

Nesting Sounds in Wild Bornean Orang-Utans (*Pongo pygmaeus*): Cultural and Functional Aspects

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Summary

In some populations, orang-utans (*P. pygmaeus*) produce sounds while building nests. In Suaq Balimbing (Sumatra) and in Scbangau (Kalimantan), a spluttering sound called raspberry occurs. In Tuanan (Kalimantan), orang-utans perform a smacking sound called nest smack, whereas in Ketambe (Sumatra), animals do not perform any sound while building a nest. In this study I wanted to investigate these nesting sounds with respect to their geographic variation in order to gain more information on functional and cultural aspects. I was collecting data and acoustic recordings in the two ecologically similar sites Tuanan and Scbangau. In Tuanan, I additionally conducted a playback experiment, comparing reactions to smacking and bird sounds.

Findings showed that all well-habituated individuals in Tuanan and Scbangau make nesting sounds. Both in Tuanan and Scbangau, these sounds are more common in the more complexly built night nests than in the simpler day nests. The hypothesis that nesting sounds occur in the late stages of nest building and might be connected to the adding of loose twigs to the nest, is supported by the obtained data. Results show that the duration of nest building as well as the building of an extra lining or pillow with loose twigs is associated with the presence of nesting sounds. However, associations with feeding smacks, which animals make while eating leaves from the Kamunda plant (*L. callicarpus*), could be rejected so far. Nesting sounds do not seem to serve as a communication signal since party associations during nest building events are rare. Moreover, these sounds are very faint and weaker than the sound of breaking branches during nest building events. In the playback experiment, immediate reactions tend to result in stronger response to the smacking than to the bird sound. Delayed reactions in the playback experiment did not clearly support a communicative function concerning nesting time regulation or distance regulation.

Overall, nesting sounds do not seem to serve a special function nor do they seem to correlate with ecological factors. Their local occurrence is high in some populations despite extreme rarity elsewhere. Nesting sounds might be a by-product of copying the behaviours of role models. These aspects suggest that nesting sounds are a cultural element of the orang-utans' behavioural repertoire.

1. Introduction

Ever since the late 1960s, intense orang-utan behaviour studies have taken place and from the start, nesting behaviour has been described by many researchers (e.g. Davenport, 1967; MacKinnon, 1974; Rijksen, 1978). Orang-utan nests are built every night for extended sleeping sessions and therefore they can be used to calculate the population density in a certain area (e.g. Maple, 1980; van Schaik et al., 2005). However, only recently some researchers paid close attention to nest building and its attributes. They noted that in some populations orang-utans produce sounds while building a nest. These sounds occur in distinct variations in the different observed populations (van Schaik et al., 2003a; Merrill 2004; van Schaik et al., 2006; S. Husson, H. Morrogh-Bernard, M. van Noordwijk, C. van Schaik, S. Wich, pers. com.). Therefore, in my study I wanted to investigate these nesting sounds with respect to their geographic variation and their possible functions. In order to examine the function, I conducted a playback experiment. Moreover, I made acoustical analyses of these nesting sounds.

1.1. *Nesting Behaviour in Orang-Utans*

1.1.1. Nesting Behaviour in Primates

For my study, nests are important as a behaviour element in the orang-utans' behavioural and cultural repertoire. Nesting behaviour, an animal's behaviour associated with the nest, is common in many animals but primarily attributed to birds (e.g. Hansell, 2000). Many primates do not ordinarily construct sleeping nests. Except for great apes, only certain species of the prosimians occasionally or regularly construct nests or shelters to deliver and raise their young (Yerkes & Yerkes, 1953; Kappeler, 1998).

In great apes, nesting is observed in gorillas, chimpanzees, bonobos and orang-utans. In Fruth and Hohmann's comparison on great ape nest building, it is reported that nest building behaviour in the four species of great apes seems to be rather uniform at all

levels of comparison (Fruth & Hohmann, 1996). All these apes build nests every evening to sleep in and usually rest from dusk to dawn. Moreover, they sometimes also build day nests to rest in during the day. Orang-utans, chimpanzees and bonobos build arboreal nests. They start their constructions by preparing a foundation of solid side branches and then bending, breaking and inter-weaving side branches crosswise. After that, detached twigs are added for an inner lining (Fruth & Hohmann, 1993; Goodall, 1965; MacKinnon, 1974; Baldwin et al., 1981). Gorillas build similarly but they build terrestrial nests (Schaller, 1963; Tutin et al., 1995; Rothman et al., 2006). While the semi social orang-utans hardly ever show accumulations of nests, chimpanzees show a wide range of building nests together, but still favour nesting in small parties (Davenport, 1967; Goodall, 1965; MacKinnon, 1974, Baldwin et al., 1981; Sugardjito, 1983). Gorillas usually stay together as whole groups and gorilla females wait until the silver back has chosen the place and has built the first nest (Schaller, 1963; Tutin et al., 1995; Rothman et al., 2006). Bonobos often congregate to form large parties (Fruth & Hohmann, 1993).

All species show differences in nest building behaviour between populations. This may indicate the range of ecological adaptation (Fruth & Hohmann, 1996; Baldwin et al., 1981; Sugardjito, 1983; Brownlow et al., 2001; Rothman et al., 2006). But if the variety of ape habitat and differences in social organization and diet is considered, nest building appears to be surprisingly uniform on the interspecific level (Fruth & Hohmann, 1996). Nest building with its basic features is shared by the four species of great apes. Because of this uniformity among these closely related species it is not likely that nest building developed independently four times during evolution (Fruth & Hohmann, 1996).

1.1.2. Nesting Behaviour in Wild Orang-Utans

All wild orang-utans build nests for their night repose, usually at a different site from the one used the preceding night. Orang-utans usually build a new nest each night but sometimes they reuse old nests (Rijksen, 1978; Sugardjito, 1983). Infants sleep with their mother at night, as do young juveniles if there is no younger sibling. Young

animals develop nesting skills long before they need to be self-sufficient in this respect. Both infants and juveniles frequently make play-nests and thus, presumably acquire skills in bending and breaking branches (MacKinnon, 1974; van Noordwijk & van Schaik, 2005).

MacKinnon (1974) describes the nest building process in detail. When an orang-utan has found a suitable site for a nest in a tree it moves in a circle bending the branches inwards with hands and feet. The back of the cupped hand is used to push branches into place and pat them down. Furthermore, branches are used in the following way:

- Rimming: branches are bent horizontally to form the nest rim and held in place by other bent branches.
- Hanging: a branch is bent down into the nest to form part of the nest bowl.
- Pillaring: a branch from beneath the nest is bent over to hold the rimming branches and to give extra support.
- Loose: a branch is snapped off the tree and put into the nest bottom. Loose branches may be gathered from several parts of the nest tree or even from another tree and carried back to the nest. Sometimes, they also build a roof above the nest with these loose branches.

In Tuanan, all observers are following the general project rules that include definitions and descriptions of the behavioural elements. Table 1.1 shows the definitions for observed nest building attributes on which data is collected at the Tuanan research station in Central Kalimantan (Rules are assorted by M. van Noordwijk and C. van Schaik).

From personal observations, I can report that orang-utans in Scbangau and Tuanan also start bending branches horizontally, sometimes also from more than one tree and that they first build a basic nest platform. After that, they start to do some additional work on the nest, most of the time they make an inner lining with detached twigs and pad them on the nest ground with the back of their cupped hands and later they lie down on it. Moreover, they sometimes spend time putting a pile of twigs at one side of the nest, thus building a pillow to put their head upon. Sometimes they even make a blanket from loose branches or leaves or they build a roof on top of the nest for the

protection against the rain. This process of additional work on the nest can go quite fast but sometimes it may also take rather long. For day nests however, most of these additional elements are missing because they are built in a very short time and mostly consist only of a basic platform (definitions of nest attributes in Table 1.1).

1.1.3. Nesting Behaviour in Rehabilitant and Captive Orang-Utans

Nest building behaviour seems to be very important for animals in captivity (Grundmann & Bomsel, 2000). Jantschke (1972) observed that many orang-utans in zoos build nests with all kind of objects, even if they are only in limited ways useful to build a nest. Behaviour elements of nest building are used in just the same way as in wild orang-utans. The nest building behaviour occurs in several variations and parts of it may also be left out. In captivity, they often build nests on the ground or on a board but not in a crotch. Also, the so called twig biting (see definition in Table 1.1) has been observed in orang-utans in zoos, where they bite off small branches and build a pillow (see definition in Table 1.1; Jantschke, 1972). However, sounds while building a nest have not been mentioned in literature of captive animals so far.

The construction of a functional, comfortable tree nest appears to be dependent on learning and experience (van Noordwijk & van Schaik, 2005). It has been reported that some older rehabilitants, adolescents and sub-adult males, were not able to construct a proper tree nest when they were first released. After some time, most individuals learnt to build a reasonably comfortable platform; however, sometimes this took many months to learn (Rijksen, 1978; Grundmann & Bomsel, 2000). Also, it was observed in a captive and isolated-reared orang-utan male that it developed nest building skills through learning on the basis of innate coordinations (Lethmate, 1977). Research at the Yerkes Regional Primate Research Center confirmed that experience is a factor in the development of nesting behaviour (Bernstein, 1969). In chimpanzees, it is also suggested that bed building is a learned behaviour that requires early experience and practice for acquisition (Videan, 2006).

