuous – and without such continuous data it cannot conclusively be stated that mosquito numbers actually oscillate that regularly. It might be that other patterns exist, but were not detected because of the gaps in data collection. That mosquito numbers decreased independently of variations in standing water is also rather contradictory to any strong relation between these two parameters. It should therefore not necessarily be concluded that the amount of standing water influences mosquito numbers two week after a given date.

That the interaction between rainfall and mosquitoes abundance usually is not a very simple one was recognized by several other studies as well. Shaman et al. (2007), for example, pointed out that "the physical effects of precipitation on environmental conditions are multiple, and the responses of different mosquito species to these effects are varied. As a result, it is often difficult to establish significant and stationary relationships between the amount of precipitation and mosquito abundance". It has to be noted that such studies usually cover several years, using means of monthly catching results and examine large regions, while this study only lasted about six months and is based on daily catching results of a very small area. Consequently the rainfall-mosquito interaction was surveyed on a very small scale which results in a lot of variation.

In summary, hypothesis 4 was not confirmed: the relationship between mosquito abundance and the amount of standing water within the forest was found to be quite complex and unpredictable. Further influences, like the flooding of the forest and the foraging of fish seem to be key factors, which also affect mosquito larva.

4.2 Nesting behaviour

Data on orangutan nests was collected to investigate differences in nesting preferences between sex/age classes or individuals (hypothesis 3) and to relate those differences to possible mosquito avoidance strategies. Data from Tuanan suggested that some differences in nesting preferences can, at least partly, be ascribed to stronger mosquito avoidance ance of certain sex/age classes (Hermann, 2010).

4.2.1 Relevance of nesting features to mosquito avoidance

As discussed above, a lot of nesting parameters at Suaq however seem to be unrelated to mosquito avoidance. Therefore first the relevance of investigated nesting features to mosquito avoidance will be discussed. Afterwards, for nesting features which obviously are unrelated to an adaption to mosquitoes, alternative explanations for findings will be suggested.

For the selection of nesting trees it was assumed that tree species with mosquito-repelling properties are generally selected more often and especially when mosquito density is higher, for example during rainfall. Results of repellency tests however show that none of the predominant nesting tree species is mosquito-repelling. Therefore choice of nesting trees is very likely not based on any mosquito-related properties of tree species tested but rather can be ascribed to structural advantages of some tree species.

It was proposed (Hermann, 2010) that nesting height is adjusted to mosquito occurrence: higher and more exposed nests are located at rather windy locations and therefore offer a better protection against mosquitoes than lower nests. Tests with mosquito traps at different heights in contrast showed that mosquito abundance was lower at 5m than at 15m or higher, so that it is unlikely that higher nests actually reduce exposure to mosquitoes. Higher nests of certain sex/age classes or individuals thus probably do not indicate an attempt to avoid mosquitoes.

Exposure of nests is thought to influence mosquito numbers through the amount of wind at the nesting site (Largo 2009, Hermann 2010). Results of respective tests however suggested that the immediate surrounding of a nest hardly influences its exposure to wind and consequently also does not determine the amount of mosquitoes at the nest. Differences

in the exposure of nests between sex/age classes or individuals thus very likely do not reflect differences in vulnerability to mosquitoes.

For pitcher plants it was assumed that the presence of such plants is accompanied by an increase of mosquito abundance. No actual tests with mosquito traps were carried out to check this hypothesis, yet it anyway seemed that orangutans did not adjust their nesting behaviour to the presence of pitcher plants. Most nests were build in areas without any pitcher plants but this rather reflected the low distribution rate of the plant. Pitcher plants usually occurred in patches, then at high density, but there were no large, continuous areas in which the plant was present at similar densities. Height and exposure of nests were hardly adjusted to the presence of pitcher plants, only mother/infant pairs and unflanged males showed slight adjustments in height. Mother/infant pairs chose to build more exposed nests in the presence of pitcher plants while unflanged males showed the opposite tendency. However, none of the differences was significant. This suggests that pitcher plants only play a minor role for the choice of height and exposure of nests. It was also my impression that the amount of pitcher plants hardly influenced mosquito abundance, probably as most mosquito species use the standing water of the ground for breeding and not pitcher plants.