Table 1.1: Definition of nest additions according to the general rules of the orang-utan project at the Tuanan research station (rules and guidelines were assorted by M. van Noordwijk and C. van Schaik).

Nesting Additions	Definition
Pillow	A pile of twigs or big leaves at one side of the nest on which the focal puts its head when lying down.
Blanket	A loose cover made from branches or leaves covering (only) the body (not the head).
Lining	A layer made on the nest from leaves or twigs on top of which the focal lies down.
Roof	A construction made from branches or twigs hanging together on top of the nest (mostly protection against rain).
Carry leaves to nest	Pick and carry leaves to nest site from other tree (e.g. Tarantang, <i>Camposperma</i> sp.) before the start of the nest building process. These leaves can be used to build the lining, pillow, roof etc.
Twig biting	Systematically passing the broken ends of leafy twigs in front of their mouth before adding the twigs to the lining of their nests. This behaviour sometimes includes actually biting the end of the twig.
Nesting in multiple trees	Building a nest by tying several smaller trees together.
Raspberry	Spluttering sounds (made by expelling air through relaxed, pouted lips) while making a nest.
Nest smack	Smacking/clicking sounds while making a nest.
Play nest	Building a day nest (mostly by immatures), in which individuals do not rest, but only play.
Day nest	Building a nest during the day to rest in.
Night nest	Building a nest in the evening to spend the night in.

1.2. Nesting Sounds

Faint nesting sounds, like smacking or spluttering while building a nest has so far never been reported for any other great apes except the orang-utans (Merrill, 2004; van Schaik et al., 2003a). The only vocalizations described that are associated with nesting context are the loud-calls frequently given by bonobos preparing to build night nests. However, these loud-calls are common between night-nesting parties and precede lone animals joining nesting parties (Merrill & White, 1996).

Nevertheless, what remains still unclear is the function of the so-called nesting sounds. Different nesting sounds have been observed so far. In Suaq Balimbing (Sumatra, Figure 1.1) Michelle Merrill (2004) observed nest raspberries, whereas she reported for Ketambe (Sumatra, Figure 1.1) no sound production at all during the nest building process (Merrill, 2004). From my supervisor Carel van Schaik and also from Serge Wich, the supervisor of the Tuanan field site (Kalimantan, Figure 1.1), it was known that orang-utans produce sounds while building a nest in Tuanan. These sounds are referred to as nest smacks and resemble a smacking or clicking sound (C. van Schaik, S. Wich, pers. com.). Also, from Helen Morrogh-Bernard and Simon Husson we heard that orang-utans in Scbangau (Kalimantan, Figure 1.1) produce nesting sounds as well. From descriptions they seem to sound similar like the ones observed in Suaq Balimbing. It is a spluttering sound and it is referred to as a nest raspberry (H. Morrogh-Bernard, S. Husson, pers. com.).

In literature, nesting sounds have only been described closer in Merrill's PhD thesis (2004). She checked for a relation between nesting sounds and several nest-building attributes. The only feature of nest building that showed any significant relationship to the production of nest raspberries in Suaq Balimbing was the duration of nest building and this was only true for night nest building. Since the nesting sounds occur in the late stages of nest building they might be connected to adding extra lining to the nests. Otherwise, Rijksen (1978) described a – what he called – “raspberry” sound, which however, was not associated with nesting behaviour but with playing infants. Also MacKinnon (1974) describes this sound but he refers to it as “spluttering” and it is described as blowing air through compressed lips. However, there is no indication

about the context of this behaviour, and especially nesting in this context has never been mentioned in literature so far.

Only recently, nesting sounds have been picked up in the cultural discussion (van Schaik et al., 2003a; van Schaik et al., 2006; see also 1.3.). Raspberries are sounds made in the final phase of nest building in Suaq Balimbing. The sounds have also been reported at Lower Kinabatangan and are there performed just before the nest building process starts and the sounds seem to announce that the sender is bedding down for the night (van Schaik et al., 2003a).

In Tuanan, data showed that although these smacks cannot clearly be heard from great distance or during rain or other loud background noise, they were recorded for half of all night nests. For day nests, the frequency of nest smack is much lower at 9,2%. They were made by virtually all focal individuals. Nest smacks were not observed elsewhere and the lack of ecological correlates strongly suggests they are innovations. Their high local prevalence, despite extreme rarity elsewhere, suggests that they have become cultural (van Schaik et al., 2006).



Figure 1.1: Different study sites in Indonesia with information about the occurrence of nesting sounds: Tuanan (Central Kalimantan, nest smacks), Sebangau (Central Kalimantan, nest raspberries), Suaq Balimbing (North Sumatra, nest raspberries), Ketambe (North Sumatra, no nesting sounds; Picture by P. van Duijnhoven in van Schaik & van Duijnhoven, 2004; modified).

1.3. Culture in Orang-Utans

One of many definitions of culture is that differences in culture should reflect variation in the complexity of innovation and the mechanisms of socially biased learning. Therefore, cultural elements may be signals involving socially transmitted, arbitrary innovations (van Schaik et al., 2003a). In the further discussion of this study also the cultural approach from Whiten et al. (1999) is used. They define culture as followed: A variant is considered cultural if it is customary (shown by most or all relevant individuals) or habitual (shown by at least several relevant individuals) in at least one site but is absent in at least one other ecologically similar site. Cultural variation among chimpanzee communities at nine long-term study sites was charted and subsequently 39 behaviour patterns were discriminated as cultural variants. This means that they were sufficiently frequent at one or more sites to be consistent with social transmission, yet absent at one or more others where environmental explanations were rejected (Whiten et al., 2001).

Nesting sounds might belong to the cultural variants of the orang-utans behavioural repertoire. Both nesting sounds, raspberries as well as smacks, might be cultural variants since they could not be attributed to ecological differences. As van Schaik et al. (2003a) state, some variants of culture like the “raspberry” vocalisation may come close to reflecting shared meaning based on arbitrary symbols (see also van Schaik & van Duijnhoven, 2004). Moreover, nest smacks were not observed anywhere outside of Tuanan, and the lack of ecological correlates strongly suggests they are innovations (van Schaik et al., 2006).

It is quite difficult to completely exclude ecological correlates. Many nesting behaviours in chimpanzees that differ between sites could be attributed to ecological variations (Baldwin et al., 1981; Whiten et al., 1999; Whiten et al., 2001). Although many nest-related behaviours, such as building a rain cover or a roof above the nest, have been suggested as cultural elements (van Schaik et al., 2003a), nesting sounds might not be a cultural but an ecological variation. Nesting sounds in Suaq Balimbing are similar to noises orang-utans make when spitting fibre after chewing lianas (*Stenochlaea palustris*). In Tuanan, similar smacking sounds were heard when focal

animals were feeding on leaves from the Kamunda plant (*Leucomphalus callicarpus*; C. van Schaik, pers. com.). Therefore, nesting sounds might be an individual association with feeding behaviour and may vary between different ecological conditions.

1.4. Orang-Utan Sounds and Vocalisations

Primates show a wide range of vocalisations – from long-distance calls to inconspicuous contact calls (Rowe, 1996). However, not all vocal elements can be considered as proper vocalisations since the vocal chord is not involved (Rijksen, 1978). Therefore, also nesting sounds are not considered as vocalisations but rather as sounds since neither raspberry nor smack seem to involve the vocal chord (pers. obs., M. van Noordwijk, pers. com.).

Most research on vocalisations in great apes has been conducted on chimpanzees. But even for this species most attention has been given to the loud pant-hoots and much less to other vocalisations (e.g. Arcadi, 1996). Up to now, only little research has been devoted to orang-utan vocal repertoire. The early orang-utan studies provided promising lists with descriptions of orang-utan vocalisations (Rijksen, 1978; MacKinnon, 1974). Unfortunately, most studies that focused on orang-utan vocalisations investigated the structure and function of the so-called long calls that are only emitted by flanged males (Mitani, 1985; Delgado, 2004). But with the Tuanan orang-utan research project this was changed. Lately, many students and researchers are investigating orang-utan vocalisations. The vocal repertoire ranges from vocalisations and sounds that are very loud as long calls to sounds as faint as nest raspberries. Long calls are the loudest orang-utan vocalisations and audible far distances apart from the calling male (Rijksen, 1978), whereas raspberries do not include any vocal chord and are only audible nearby (pers. obs.).

1.5. **Playback Experiment**

To better understand the meaning of these nesting sounds, a playback experiment was conducted to test the function of this vocal signal. Playbacks were carried out with nest smacks and birdsongs (as a control sound) to observe the reactions of the animals.

1.5.1. History and Importance of Playback Experiments

A playback is defined as an experimental technique in which natural or synthetic signals are broadcasted and the response of animals are noted down (McGregor, 2000). Already in the early 1890's, R.L. Garner started doing playback experiments. He wanted to learn more about the function of the sounds by replaying the vocalizations to animals and watching their reactions (Garner, 1892). Over the years, playback experiments have become the most important technique for studying animal vocal communication. A stimulus is presented to the subject and an elicited response is measured. Moreover, with today's possibilities, the computer broadened the potential of playback studies by making it possible to manipulate and synthesize acoustic signals, constructing precise stimulus sequences on tape and directly control stimulus presentation in field trials (Hopp & Morton, 1998).

1.5.2. Playback Studies in Primates

Playback studies have been conducted with several animals, such as for example birds (e.g. Leavesley & Magrath, 2005), elephants (e.g. Poole, 1999) or primates (e.g. Cheney et al., 1996). With primates, research using playback experiments has so far been mainly done on alarm call systems (e.g. Zuberbühler, 2000; Wich et al., 2002a; Wich et al., 2002b; Kirchof & Hammerschmidt, 2006).

Functions and mechanisms of many of primate communication systems have been elucidated by playback experiments. Playback experiments in baboons (*Papio*

cynocephalus ursinus) suggest that females primarily ‘answer’ their close relatives’ contact barks when they themselves are separated from other females or if they are at the end of the group progression (Cheney et al., 1996). Another study on Thomas langurs (*Presbytis thomasi*) shows that males react more vigorously towards calls from strange than neighbouring males (Wich et al., 2002a; Wich et al., 2002b). With Tamarins (*Saguinus fuscicollis*, *Saguinus mystax*) playback experiments showed that alarm calls contain information about the predator type (Kirchhof & Hammerschmidt, 2006).

Playback experiments in orang-utans have so far only been done with long calls. Long calls are the best studied vocalization of the orang-utans (Mitani, 1985; Delgado, 2003). These sex-specific loud vocalizations are emitted only by males and might be heard long distances over one kilometre (Rijksen, 1978). Long calls were also analysed by acoustical structure very well (e.g. Delgado, 2003; Ross, 2004). Mitani’s playback experiments support the male-spacing hypothesis where it was shown that long calls regulate spacing between males through an approach-avoidance system based on dominance relationships. On the other hand, the experimental playbacks also demonstrate that sexually active females do not move towards long calls. Therefore, there is no support of the mate-attraction hypothesis (Mitani, 1985). Delgado’s playback experiments provide evidence that orang-utans can distinguish familiar and unfamiliar flanged males through their vocalisations. Moreover, the variance in the speed of the call suggests that long-calls might reflect a male’s motivational state (Delgado, 2003; Delgado, 2004).

1.6. Objectives

Since there is not much known about nesting sounds in orang-utans, the aims of this study are

- 1) to generate an overview of nesting sounds in Tuanan and Sebangau,
- 2) to investigate on cultural and functional aspects of nesting sounds by testing some hypotheses on nesting sound correlates and
- 3) to conduct and analyse a playback experiment in Tuanan.

1.6.1. Nesting Sounds in Tuanan and Sæbangau

In the first part I will provide some basic information on nesting sounds. Since nesting sounds in Tuanan and Scbangau are not yet officially defined, I will attempt to describe both sounds and point out some differences by analysing their acoustical structure. Moreover, I would like to look at the distribution pattern of nesting sounds within the two investigated populations and also between day and night nests. To get a broader view, I will also look at the number of nesting sounds that individuals make while building night nests.

1.6.2. Nesting Sound Correlates

In the second part, I test some hypotheses to get to know more about the cultural and functional aspects of nesting sounds in orang-utans.

As Merrill (2004) stated in her study, the only feature of nest building that showed any significant relationship to the production of nest raspberries in Suaq Balimbing was the duration of nest building and this was only true for night nest building. Since the nesting sounds occur in the late stages of nest building they might be connected with adding extra lining to the nests.

Therefore, I checked for a relationship between a) day and night nest building duration and the production of nesting sounds, b) the production of nesting sounds and building a pillow or extra lining in night nests, and c) rebuilding old nests for night repose and the production of nesting sounds.

The lack of associated nest building or social features with nesting sound production in Merrill's thesis (2004) make this behaviour a candidate for classification as a cultural "convention". A convention would be a behaviour that is wide spread in a population due to social transmission, but does not serve any adaptive or social function. Such behaviours may be a by-product of the propensity to mimic behaviours of others (Merrill, 2004). Both nesting sounds, raspberries as well as smacks, might

be cultural variants since they could not be attributed to ecological differences (van Schaik et al., 2003a; van Schaik et al., 2006).

Alternatively, nesting sounds might not be cultural, but an ecological variation. In Tuanan, similar smacking sounds were heard when focal animals were feeding on leaves from the Kamunda plant (*L. callicarpus*; van Schaik, pers. com.). Therefore, nesting sounds might be an individual association with feeding behaviour.

Consequently, I checked for a) possibilities of social transmission, namely the relation of being in a social association during nest building events and the production of nesting sounds, and b) the distribution status of the nesting sounds in the two population, and c) the amount of Kamunda (*L. callicarpus*) in each individuals diet and the frequency of nesting sound production of each individual.

1.6.3. Playback Experiment

First, differences in immediate reactions to the smacking sound and the bird sound (control sound) were tested. Therefore, I noted the direction of looking of the focal animal for ten minutes after the start of the experiment. Then the aim was to test three hypotheses about the possible functions of nesting sounds, which might take place not immediately after the experiment but delayed. There might also be other possibilities about the function of these sounds and the observers might not recognize reactions. However, in this experiment, I considered the following possibilities, which are also listed in Table 1.2.

- Distance regulation signal

If we assume that nesting sounds are distance regulation signals indicating that another orang-utan is already building its nest in this spot, then we would expect that after the smacking experiment the focal animal moves away and builds its nest in a spot further away after the smacking than after the bird experiment.

- Nesting time signal

If we assume the nesting sound to serve as a communication signal that indicates that it is time to settle down for the night repose (synchronisation), then we would expect the animal to start building its nest and settle down for night rest sooner after the smacking experiment than after the control experiment.

- Functionless signal

Since there is no hint on the function of these sounds it is also suggested to be a signal without a function and we would expect to receive no reaction, neither after the nesting sounds nor after the bird sounds (control experiment).

Table 1.2: Expected (delayed) reactions in the playback experiment.

	Distance Regulation	Time Regulation	Functionless
Nest smack	move away	build nest	no reaction
Bird song (control)	no reaction	no reaction	no reaction

2. Material and Methods

2.1. Study Sites

Research was conducted at Tuanan and Scbangau, two established research sites in Central Kalimantan, Indonesia (Figure 2.1). Both sites contain populations of wild Bornean orang-utans, *Pongo pygmaeus wurmbii*. Central Kalimantan comprises the largest continuous peat swamp and flood plains of western Indonesia. Three major rivers are separating the two sites from each other: The Kahayan River, the Kapuas River and the somewhat smaller Scbangau River (Rijksen & Meijaard, 1999).

The study site Tuanan (2°09' S, 114°26' E) is located in the Mawas Reserve in Central Kalimantan, Indonesia. The Mawas Reserve is managed by BOS (Bornean Orang-Utan Survival Foundation). This site consists of peat swamp on shallow peat of varying thickness, up to about 2 m. The area is disturbed, as it has been subject to selective commercial logging in the early 1990s, followed by the informal logging by local entrepreneurs. Orang-utan research started in January 2003 (van Schaik et al., 2005; van Schaik et al., 2006). The research area includes a grid system of approximately 500 ha with trails and a boardwalk to get access to the forest.

The study area Scbangau (2°20' S, 113°55' E) is located in the P.T. Setia Alam Jaya timber concession, 20 km southwest of Palangkaraya, the Provincial capital of Central Kalimantan. It is located in the upper catchment of the river Sungai Scbangau, which is part of a very large peat-covered landscape between the river Sungai Katingan and the river Sungai Kahayan. Most of this area is covered with peat swamp forest, although there has been some land development for agriculture and settlement (Morrogh-Bernard et al., 2003). The area is managed by EKOVTQR. Indonesia. In 2004, Scbangau was established as a research area. The research area includes a grid system of approximately 400 ha with trails and a boardwalk to get access to the forest.

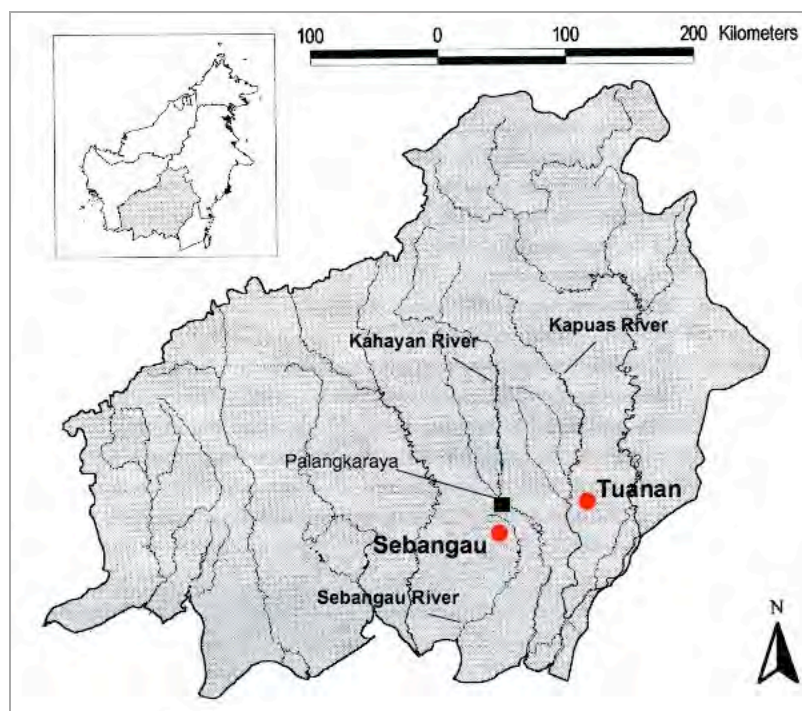


Figure 2.1: Central Kalimantan province (Borneo, Indonesia) with the two research sites Sebangau and Tuanan as well as the provincial capital Palangkaraya and the rivers that separate the two sites: Kapuas River, Kahayan River and Sebangau River (Picture from Rijksen & Meijaard, 1999; modified).