The amount of standing water at the nest site might be a better predictor of the amount of mosquitoes within a certain area and consequently might be more relevant for mosquito avoidance. At first sight the results also guite nicely seem to reflect the assumed differences in vulnerability to mosquitoes: adolescents and mother/infant pairs nest in rather dry areas whereas flanged and unflanged males build their nests in areas with more standing water (see Figure 3-11). Furthermore, many nests of flanged males were built in areas close to the river, which are characterized by a wetter ground and often accompanied with a higher mosquito density. For the overall result it, however, has to be considered that the amount of standing water was strongly dependent on the amount of standing water within the forest during that time (see 3.3.7). Whether orangutans really had the possibility to find a dry site for nesting thus was mainly determined by the seasonality in rainfall and less by own preferences. For the interpretation it therefore has to be considered during which part of the study period nesting data for the different sex/age classes was collected. The data revealed that most of the high values for standing water originated from November, when the water level within the forest was nearly constantly high. During that time a comparatively large amount of data for nests of unflanged males was collected which explains the high mean value for this sex/age class. In contrast, not a single nest of a mother/infant pair was measured during that time of a high water level. This bias of data collection thus very likely also accounts for the low mean value of mother/infant nests. The amount of flanged male nests was neither larger nor smaller during November, so that their mean value more likely is based on the fact that flanged males quite often travelled and also nested in areas close to the river. Such a trend indeed might imply that large animals are less disturbed by the high mosquito density close to the river. Yet, that flanged males built many nests in such an area and other sex/age classes rather avoided the area probably has some different reasons as well: flanged males, for example, might travel more within the floodplain because they are more confident travelling in rather open areas with lower tree densities and also mostly smaller trees than adolescents and mother/infant pairs. Also food preferences or food availability often play an important role in travelling routes of orangutans.

Altogether it seems as if the water level at the nest site also is a factor which orangutans do not, respectively can not, take into account for mosquito avoidance, possibly because their choice is quite restricted by seasonal influences in rainfall.

The inclusion of lianas into nests in contrast to all other nesting features, very likely is a factor which is relevant to mosquito avoidance. Certain liana species seem to intentionally be included into nests and this mostly during nights of rainfall when mosquito numbers usually increase. That this possibly is an attempt to minimize exposure to mosquitoes is supported by repellency tests which found one liana species, Akar melinjo, to be mosquito-repelling. The result for the repellency test for Akak melinjo was significant and the comparison of inclusion between rainy and dry nights showed a trend as well.

In six out of eight cases of active inclusion of liana species nests were constructed by adolescents which implies that this behaviour is not equally often found in all sex/age classes. A preference of adolescent individuals for inclusion of lianas might confirm that this sex/age class is especially vulnerable to threats accompanied by mosquitoes. However, mothers with small infants should then also show liana inclusion, which was not observed. Yet, during the study period most of the nests investigated were build by adolescents (n=32) and fewer by other sex/age classes, for mother/infant pairs it were 19 nests. So maybe if more nests by mother/infant pairs, or more nests of other sex/age classes in general, were examined, then inclusion of lianas would have been found more often for those other sex/age classes as well. Also, as fewer nests of other sex/age classes were measured, there were fewer cases of nests built during rainfall – and as rainfall seems to be a main trigger for liana inclusion, consequently less cases of liana inclusion were reported for other sex/age classes. The presence of this behaviour in adolescents and the absence in mother/infant pairs still is quite surprising. Young orangutans generally acquire a lot of information from their mothers, for example about dietary choices or food-processing skills (Jaeggi et al., 2008), thus it seems plausible that they acquire nest building skills from their mothers as well. Further, as four different adolescent individuals showed the behaviour of including lianas it seems very unlikely that they all invented this behaviour by themselves. Consequently mothers should practice the inclusion of lianas as well on appropriate occasions. More data is necessary to decide whether this finding is due to a bias of nests investigated or actually reflects a preference of adolescent individuals.

On the basis of findings hypothesis 3 thus is only partly confirmed: there are differences in nesting preferences between sex/age classes in terms of certain properties of the nests. Most of the nesting properties at Suaq however cannot be related to any form of mosquito avoidance – thus differences in these properties are very likely based on other reasons than differences in vulnerability to mosquitoes between sex/age classes.

Now that for nearly all nesting features the influence of mosquito foraging can be excluded, other possible explanations for the findings will be discussed.

4.2.2 Alternative explanations

Considering all nest features which were investigated, most differences were found between sex/age classes. Thus for each sex/age class quite a distinct "preference profile" can be compiled:

Adolescents on average built the highest and most exposed nests, whereby these two parameters strongly correlate. With a mean height of 20m adolescents built significantly higher nests than all other sex/age classes. Building a night nest high in the canopy generally is ascribed to predator avoidance (Hamilton, 1982), arguing that nests build in a high position enhance detection of an approaching predator and also reduce accessibility for such threats. This argumentation, however, dose not or only restrictedly work for orangutans (see page 7). An alternative explanation for such high nests might be protection against other individuals of the orangutan population. Gibson (2005) suggests that orangutans of lower hierarchical positions try to avoid confrontation and harassment through higher-ranking individuals. All adolescent individuals of this study were young females and young females are often at risk from forced copulations (Gibson 2005). Gibson reports that an adult female at Sabangau National Park, Kalimantan strongly altered her nesting behaviour during a period of harassment by a sub-adult male. Thus, it seems plausible that

lower-ranking, more vulnerable individuals are more cautious and prefer to nest at less accessible locations while they are asleep. It was also my impression that adolescents which were not yet very familiar with travelling alone and therefore less confident, tried to travel or nest in party with other adolescents or mother/infant pairs. This observation supports the idea that adolescents are more timid and therefore more comfortable in high nests.

The higher exposure of adolescent's nests is very likely to a great extend caused by nesting height: as adolescents prefer to nest high, they in return have to accept less cover for nesting.

Adolescents showed a strong preference for the tree species Ubar. In this tree species nests were very often constructed very close to the top of the tree which suggests that this tree species is especially suitable for high nests. Furthermore Meranti batu was selected more often than by other sex/age classes, yet this difference mainly is due to the preference of one individual (Chindy) who built her nests exclusively in Meranti batu.

A comparison to nesting preferences of adolescent individuals at Tuanan reveals similarities in nesting height but differences in terms of exposure: at Tuanan adolescents usually build higher nests than other sex/age classes as well, even though the difference is not as pronounced as at Suaq. With a height of about 10m they do not differ very much from mother/infant pairs or unflanged males (Herman, 2010). The trend, however, is a similar one, supporting the idea that immature orangutans are the most vulnerable animals of the population. The range of mean nesting heights at Suaq generally is wider than at Tuanan. There mean nesting heights only ranged between seven to twelve meters (Hermann, 2010), which reflects the height of trees at Tuanan.

Preferences in exposure, in contrast, differ a lot between the two sites. While at Suaq adolescents built the most exposed nests, at Tuanan flanged males prefer mostly exposed nests. This is contradictory to the assumption that larger animals are less affected by heat loss. This hypothesis implies that large flanged males have a lower surface to volume ratio and therefore radiate less body heat per kilo than a smaller individual (Largo 2009). The model nicely explained the large amount of exposed nests build by flanged males at Tuanan, but why do at Suaq rather small bodied adolescents prefer exposed nests? The heat-loss model assumes that radiation of body heat is connected to convection currents in the respective position of the nest. Results of wind measurements, however, have shown that wind gusts are rather rare within the peat-swamp forest of Suaq, especially at night. Also, not the immediate surrounding of a nest but rather extended areas determine the presence and amount of wind gusts. Thus orangutans at Suaq in general might not be affected that much by heat-loss as there hardly are any wind gusts which could lead to such an energetic loss. In case of a windy night adolescents could still pick an exposed nesting site, as long as the extended area around the nesting tree offers enough vegetational cover as protection against strong wind.

Mothers with infants on average built quite high nests as well – with a mean height of 17m they clearly rank above the height of nests by males. Similar to adolescents this might be a measure to reduce the possibility of confrontation with males who may pose a risk to them and their infants. The exposure of nests built by mothers with infants is quite similar to exposure of nests by males (see Fig. 3-23), even though nests of males are distinctly lower. Thus mothers try to construct nests at high sites which are still well sheltered. Lower nests often were designed even more concealed. This maybe reflects the particular vulnerability of infants. Tree species selection of mother/infant pairs revealed a preference for Ubar and Puin which usually are large and stable trees. Nests in theses two tree species mostly were type 1 and type 2 nests close to the main stem – thus enable stable nests at high nesting sites.