2.2. Identified Individuals

In Tuanan already 41 different individuals have been recognised (S. Wich, M. van Noordwijk, pers. com.), including adult females with offspring, flanged males, unflanged males and adolescents. There are seven infants (three males and four females).

In Sebangau there are 34 individuals that have been recognised (H. Morrogh-Bernard, pers. com.), including adult females with offspring, flanged males, unflanged males and adolescents. There are four infants (one female, one male, two unknown).

For this study, independent individuals were grouped into different age/sex classes as shown in Table 2.1. Numbers of identified individuals do not include dependent infants (AF: adult females, Adol F: adolescent females who are just recently

independent but not yet sexually mature, AM: adult flanged males, SAM: sub-adult, unflanged, but sexually mature males, Adol M: adolescent males who are recently independent, but not sexually mature yet).

Table 2.1: Total number of identified focal individuals by age/sex classes at each site (Tuanan and Scbangau) and the number of focal individuals with data collected for this study (**bold**) at each site.

Class	Definition	Tuanan		SUBangau	
AF	Adult Female	9	7	6	2
AM	Adult Male (flanged)	13	10	7	3
SAM	Sub-Adult Male (unflanged, sexually mature)	8	7	10	1
Adol F	Adolescent Female (independent, not sexually mature)	3	1	5	2
Adol M	Adolescent Male (independent, not sexually mature)	1	1	2	0
Total		34	26	30	8

There is a lot less data for the Scbangau research site for several reasons: 1) data sampling on nest data necessary for this study covers only two months at the Scbangau site. There is on the other hand a large data pool for the Tuanan site, which includes data starting in July 2003 that has been collected by many researchers and assistants; and 2) in Scbangau, the animals were more spread across the area and therefore were not as often found and followed as animals in Tuanan. Moreover, there were much fewer researchers and assistants to search and then follow and collect data.

2.3. Field Data Sheets

To collect data for this study, datasheets with information regarding nesting behaviour were used at each site (definitions of nesting behaviour elements see Table 1.1). Also *ad libitum* data was taken on special occasions. Only independent orang-utans were used as focal animals.

For each day or night nest that was built by a focal animal, a check list (Figure 2.2) was filled out – including the starting time as well as the ending time of the nest building process, and the time when the focal lies down (to the nearest minute, building times under one minute were rounded up to one minute). Also, tree species, height and DBH (diameter at breast height) of the tree were noted. The height of the nest, the nest position and whether it was a rebuilt nest or newly built nest was noted. Occurrence of building a pillow, a blanket, a roof or a lining was recorded regularly in Tuanan but not in Scbangau. This additional data was collected especially during my stay at the Scbangau research site during the time period from April 14th through June 2nd 2005. The presence of nesting sounds and any other vocalisations during nest building was noted and sometimes also the number of nesting sounds was recorded. Other data was taken if there was rain during the nest building process, if the nesting tree has been likewise used as a feeding tree before, if there was a party and if so, who built the nest first and also, whether the infant was in the nest of the mother.

For analysis, data sheets from Tuanan recorded between July 2003 until July 2005 were used and in Scbangau, datasheets recorded between April 2005 until June 2005 were used (unless otherwise mentioned).

sarang sore	
jam buat	15.34
jam selesai	15.42
jenis pohon	agula
keliling pohon	45 cm
tinggi pohon	10+
tinggi sarang	5+
posisi sarang	7
baru/diperbaiki yg tua	tua
bantal	ya <input checked="" type="radio"/> tidak <input type="radio"/> tidak tahu <input type="radio"/>
selimut	ya <input type="radio"/> tidak <input checked="" type="radio"/> tidak tahu <input type="radio"/>
pakai atap?	ya <input checked="" type="radio"/> tidak <input type="radio"/> tidak tahu <input type="radio"/>
pakai alas?	ya <input type="radio"/> tidak <input checked="" type="radio"/> tidak tahu <input type="radio"/>
ada nyeletok?	ya <input checked="" type="radio"/> tidak <input type="radio"/> tidak tahu <input type="radio"/>
hujan di waktu bikin sarang?	tdk
pohon makan sebelumnya	tdk
party: yg pertama	
jarak antara sarang party	
jam golek	15.46

Figure 2.2: Table of data sheet to collect night nest information. From top to bottom: starting time, ending time, tree species, height of the tree, height of the nest, position of the nest, new or rebuilt nest, pillow, blanket, lining, roof, nest smack (yes, no, unknown), rain, feeding tree, party members, time of bedding down.

2.4. Recordings and Measurements

2.4.1. Tape Recordings in the Field

During the following of focal animals, recordings of all orang-utan vocalisations and sounds were made and there is now quite a large data pool of orang-utan vocalisations and sounds for Tuanan, including many recordings made by all people of the vocalisation team at Tuanan. Other vocalisations and sounds are analysed in other studies. In Scbangau, on the other hand, I was the only person recording vocalisations. Sometimes also long calls were recorded in Scbangau, but no other vocalisations or sounds were recorded in general.

Sounds in Scbangau were recorded with a XLR microphone and a Sony DAT recorder. In Tuanan however, recordings were made with the Sony DAT recorder as well as with a Marantz analogue cassette recorder and a XLR or an EMC Sony microphone. Regular analogue tapes as well as DAT tapes between 60 and 120 minutes recording time were used for the recordings.

2.4.2. Sonograms

Recordings were digitized using the Raven 1.2.1 Software program (Charif et al., 2004) on Macintosh Power Book in Tuanan where some parts of the vocalisations and sounds were already digitized. Back in Zurich, a Power Macintosh was used. To acquire signals, the input settings in Raven were as follows: Sample rate 44100 Hz, Channel: left, Sample Format: 16-bit signed PCM.

Measurements to analyse sounds were made via a spectrogram view. To configure a spectrogram view, the waveform sonograms were then established by Fast-Fourier Transformation with parameters adjusted as listed in Table 2.2.

Table 2.2: Configuration settings to convert the waveform into the spectrogram view (in Raven 1.2).

Window	
Type	Hann
Size	1024 samples
3 dB Filter Bandwidth	124 Hz
Time Grid	
Overlap	90 percent
Hop Size	256 samples
Frequency Grid	
DFT Size	512 samples
Grid Spacing	86.1 Hz

2.4.3. Sound Analysis

Sounds were analysed using the Raven software package for Macintosh (Charif et al., 2004). Of all recordings, 173 nests smacks and only seven nest raspberries were used to analyse. Especially for Scbangau a very limited sample was available that was useful for analysis. Many recordings could not be used due to the following problems. There were quite a lot of background sounds that decreased the value of many recordings. It was difficult to find the desired nesting sound in the sonogram, since nest smacks and raspberries are quite faint compared to louder vocalizations such as for example kiss-squeaks or long calls. There was noise produced by cicadas, crickets, mosquitoes and other insects, but also many birds and gibbons vocalized during tape recordings. Moreover, during recording of nesting sounds, orang-utans were handling branches and also breaking them, which sometimes makes it impossible to hear these faint nesting sounds or to find their exact starting and ending points in the sonogram. Feeding smacks could not be analysed. There were not enough recordings and the few recordings were difficult to analyse. While recording feeding smacks, falling fruits were often producing noise in close distance to the microphone and sometimes also rain and wind made it difficult to obtain good quality recordings.

After the desired part of the recording was selected in the sonogram, the following recording measurements were applied for analysing the sounds (definitions are taken from the Raven Manual).

- Max Frequency

This is the frequency at which *Max Power* occurs within the selection. Units: Hz (Charif et al., 2004). This parameter is used to look at differences between the two different nesting sounds in Tuanan and Scbangau, since they were quite clear to determine. It is the darkest point in the selection (see *Max Power*).

- Max Power

This is the maximum power in the selection. In a greyscale spectrogram, the maximum power in a selection is the power at the darkest point in the selection. Units: dB re 1 dimensionless sample unit (Charif et al., 2004).

- Delta Time

It is the difference between *Begin Time* (time at which the selection begins) and *End Time* (time at which the selection ends) for the selection. Unit: seconds (Charif et al., 2004). Due to many background noises, this parameter should be used with caution since it was difficult to decide where exactly the starting and the end point of the sound are located.

2.5. Data Analysis

For my analysis I considered 13 individuals who were observed while they were building nests both with and without nest smacks at Tuanan as well as 6 individuals who were observed building nests with and without nest raspberries at Scbangau. Samples for most focal animals were limited, especially for Scbangau.

First of all, I considered the fact that there does not yet exist any analysed data on nest smacks in Tuanan or nest raspberries in Scbangau. A definition was worked out by

the whole vocalization team in Tuanan. An inventory list on the presence and absence of nesting sounds produced by the observed individuals was prepared to gain more information about the distribution patterns within the populations and also between day and night nests. Moreover, age/sex classes and populations were compared. Unless otherwise mentioned, only new built nests were considered for counting frequencies. Furthermore, the number of nesting sounds in all individuals were counted and compared between sites.