At Tuanan mother/infant pairs were also characterized by rather unexposed nests. The nests, however, were built quite low, at about the same height as unflanged males. This result quite likely simply reflects the forest structure at Tuanan: there nests of all sex/age classes lie within a range of heights of 7–12m with a mean nesting height of 8,5m (Hermann 2010). At Suaq in contrast mean nesting height is about 15m and nesting heights range from 5-25m. The forest at Suaq is more heterogenous in terms of tree heights and thus the possibilities for nesting heights are more diverse as well.

The nests of unflanged males for most nesting parameters ranged between values for flanged males and the other two sex/age classes, which reflects their hierarchical position within the population and their constitution. They are not as vulnerable as adolescents or mother/infant pairs, yet in social hierarchy they rank below flanged males. Accordingly, nests were built notably lower than the ones by mother/infant pairs but not as low as the ones by flanged males. For exposure, nests of unflanged males did not differ a lot from nests of flanged males or mother/infant pairs. That exposure values do not differ as much as nesting heights might however also be ascribed to how the index is generated and that possibilities to achieve differences in exposure are restricted. While for the nesting height orangutans can choose from a wide range of different trees, the range of exposure of nests will always be within a certain restricted span – nests with a value below 0,2 are vir-

tually impossible and a value above 0,8 is also quite unlikely. Yet, the results show that preferences for certain heights are more pronounced than preferences for nests of a certain exposure: nesting heights for individuals of a certain sex/age class were usually quite similar whereas exposure of nests varied a lot, even for nests built by the same individual. This finding implies that exposure is much more adjusted to respective conditions of the nesting site, like tree species or surrounding of the nesting tree, and possibly also to weather conditions.

Unflanged males showed a preference for type 2 and type 4 nests: most unflanged males are smaller and lighter than flanged males, thus they do not need to construct especially stable nests of type 4. For the same reason nest at higher sites are still possible while for heavy flanged males higher nest sites are critical. The tree species preferences lie in between flanged males and other sex/age classes as well: Ubar was used occasionally, otherwise other, smaller tree species were chosen. At Tuanan unflanged males show a similar nesting behaviour with a nesting height and exposure comparable to flanged males and mother/infant pairs (Hermann, 2010). At Tuanan type 4 nests are the most preferred nest type overall (Largo, 2009). This tendency however is an exception which can only be found at Tuanan and Sabangau in Central Kalimantan (Prasetyo et al., 2009).

Flanged males on average built the lowest nests (10m) and showed a strong preference for type 4 nests. This result can probably be ascribed to low vulnerability to any kinds of threats and their high body weight. Most flanged males used various smaller tree species, like Medang baru or Medang lede, for nesting by combining several trees into a nest. This behaviour very likely aims at constructing a particular large and stable nest to support the weight of a fully grown flanged male. Nesting height thus is also restricted by the availability of suitable nest sites for flanged males. Individuals of this sex/age class thanks to their body weight anyway do not have to fear attacks by predators and therefore can also afford to nest that low. Exposure of flanged male nests did not differ notably from nests of unflanged males or mother/infant pairs. Flanged males often nested in clusters of small to medium-sized trees so that even if they used a large amount of leaves and branches for cushion, still some cover of surrounding trees was present.

At Tuanan flanged males also nest lowest, at only about 6m. Their nests however are rather exposed. Maybe their nests are so far away from the canopy above that cover by vegetation at their nests is usually low. It might as well be that flanged males at Tuanan have developed other preferences than flanged males at Suaq for some reason.

An interesting difference between the two sites of Suaq and Tuanan was revealed for tree species preferences: while at Tuanan the choice of tree species is quite similar in all sex/age classes (M. blawau contributed to the majority of night nests in all sex/age classes), at Suaq there are distinct differences in tree species selection between sex/age classes. This finding might be related to more pronounced height preferences of sex/age classes and the forest structure at Suaq: as adolescents and mother/infant pairs prefer to nest rather high they choose other tree species for nesting than males who generally nest lower. Since the differences in nesting height are much larger at Suaq, tree species choices also diverge more than at Tuanan.