To examine the possible functions of nest smacks in Tuanan and nest raspberries in Scbangau, several nest-building attributes were compared in the presence or absence of nesting sounds. This analysis is partly the same as the one performed by Michelle Merrill for her PhD thesis (2004) in order to compare my data to her findings in Suaq Balimbing and Ketambe (Gunung Leuser National Park, Sumatra, Indonesia).

I calculated the average duration of nest building for each individual when nesting sounds were present or absent in day as well as in night nests to investigate whether the difference in nesting sound production was linked to a difference in nest building duration. Additionally, results obtained from the two populations were compared. Moreover, I investigated whether the nesting attributes such as building a pillow and an inner lining are associated with the occurrence of nesting sounds. I also checked whether individuals are in a social association during nest building events. For focal animals in Tuanan, average frequencies of nesting sound occurrence in night nest building were correlated to the average frequency of building a pillow or a lining during night nest events.

If old nests are reused by orang-utans, a basic platform already exists but they often improve it with an extra lining of loose twigs. If nesting sounds are associated with adding such loose twigs then individuals should also perform nesting sounds while rebuilding an old nest.

In Tuanan, similar smacking sounds occur while eating leaves from the Kamunda plant (*Leucomphalos callicarpus*). Therefore, the time of eating Kamunda (% of total

time spent feeding) was calculated and put in relation to the frequency of performing nest smacks.

2.6. Statistics

All calculations were generated by Microsoft Excel 2004 for Mac OS X. Also all graphs, figures and tables were made with Microsoft Excel or SPSS 11. To conduct non-parametric statistical tests, SPSS 11 for Mac OS X was used. The null hypothesis was rejected whenever significance tests produced a probability of less than 0.05. All tests were two-tailed. The following non-parametric tests were used for statistical analyses:

- Kruskal Wallis Test

The Kruskal Wallis test is used to decide whether k independent samples are from different populations. The differences among the samples signify genuine population differences or whether they represent merely the kind of variations that are to be expected among random samples taken from the same population (Lamprecht, 1999; Siegel & Castellan, 1988).

- Wilcoxon Signed Ranks Test

The Wilcoxon Signed Ranks Test is applicable to the case of two related samples whenever the experimenter wishes to verify that two conditions are different (Lamprecht, 1999; Siegel & Castellan, 1988).

- Mann Whitney U Test

The Mann Whitney U Test is used to test whether two independent samples have been drawn from the same population (Lamprecht, 1999; Siegel & Castellan, 1988).

- Spearman Rank-Order Correlation

The Spearman Rank-Order Correlation is a measure of association between two variables (Lamprecht, 1999; Siegel & Castellan, 1988).

- Chi-Square Test for Association

The Chi-Square Test is used to test whether two groups differ with respect to some characteristic and, therefore, with respect to the relative frequency with which group members fall in several categories (Lamprecht, 1999; Siegel & Castellan, 1988).

2.7. Playback Experiment

2.7.1. Playback Stimuli

Focal animals were subjected to two sets of sounds. One set consisted of three nest smacks and the other set was a control set and consisted of three parts of birdsongs. In both sound sets there was an interval of 15 seconds between the smacks or the birdsong parts. This is similar to the natural time lapse between nest smacks while building a night nest. Nest smacks as well as bird songs were presented to the focal in a single trial only. A non-random design was chosen to maintain a maximum amount of variation in the sequence of the experiments. Three of the six tested individuals were exposed to the control sound first, whereas the other three individuals were exposed to the nest smacks first. On a different day – at least two days after the first exposure – the individuals were exposed to the other sequence.

2.7.2. Pseudoreplication

Pseudoreplication arises when there is confusion between the number of measurements made and the number of statistically independent replicates available for a statistical test. The result of such a confusion is that the sample size (N) used in a statistical test is not appropriate to the hypothesis that is being tested (Hurlbert, 1984). I tested my different focal animals with different stimuli to avoid over-generalisation of the result. To avoid pseudoreplication, all individuals were subjected to different nest smacks and bird sounds. Nest smacks as well as bird sounds were recorded in the study area with a DAT or Analogue Recorder and an EMC Sony microphone. From

our data collection, I randomly chose stimuli of smacks from six different individuals. The reason that we needed multiple exemplars randomly chosen, is to try and ensure that the only difference in common between the two sets of stimuli is that one shows smacking (in all their variable forms) and the other one shows bird songs (in all their variable forms; McGregor, 2000).

2.7.3. Data Collection

With the Raven 1.2 software package, playback sounds were cleaned from disturbing background noises, such as cicadas and branch breaking as much as possible. Sounds were amplified with a Nagra-Kudelski DSM speaker connected to a Sony DAT Recorder. The volume was adjusted to the natural loudness of a nest smack from a male (app. 47 dB at approximately 15 meters, A. Lameira, pers. com.). All playbacks were conducted from about 10 to 20 meters distance (depending on the habitat structure) and at a height of about 1.5 meters. Sound level settings were the same for all experiments. Playbacks were conducted in the afternoon hours between 14:00 and 15:30 when it would also be natural for an individual to start building its nest. The experiment was not conducted when a test individual was in a party with another orang-utan or if the weather conditions were not appropriate, e.g. if it was raining. On the one hand, the expensive and sensitive equipment could be damaged due to the humidity and on the other hand, the smacks were not well audible. Moreover, the experiment was not started if the conditions necessary to start the experiment were not given, e.g. if the orang-utan was travelling on, if the observer taking data could not see the orang-utan's face, or if the orang-utan was positioned too high up in the tree.

Data was collected on direction of looking, time of nest building and distance travelled after the experiments to compare reactions between the smacking experiment and the bird song experiment (control).

2.7.4. Set Up

The playback speaker (■) was positioned about 10 to 20 meters away from the focal in the opposite direction of the orang-utan's direction of looking. The focal animal (●) should not see the person playing the recorder (2), nor should it see the speaker. The observer taking data (1) is positioned facing the focal. Set up and playback speaker are shown in Figure 2.3. Most of the times, there were two other observers who were taking regular focal data and sometimes also helping with the experiment, or otherwise taking their own data. The playback speaker was hidden in the vegetation and got covered with a green T-shirt after the experiment. One observer was responsible for preparing the playback stimulus and then for playing the sound. This observer was more or less hidden in the vegetation and could not see the orang-utan. He or she started the experiment after a signal of the observer taking data. The other observer was taking data for ten minutes after the start. With the compass, data was taken every 30 seconds during the period of ten minutes on the direction of looking or moving. Likewise, the distance to the focal animal, angle between focal and speaker, activity and any special behaviour of the focal (e.g. vocalisations, scratching) as well as place and time of night nest building were recorded. Directions of looking were transformed into sectors A (closest to the speaker) through D (furthest away from the speaker).

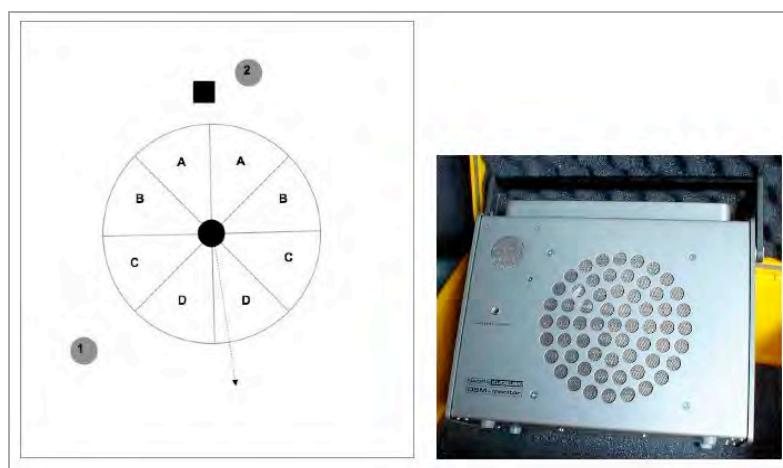


Figure 2.3: Set-up playback experiment (left picture): The focal animal is located in the centre (●), the playback speaker (■, right picture) and observer (2) are opposite of the focal animal's direction of looking (→), data-taking observer (1) is facing the focal.

2.7.5. Study Site and Focal Animals

Six individuals from the wild orang-utan population at the study site Tuanan were used to conduct the playback experiment:

- Mindy: adult female with offspring (Milo, female, born in 2001)
- Jinak: adult female with offspring (Jerry, male, born in 2003)
- Kerry: adult female with offspring (Kondor, female, born in 1999)
- Fugit: flanged male
- Juni: adult female, never gave birth to an offspring before
- Nanio: adolescent male

The choice of focal animals for the playback experiment depended mainly on the availability of focal animals. This depended on what individuals we found and were allowed to follow in the period of June 30 until July 25, 2005 (focal follows lasted a maximum of ten days in a row). The choice also depended on other experiments carried out on focal animals (e.g. tiger experiment and/or long call experiment).

Playback experiments were carried out from June 30 2005 until July 22 2005. Playback experiments were only conducted at the Tuanan study area in the Mawas Reserve, Central Kalimantan, Indonesia (see description of site in 2.1). In Scbangau there was not enough time and not enough orang-utans around to conduct a playback experiment. Also, playback experiments were not done as planned with both nest smacks and nest raspberries, but were only done with nest smacks since the raspberries are too faint and it is difficult to find this sound in the spectrogram and clean out background noises without changing the characteristics of the sound.

2.7.6. Material

The following material was used to conduct the playback experiment:

- The Raven Software Program 1.2.1 to first put the sounds from either the DAT or analogue tape into the computer and digitalize them and then clean from background noises and cut to the appropriate length.

- A DAT recorder to playback the sound, connected to the Nagra playback speaker to amplify the sound.
- A tape with six sections nest smacks Tuanan and six sections bird sounds. To avoid pseudoreplication, a different section was used for each focal (see 2.7.2).
- An analogue recorder with Sony microphone to record possible vocalisations as a reaction to the playback experiment.
- A compass to write down the direction of looking or moving of the focal every 30 seconds during the period of ten minutes and to define the position of the speaker relative to the focal.
- A green shirt to cover the playback speaker after the experiment. To avoid further disturbance, the speaker was only moved away after the focal already had moved away from the place of the experiment.
- Maps from regular daily data sheets were used to locate the place of experiment and the place of nest building and measuring the distances in between.

2.7.7. Statistics and Analyses

Due to small sample sizes differences in immediate and delayed responses were analyzed using non-parametric statistical tests. The null hypothesis was rejected when significance tests produced a probability of less than 0.05. Reactions after the smacking experiment were compared to reactions after the bird experiment (control experiment) using a Wilcoxon Signed Ranks Test (Siegel & Castellan, 1988; see also 2.6).

3. Results

3.1. *Nesting Sounds in Tuanan and SUBangau*

3.1.1. Definition of Nesting Sounds

Definitions of the orang-utan vocalisations and sounds have been worked out with the whole vocalisation group consisting of Agatina Naso, Natascha Nieuwenhuis, Madleine Hardus, Adriano Lameira and Serge Wich, and with the help of Maria van Noordwijk. In the following section the definitions of nest smacks and nest raspberries that have been worked out by the whole team are presented, with some personal additions from my own observations and findings from sound analysis and nest analysis.

3.1.1.1. *Nest Smacks in Tuanan*

Nest smacks are a soft smacking sound that can be produced by infants, immature and adults during the nest-building process. This sound is most often heard during the construction of the evening nest; however, it can also occur while building a day- or play nest. The sound is probably made during the late stage of nest building when breaking of smaller twigs occurs and also while padding the nest with loose twigs and branches to build a pillow or an inner lining. Sometimes, the twigs are wiped through the mouth before they are being put down on the nest (this behaviour is referred to as twig biting, see Table 1.1). So far these smacks are only known to occur at the Tuanan site. However, in Scbangau (Central Kalimantan), where normally the raspberry sound occurs, a similar smacking sound has been observed with two individuals (but these two individuals were also and most often performing the raspberry sound). Otherwise, similar smacking sounds have only been heard during solitary play by infants with a twig or a branch. Figure 3.1 shows a sonogram of three smacking sounds made by the flanged male Fugit at the Tuanan research site.

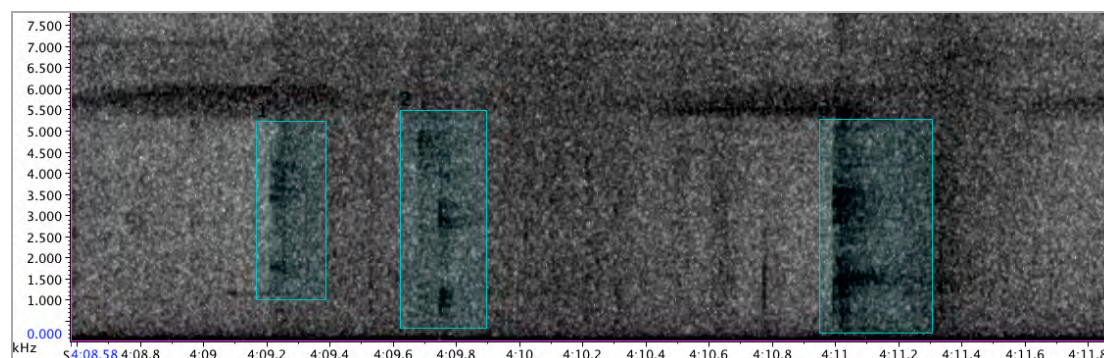


Figure 3.1: Raven Sonogram of three nest smacks (selections 1, 2 and 3) made by the flanged male Fugit (axes show kilohertz and seconds; horizontal bands between 5.500 and 6.000 kHz are insects).

3.1.1.2. *Nest Raspberries in Sæbangau*

Nest raspberries are defined as faint exhalatory spluttering sounds that can be produced by infants, immatures and adults during nest building. This sound is most often heard during the construction of the evening nest; however, it can also occur while building a day or play nest. Raspberries occur in the same context as nest smacks in Tuanan (Central Kalimantan); however, up to now they have never been heard in Tuanan. On the other hand, Michelle Merrill (2004) observed raspberry sounds during nest building processes also in Suaq Balimbing (Sumatra). Although no sonograms are available for Suaq Balimbing, descriptions suggest that these sounds sound just about the same as the raspberries in Scbangau. MacKinnon (1974) refers to raspberries only as calls occasionally made by juvenile animals in the same context as kiss squeaks (annoyance). Rijksen (1978) describes the spluttering sound in rehabilitant orang-utans who saw food but could not get it. Figure 3.2 shows a sonogram of a nest raspberry made by the flanged male Beethoven at the Scbangau research site.

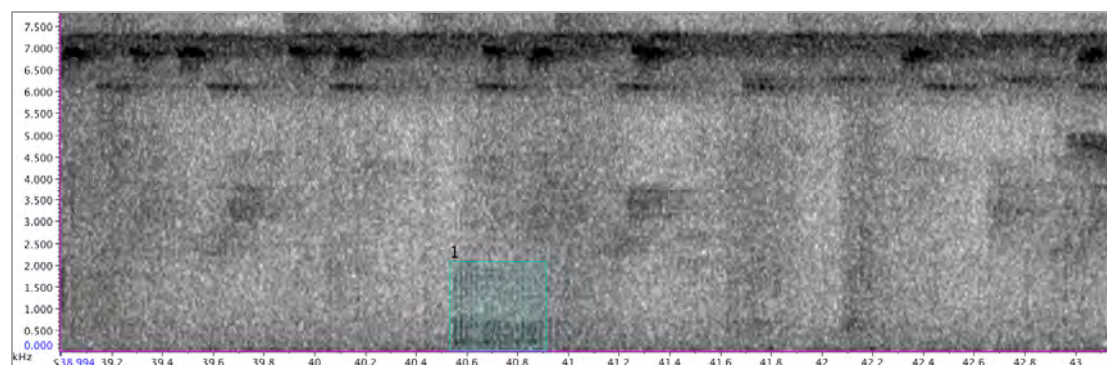


Figure 3.2: Raven Sonogram of a nest raspberry (selection 1) made by the flanged male Beethoven (axes show kilohertz and seconds; horizontal bands at around 7.000 kHz are insects).

3.1.2. Sound Analysis of Nesting Sounds

To get to know more about the nesting sounds and how they differ from each other, I examined some measurements and sound parameters with the Raven 1.2 sound program (Charif et al., 2004). As already mentioned in the chapter Material and Methods, descriptive parameters are limited to *Maximal Frequency* and *Delta Duration*. A trade-off between resolution of the sonogram and the size of the sound in the picture was necessary.

Table 3.1 shows the mean delta duration and the mean maximum frequency of individuals of which nesting sound recordings could be made in Tuanan and in Scbangau respectively. From my own observations I can say that these two sounds sound very different to the human ear as described in chapter 3.1.1. Sonograms also show that their acoustical features in the spectrogram are different, e.g. the frequency range of the smack is wider than that of the raspberry (Figure 3.1 and 3.2).

Lowest maximum frequency of a nest smack in Tuanan is 344.5 Hz and highest maximum frequency is 7579.9 Hz (both smacks are made by the female Jinak, total N = 173 smacks of eight different individuals were analysed). Mean maximum frequency of smacks in Tuanan is 1206.5 Hz (Table 3.1). Mean maximum frequency of raspberries in Scbangau is 296.1 Hz (Table 3.1). Mean maximum frequencies of

smacks in Tuanan are significantly higher than mean maximum frequencies of raspberries in Scbangau (Mann Whitney U Test, $U = 0$, $p = 0.006$, $N_1 = 8$, $N_2 = 4$).

The mean delta duration of Tuanan individuals is 0.123 seconds whereas mean delta duration of Scbangau individuals is 0.156 seconds. For all individuals, mean delta duration does not differ significantly between the two sites (Mann Whitney U Test, $U = 9$, $p = 0.345$, $N_1 = 7$, $N_2 = 4$). As already mentioned, this parameter has to be handled with caution since measurements may not be completely accurate.

Table 3.1: Mean delta duration (seconds) and mean maximum frequency (Hertz) for eight individuals in Tuanan and four individuals in Scbangau.