The investigation of liana presence at nests revealed that males, especially flanged males, clearly show less avoidance of trees vegetated by lianas. For males, trees were often covered by more lianas and liana species more often were associated with ants. Adolescents and mother/infant pairs seemed to avoid nesting sites with lianas, especially if the liana species was associated with ants (Akar pakis). The difference between sex/age classes was quite distinct which suggests that flanged and unflanged males indeed are less disturbed or less vulnerable to threats associated with insects. Nests of adolescents and mother/infant pairs usually were built higher within the tree which led to fewer or less dense vegetation of lianas at the nest site as most liana species start growing from the ground. Nests in trees with lianas however were not built notably higher, thus orangutans probably did not adjust the height of nests to the presence of lianas after selecting a tree for nesting.

Taken together it can be concluded that most differences between sex/age classes can be ascribed to the hierarchical position of individuals within the orangutan population and physical properties of the animals. Differences in nesting behaviour between the two sites of Suaq Balimbing and Tuanan in most cases reflect differences in forest structure.

4.2.3 Influence of rainfall and mosquito seasonality

Rainfall and mosquito season both affect mosquito numbers and might therefore influence orangutan nesting behaviour. Nesting height, exposure of nests and tree species selection between rainy/dry and mosquito high/low season were compared.

Rainfall seemed to influence exposure of nests: nests were built significantly more exposed during rainy nights. This is surprising, because it was assumed that orangutans try to protect themselves with more leaf cover during rainy nights. Exposure of nests was found to not affect mosquito numbers at the nest, therefore the attempt to avoid mosquitoes by means of a more exposed nest can be excluded. Maybe the exposure of nests during rainy nights is connected to tree species choice: the comparison also revealed, that Meranti batu is chosen more often during rainfall and Meranti batu was found to offer comparable few cover (see Fig. 3-25). Thus, nests might be more exposed during rainy nights because they were constructed in Meranti batu. Tree species selection during rainy nights might also be related to occurrence of lianas on trees. Since orangutans included lianas more often during rainy nights, they might have selected certain trees due to lianas growing on these trees, not because of the tree species itself.

The comparison of mosquito high and low season also revealed differences in tree species selection and exposure while nesting height did not vary. Meranti batu was selected significantly more often during the mosquito low season. This is in line with results of repellency tests, which identified Meranti batu as mosquito attracting compared to the other three tree species. Thus, orangutans might use Meranti batu more often during times of low mosquito abundance because of its mosquito-attracting properties. Further, the increased usage of Meranti batu during the mosquito low season partially was caused by one focal (Chindy) who was only followed during mosquito low season and built her nests exclusively in Meranti batu. Her preference already accounts for four out of ten nests during the mosquito low season, the other six were build by several other individuals. That they used Meranti batu more often than before may be connected to the avoidance of fruiting trees, since during that time Puin produced fruit and also Ubar began to fruit.

Exposure of nests was found to be significantly higher during the mosquito low season. This is contradictory to the assumption that more exposed nests are build during times of high mosquito numbers (Hermann, 2010). Yet, results of exposure tests of this study showed that exposure is unlikely to affect mosquito numbers at the nest. Differences between the mosquito high and low season therefore are more likely to originate from the contribution of different individuals to each respective season.

Data from Tuanan was more in line with proposed hypotheses: one tree species, which was identified to be mosquito-repelling, was used significantly more often for nesting during the mosquito season (Hermann, 2010). Also nesting height changed accordingly to expectations: Some sex/age classes built significantly higher nests during the mosquito sea-

son (Hermann, 2010). The definition of high and low season , however, was based on rainfall measurements, plus mosquito numbers generally were a lot smaller. Therefore a comparison between the two sites concerning differences between high and low season is hardly conclusive.

4.3 Conclusion

The aim of this study was to relate nesting features, especially tree species preferences, to avoidance of mosquitoes. To investigate this, several tests with mosquito traps were carried out and data on nest building behaviour of this population was gathered.