Focal	Mean Delta Duration (s)	Mean Max Frequency (Hz)
Mindy	0.177	1339.4
Jinak	0.121	1537.8
Sumi	0.079	904.4
Juni	0.150	998.3
Fugit	0.164	1733.4
Rambo	0.077	1243.6
Gismo	-	1205.9
Preman	0.096	689.1
Mean Tuanan (N=8 individuals)	0.123	1206.5
Indah	0.160	258.4
Indy	0.070	387.6
Ella	0.189	258.4
Beethoven	0.214	279.9
Mean SUBangau (N=4 individuals)	0.158	296.1

3.1.3. Distribution of Nesting Sounds Within Populations

3.1.3.1. *Presence and Absence of Nest Raspberries in Sæbangau*

Since the time to take data on nesting behaviour in Scbangau was limited, I used an extended data set from December 7th 2004 until June 2nd 2005 to get an overview of

the performance of nest raspberries during **night** nest building events in Scbangau (Figure 3.3). During this time, data was collected about the presence or absence of nest raspberries during **night** nest building processes. However, there was no data on nest additions like making a pillow or a lining (definitions see Table 1.1) and also not on the number of sounds that occurred during a nest building event.

Figure 3.3 shows the number of **night** nest observations and the occurrence of raspberries. Raspberries were made by most of the observed individuals. Only one individual (Drake) never made nest raspberries, neither during day nor night nest building. However, he was only recently identified and still unhabituated. Moreover, it must be considered that there are individuals with as much as 15 **night** nest observation events (Beethoven) and others with only one **night** nest observation (Franky). The female Indah with her daughter Indy and the flanged male Beethoven as well as the adolescent female Feb are the ones that were followed most in this time period.

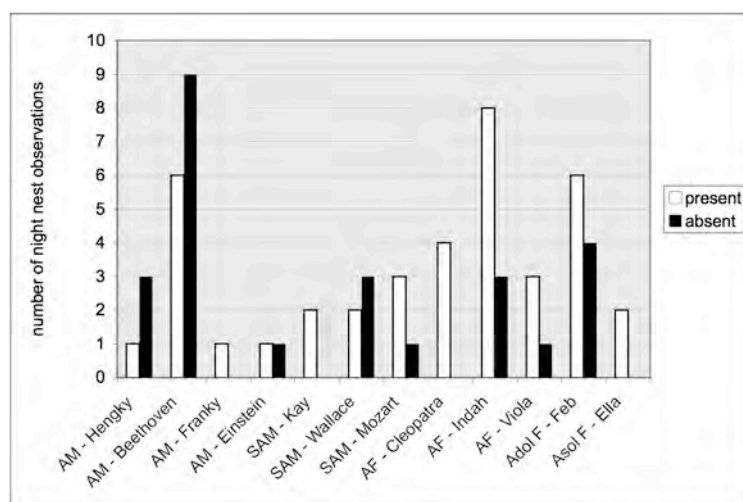


Figure 3.3: Number of night nest building observations of 13 individuals at the Scbangau research site when raspberries were present or absent (extended data set; AM: adult male, SAM: subadult male, AF: adult female, Adol F: adolescent female).

For any further analysis I solely used the data from April 14th 2005 until June 2nd 2005. This was actually the time I spent at the Scbangau research site and collected data on nesting behaviour. During the study period from April 14th until June 2nd 2005, we followed eight individuals, but only six individuals were observed building nests both with and without raspberries. Table 3.2 shows the observed frequencies of **day** and **night** nest building events when raspberries were present, absent, or unknown. One individual (Portret) was only followed once and did not make any nest raspberries while building a **day** nest. There are no **night** nest observations for this focal animal at all and moreover, identification of this animal is not sure. And, as already mentioned, the still unhabituated flanged male Drake was a never observed making nest raspberry neither while building a day or a night nest (Table 3.2).

Table 3.2: Number of nest building events and frequencies when raspberries are present, absent, or unknown during day and night nest building observations events at Scbangau (? : unknown, A: absent, P: present; only new built but not rebuilt nest were considered; AF: adult female, AM: adult male, SAM: subadult male, Adol F: adolescent female).

Focal	Class	Day Nest Events			Total	Night Nest Events			Total	Grand Total
		?	A	P		?	A	P		
<i>Beethoven</i>	AM	0	0	0	0	0	5	4	9	9
<i>Mozart</i>	SAM	0	1	0	1	0	1	3	4	5
<i>Viola</i>	AF	1	3	0	4	0	1	2	3	7
<i>Indah</i>	AF	0	1	1	2	0	1	7	8	10
<i>Ella</i>	Adol F	0	1	0	1	0	0	2	2	3
<i>Feb</i>	Adol F	0	0	0	0	1	0	4	5	5
		1	6	1	8	1	8	22	31	39
		0.125	0.750	0.125		0.032	0.258	0.710		
Drake	AM	0	4	0	4	0	2	0	2	6
Portret	AM	0	1	0	1	0	0	0	0	1
Grand Total		1	11	1	13	1	10	22	33	46

For further analysis, data from Drake and Portret were disregarded and only the data from the six remaining well-habituated individuals (*italic* in Table 3.1) who were observed building nests both with and without nest raspberries were considered. Even

though Drake had more observation events compared to individuals such as the adolescent females Ella or Feb, they were both considered well habituated by experienced researchers in Scbangau who had been following them also before this data period. Drake, however, was newly found in this region and never followed before and still intensely kiss-squeaking towards observers. He is therefore still considered to be unhabituated. There is no comparison between age/sex classes since the data sample is too small to use for within group analysis. With a larger sample these groups could perhaps be compared more accurately.

In Scbangau, nest raspberries are more common in **night** nest than in **day** nests (Wilcoxon Signed Ranks Test, $Z = -2.201$, $p = 0.028$). In individuals across all age/sex classes at Scbangau ($N=6$ individuals), nest raspberries were confirmed for 12,5% of all **day** nests ($N=8$ day nest observations) and 71% of all **night** nests ($N=39$ night nest observations).

3.1.3.2. *Presence and Absence of Nest Smacks in Tuanan*

For Tuanan there exists – compared to the small data set for Scbangau – a large data pool starting in July 2003. In my study I used data until July 2005, the end of my six months fieldwork period.

Table 3.3 shows the number of nest building events when nest smacks were present, absent, or unknown during day and night nest building events at Tuanan. In Tuanan, only three individuals were never observed performing nest smacks during neither **day** or **night** nest building processes. However, these three focal animals (Cipto, Ekko and Ucok) only had three **day** nest observations and zero, one or two **night** nest observations. They were not found and followed often in the two years of data collection and are therefore also not very habituated yet (M. van Noordwijk, pers. com.).

Table 3.3: Number of nest building events and frequencies when raspberries are present, absent, or unknown during day and night nest building observations events at Scbangau (? : unknown, A: absent, P: present; only new built but not rebuilt nest were considered; AF: adult female, AM: adult male, SAM: subadult male, Adol F: adolescent female).

Focal	Class	Day Nest Events			Total	Night Nest Events			Total	Grand Total
		?	A	P		?	A	P		
<i>Jinak</i>	AF	44	40	11	95	45	8	117	170	265
<i>Juni</i>	AF	24	9	8	41	15	4	47	66	107
<i>Kerry</i>	AF	8	4	2	14	29	9	30	68	82
<i>Mindy</i>	AF	9	20	15	44	14	11	81	106	150
<i>Sumi</i>	AF	13	18	0	31	64	34	21	119	150
		98	91	36	225	167	66	296	529	754
		0.436	0.404	0.160		0.316	0.125	0.560		
<i>Fugit</i>	AM	6	2	0	8	0	1	15	16	24
<i>Henk</i>	AM	6	1	3	10	2	2	12	16	26
<i>Niko</i>	AM	0	1	0	1	1	1	7	9	10
<i>Rambo</i>	AM	8	2	2	12	1	1	10	12	24
<i>Wodan</i>	AM	3	3	0	6	2	2	4	8	14
		23	9	5	37	6	7	48	61	98
		0.622	0.243	0.135		0.098	0.115	0.787		
<i>Dayak</i>	SAM	5	17	0	22	7	4	6	17	39
<i>Gismo</i>	SAM	7	1	0	8	8	1	8	17	25
<i>Preman</i>	SAM	15	4	1	20	10	1	18	29	49
		27	22	1	50	25	6	32	63	113
		0.540	0.440	0.020		0.397	0.095	0.508		
Total		148	122	42	312	198	79	376	653	965
		0.474	0.391	0.135		0.303	0.121	0.576		
Lolo	Adol F	4	1	0	5	2	0	1	3	8
Nanio	Adol M	0	0	0	0	5	1	1	7	7
Desy	AF	0	1	0	1	2	0	5	7	8
Inul	AF	0	0	2	2	0	0	1	1	3
Aqil	AM	3	0	0	3	0	0	1	1	4
Kay	AM	2	0	0	2	1	1	1	3	5
Teju	AM	2	0	0	2	0	0	1	1	3
Ucok	AM	0	3	0	3	0	0	0	0	3
Zeke	AM	2	0	0	2	2	0	1	3	5
Cipto	SAM	3	0	0	3	2	0	0	2	5
Ekko	SAM	2	1	0	3	1	0	0	1	4
Yoga	SAM	0	3	0	3	1	1	2	4	7
Ogun	SAM	2	0	0	2	2	0	1	3	5
Grand Total		168	131	44	343	216	82	391	689	1032

23 individuals performed nest smacks during **night** nest building and of these 23 animals only eight individuals (Henk, Inul, Jinak, Juni, Kerry, Mindy, Preman and Rambo) were observed also making nest smacks during **day** nest building as well. Moreover, of these eight individuals making nest smacks during **day** nest building, five (Henk, Inul, Kerry, Preman and Rambo) were only observed during one, two or three nest building observations making smacks while building a **day** nest. The other three individuals that were observed performing nest smacks more regularly while building a **day** nest (Jinak, Juni and Mindy) were all adult females, two of them still having a dependent infant with them (Jinak with Jerry, Mindy with Milo; Table 3.3).