The main test set-up was used to check preferred nesting trees for possible mosquitorepelling properties. The hypothesis under investigation was that tree and liana species used for nesting differ in their ability to repel mosquitoes, based on the secondary compound properties of their leaves and bark. Therefore, the influence of leaves of several tree and liana species on mosquitoes was compared to the effect of plastic leaves.

Results of this test quite clearly show that the selection of certain tree species for nesting is not related to mosquito-repelling properties of preferred tree species. For none of the most popular tree species an indication of mosquito-repelling properties could be found. Instead, nesting trees might be selected due to structural advantages. A basic analysis of structural parameters for the four most popular nesting tree species revealed that orangutans at Suaq might prefer tree species with many, rather thin branches and regular foliage over tree species with rather few, large branches and leaf clusters. More extensive and detailed data on structural parameters, however, are needed to conclude whether structural advantages actually are the main reason for tree species preferences at Suaq.

The most interesting finding of this study was the identification of a mosquito-repelling liana species: Akar melinjo. For this liana species significantly less mosquitoes were caught inside the test traps, compared to a control with plastic leaves. Investigation of nests revealed that orangutans include this liana species mostly during rainy nights, when mosquito density is higher. This is a very promising observation and deserves further investigation.

Further nesting features, like the height of a nest within the tree and exposure of a nest to wind, are suggested to be related to avoidance of mosquitoes as well (Hermann, 2010). Therefore, additional tests with mosquito traps were carried out and compared to the nest-building behaviour of orangutans of this population. Test with mosquito traps at different heights found significantly fewer mosquitoes at low locations (5m) compared to higher ones (15, 20, 25m). Differences in nesting height of orangutans, however, were best predicted by the sex/age class of the nest builder. This suggest that nesting height is mainly driven by the hierarchical position of individuals within the population and not by mosquito

avoidance. The results of comparisons between rainy/dry nights and mosquito high/low season support this interpretation: orangutans did not adjust nesting height to conditions of higher mosquito density.

Another test set-up with mosquito traps in positions of different exposure showed that the position within a tree is not related to the amount of mosquitoes in respective positions. Thus, exposure of nest very likely is not related to mosquito avoidance. However, the enlarged area around the nesting site seemed to influence mosquito occurrence. More open areas with a less dense vegetation appeared to be avoided by mosquitoes as they offer less cover and probably are more windy.

The exposure of nests was found to be very variable, also for the same individuals, indicating that exposure is always adjusted to respective conditions of the nesting site, like tree species or surrounding of the nesting tree, and possibly also to weather conditions.

Further, mosquito-related parameters of the nest and nest site were investigated, e.g. the amount of standing water at the nest site and the presence of pitcher plants. For these factors no distinct influence on nesting behaviour could be found either. For nest site selection other factors might be more influential, like the distance to feeding trees or energet-ic constraints to travelling.

Finally, the investigation of the relationship between mosquito abundance and rainfall and standing water within the forest revealed a quite complex interaction. Mosquito numbers declined after the study started, independent of the amount of standing water. Rainfall only had a short-term effect on mosquito numbers. Further influences, like the flooding of the forest and foraging behaviour of fish seem to be key factors which affect mosquito larva.

The comparison of this study to tests carried out at Tuanan is only to a limited extent useful, since test set-ups were fundamentally different. For nesting features, like nesting height or exposure, most differences between sites can probably be ascribed to differences in forest structure.

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7) Appendix



7.1 Growth of lianas on tree species

Fig. 7-1: The amount of nests where lianas were present and absent for the different tree species

Some tree species were vegetated more often by lianas than others. Figure 7-1 shows that Ubar quite often was vegetated by lianas, if so however with rather few (Figure 7-2). Rengas and Meranti batu were less often vegetated by lianas, yet the amount of lianas was larger, always class 2 (6-10 lianas) or class 3 (more than 10 lianas). For Puin in contrast only one out of eleven nesting trees was vegetated by lianas and in that cases it were only very few lianas (class 1). Thus selection of a certain tree species for nesting also to some extend determines the likelihood that lianas are present at the nesting site.



Fig. 7-2: The amount of lianas present at the nest for the different tree species

7.2 Height of nest types

There was a statistically significant difference in height between the four classes of nest type as determined by a one-way ANOVA (F(3, 79)=5,27; P=0,002). A Scheffe post-hoc test revealed that this difference is mainly based on the low height of type 4 nests: those were significantly lower than type 1 (P=0,008) and type 2 (P=0,045) nests (Fig. 7-3). For type 3 there were only three nests and thus no statistically significant differences to other nest types could be found.



Fig. 7-3: The four nest types in relation to nesting height Type 1 and type 2 nests were usually constructed at about the same height, while type 4 nests were built significantly lower.

7.3 Raw data for repellency tests

Table 7-1: Catching results for Ubar and Rengas for all trouble-free nights The tables 4-6 illustrate how catching results for repellency test varied: during most nights more mosquitoes were found inside test traps, sometimes however more inside control traps. Notice how mosquito numbers declined by the end of the study period. This probably explains why for Rengas overall fewer mosquitoes were caught inside the test traps.

Test night -	Ubar		Re	Rengas		
	Test trap	Control trap	Test trap	Control trap		
1	31	31	28	62		
2	17	9	96	29		
3	17	15	25	10		
4	85	94	43	34		
5	384	254	18	43		
6	104	55	102	47		
7	34	16	22	29		
8	22	12	13	63		
9	18	17	17	10		
10	16	5	10	10		
11	27	18	35	23		
12	20	31	10	17		
13	45	22	7	27		
14	30	21	6	13		
15	14	7	10	44		
16	27	6	0	55		
Sum	891	613	442	516		

Test night	Puin		Meranti batu
	Test trap	Control trap	Test trap Control trap
1	75	62	108 37
2	25	27	177 50
3	36	16	65 12
4	25	25	161 81
5	25	13	64 37
6	7	7	99 27
7	9	5	31 25
8	115	49	31 61
9	26	42	80 39
10	40	2	16 48
11	49	3	31 2
12	5	0	32 7
13	8	1	
Sum	445	252	895 426
Test night	Akar melinjo		Akar kekait
	Test trap	Control trap	Test trap Control trap
1	2	13	17 39
2	30	64	4 49
3	48	53	16 13
4	60	65	7 9
5	31	51	15 65
6	32	24	26 23
7	17	27	18 6
8	13	9	11 7
9	16	29	
10	14	17	
11	14	28	
12	5	20	

Table 7-2: Catching results for Puin, Meranti batu and the liana species Akar melinjo and Akar kekait

7.4 Raw data for the exposure test at J25

Test night	Exposed	Unexposed
1	7	17
2	39	60
3	40	46
4	34	45
5	34	36
6	25	22
7	21	25
8	30	17
9	7	17
10	5	3
11	19	13
12	10	21
13	12	5
14	18	3
15	7	2
16	2	23
17	31	37
18	16	16
19	11	9
20	12	8
21	5	2
Sum	385	427

Table 7-3: Results of the exposure test at J25 Mosquito numbers generally were lower at this test site

7.5 Data phenology plot

Table 7-4: Phenology plot of the three transects U,X and H – the data give an approximation to which proportion each tree species contributes to the body of the forest. Each transect is made up of about 500 trees; prepared by Andrea Permana, 2010

Local name	Saiantifia nama	Family	Trees	% in plot
		гашну		
Rengas	Gluta renghas	Anacardiaceae	375	25,07
Jambu air	Syzygium densiflora	Myrtaceae	139	9,29
Meranti batu	Shorea teysmanniana	Dipterocarpacreae	126	8,42
Ubar	Horsfieldia polyspherulla	Myristicaceae	98	6,55
Resak biasa	Parastemon urophyllus	Chrysobalanaceae	97	6,48
Medang baru	Litsea gracilipes	Lauraceae	75	5,01
Resak payo	Dialium patens	Fabaceae	70	4,68
Malaka	Tetramerista glabra	Tetrameristaceae	64	4,28
Puin	Sandoricum beccarianum	Meliaceae	64	4,28
Kuli jambu	Garcinia sp.1	Clusiaceae	59	3,94
Mangga hutan	Mangifera gracilipes	Anacardiaceae	37	2,41
Gersang	Jackiopsis ornata	Rubiaceae	26	1,74
Medang kersik	Platea excelsa	Icacinaceae	24	1,6
Bunga piring	Dillenia pulchella	Dilleniaceae	20	1,34
Medang glue	Nothaphoebe umbellifrora	Lauraceae	17	1,14
Pala hutan kecil	Gymnacranthera contracta	Myristicaceae	17	1,14
Tapis batu	Garcinia havilandii	Clusiaceae	17	1,14
Sepang	Sterculia oblongata	Sterculiaceae	16	1,07
Medang lede	Elaeocarpus petiolatus	Elaeocarpaceae	12	0,8
Kayu kacang	Xylopia malayana	Annonaceae	11	0,74
Medang nangka	?	?	11	0,74
Tampu licin	Macaranga hosei	Euphorbiaceae	11	0,74
Timah-timah kecil	?	?	8	0,53
Medang hitam	?	?	7	0,47
Basong	Alstonia pneumatophora	Apocynaceae	6	0,4
Jambu lepo	Syzygium Ocneocarpum	Myrtaceae	6	0,4
Medang singkat	Campnosperma auriculatum	Anacardiaceae	6	0,4
Sebras	?	?	6	0,4
Cempedak	Artocarpus teysmanii	Moraceae	6	0,4

Peradah	Garcinia celebica	Clusiaceae	5	0,33
Kayu karing	Eugenia sp.1	Myrtaceae	5	0,33
Cemengang	Neesia aquatica	Bombaceae	3	0,2
Kopi-kopi kecil:	Gynotroches axillaris	Rhizophoraceae	3	0,2
Resak ubar	Brackenridgea palultris	Ochnaceae	3	0,2
Sansewan	?	?	3	0,2
Sitapeh	?	?	3	0,2
Gajabing	Syzygium zeylanicum	Myrtaceae	3	0,2
Kayu Kelumit	Glochidion rubrum	Euphorbiaceae	2	0,13
Kayu Gelombang	Xanthophyllum incertum	Polygalaceae	2	0,13
Kuli batu	Polyalthia glauca	Annonaceae	2	0,13
Sibras	Timonius wallichianus	Rubiaceae	1	0,07
Simasam	?	?	1	0,07
Tampu gajah	Macaranga motleyana	Euphorbiaceae	1	0,07
unknown			27	1,8
Total			1496	

7.6 Usage of tree species for nesting

Table 7-5: Overview of the tree species used for nesting, compared to abundance within the forest (last column). Uneven numbers for nesting events result from usage of multiple trees for one nest. In case of two trees of different species each tree species was rated with a value of 0,5; in case of three species each was rated with a value of 0,33 etc.

Local name	Scientific name	Nesting events	% of nests	% in plot
Ubar	Horsfieldia polyspherulla	21,83	26,57	6,55
Puin	Sandoricum beccarianum	11,83	14,4	4,28
Meranti batu	Shorea teysmanniana	11,83	14,4	8,42
Rengas	Gluta renghas	9,17	11,16	25,07
Medang baru	Litsea gracilipes	5,83	7,1	5,01
Resak biasa	Parastemon urophyllus	4,5	5,48	6,48
Jambu air	Syzygium densiflora	3,5	4,26	9,29
Kuli jambu	Garcinia sp.1	1,83	2,23	3,94
Gersang	Jackiopsis ornata	1,5	1,83	1,74
Sepang	Sterculia oblongata	1	1,22	1,07
Malaka	Tetramerista glabra	1	1,22	4,28
Medang sp. 2	?	1	1,22	?
Kayu kacang	Xylopia malayana	1	1,22	0,74
Semasam	?	1	1,22	0,07
Resak payo	Dialium patens	1	1,22	4,68
Cemengang	Neesia aquatica	1	1,22	0,2
Medang lede	Elaeocarpus petiolatus	0,83	1,01	0,8
Peradah	Garcinia celebica	0,5	0,61	0,33
Medang kersik	Platea excelsa	0,5	0,61	1,6
Jambu lepo	Syzygium Ocneocarpum	0,5	0,61	0,4
Pala hutan kecil	Gymnacranthera contracta	0,5	0,61	1,14
Timah-timah kecil	?	0,5	0,61	0,53