For further analysis, data from all well habituated individuals in Tuanan with more than a total of ten nest observations were used. Therefore, data was used from thirteen well-habituated orang-utans at Tuanan who were observed building nests both with and without nest smacks within their observed nesting events (*italic* in Table 3.3).

Nest smacks are more common in **night** than in **day** nests (Wilcoxon Signed Ranks Test, $Z = -3.188$, $p < 0.001$). In Tuanan, nest smacks were confirmed across all age/sex classes ($N = 13$ individuals) for 13,5% of all **day** nests ($N = 312$ observed day nest events) and 57,6% of all **night** nests ($N = 653$ observed nest events; Table 3.3).

Individuals were split up into age/sex classes (see chapter 2.2) to compare findings between these groups. However, there is not enough data to create categories for adolescent males and adolescents females. Classes only include adult males (AM) and adult females (AF) as well as subadult males (SAM).

In all age/sex classes, nest smacks are more common in **night** than in **day** nests. For adult flanged males, nest smacking was present in 78,7% of all **night** nest building observations (total $N = 61$ observations) – compared to the adult females where nest smacking was present only in 56% of all **night** nest building observations (total $N = 529$ observations). Subadult males were the ones with the lowest presence of nest smacks during nest building observations. Nest smacking was present in 40,8% of **night** nest building events (total $N = 63$ observations; Table 3.3, Figure 3.4, Figure 3.5). The frequency of presence of nest smacks during nest building observations was

not significantly different between age/sex classes (Kruskal-Wallis Test, $H = 4.478$, $p = 0.107$ for **night** nests, $H = 2.599$, $p = 0.273$ for **day** nests). However, the samples of the three groups are quite small (AF: $N = 5$, AM: $N = 5$, SAM: $N = 3$).

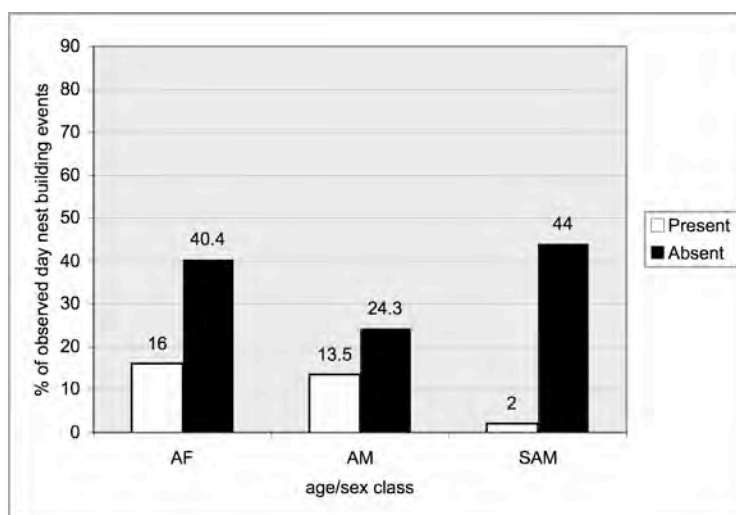


Figure 3.4: Presence and absence of nest smacks at the Tuanan site for the different age/sex classes in **day** nests (in % of total observed nesting events; P: present, A: absent; nests with unknown occurrence of nesting sounds are not listed; AF: adult female, total $N = 225$ observations; AM: adult male, total $N = 37$ observations; SAM: subadult male, total $N = 50$ observations).

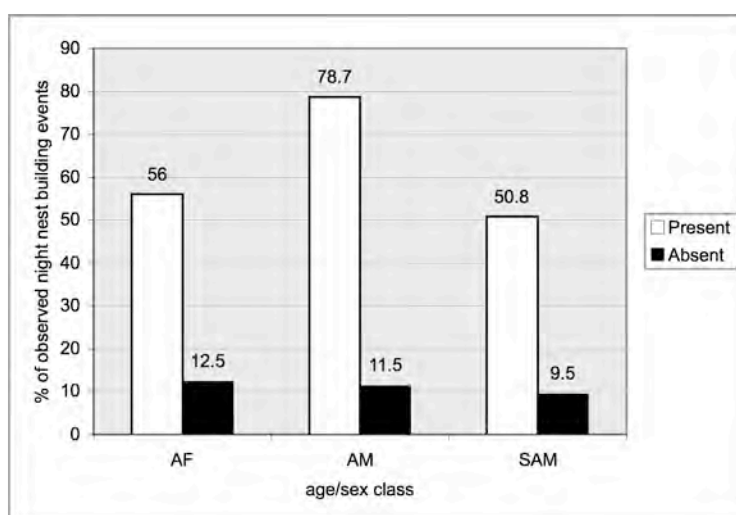


Figure 3.5: Presence and absence of nest smacks at the Tuanan site for the different age/sex classes in **night** nests (in % of total observed nesting events; P: present, A: absent; nests with unknown occurrence of nesting sounds are not listed; AF: adult female, total $N = 529$ observations; AM: adult male, total $N = 61$ observations; SAM: subadult male, total $N = 63$ observations).

3.1.3.3. *Presence and Absence of Nesting Sounds Compared Between Tuanan and Sæbangau*

Nesting sounds are produced by almost all observed and well-habituated orang-utans at least once during day or night nest building process in Tuanan as well as in Scbangau.

Figure 3.6 shows that in **night** nest building processes, nest smacks are less often present in Tuanan (57,6%) than in Scbangau (71 %). However, differences in presence of nesting sounds while building a **night** nest are not significant (Mann Whitney U Test, $U = 24.5$, $p = 0.203$, $N_1 = 13$, $N_2 = 6$). This difference in **night** nests might be due to different sizes of the data pool and also to many question marks in the observation of presence or absence of nesting sounds in Tuanan. In Tuanan, one individual (Sumi) had most of the question marks (53.8%). She was often found outside the forest along the riverside and could not be followed very closely. Therefore, observers often were not able to hear whether she made sounds while building a nest (M. van Noordwijk, pers. com.).

Figure 3.6 shows also that presence of nesting sounds while building **day** nests is almost the same for Tuanan (13,5%) and Scbangau (12,5%). Also for **day** nests, presence of nesting sounds in Tuanan and Scbangau is not significantly different (Mann Whitney U Test, $U = 28$, $p = 0.283$, $N_1 = 13$, $N_2 = 6$).

Findings in Scbangau seem to be very similar to the results from Michelle Merrill (2004), who observed that nest raspberries were confirmed for 11% of all day nests and 73% of all night nests at Suaq Balimbing.

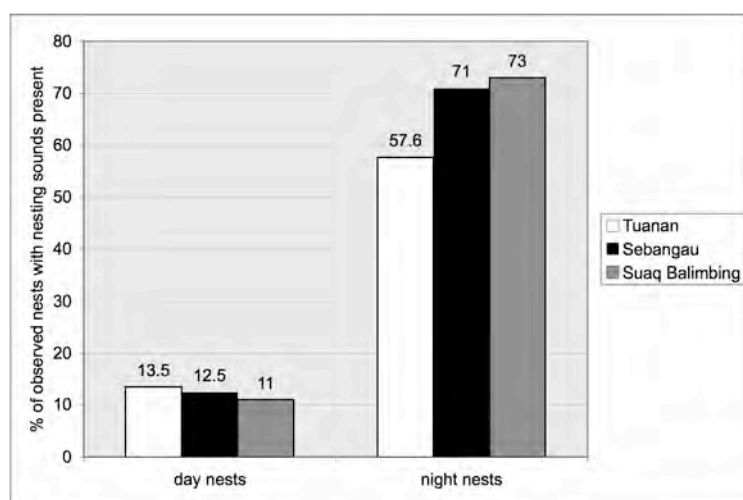


Figure 3.6: Presence of nesting sounds in % of total observed nest building events for day nests and night nests (across all age/sex classes) at Sebangau (total N = 8 day nest observations and 31 night nest observations) and Tuanan (total N = 312 day nest observations and 653 night nest observations). To compare, data from Suaq Balimbing is added (Merrill, 2004; with permission of C. van Schaik).

3.1.4. Number of Nesting Sounds per Nesting Event in Tuanan and Sebangau

Whenever possible, the number of raspberries was counted, however, noise of insects, branch and twig breaking, wind, rain, moving observers etc. made it hard to hear this faint noise. Only new built **night** nests were considered for counting the number of nesting sounds.

In Sebangau, **night** nest building events included the occurrence of up to nine raspberries (Indah). The average amount of raspberries as well as the median and range for the six observed individuals are shown in Table 3.4.

In Tuanan, **night** nest building events included the occurrence of 59 nest smacks (Juni). Table 3.5 shows the amount of smacks as well as the median and the range for the thirteen observed individuals in Tuanan.

Table 3.4: Average amount of raspberries as well as median and range for six individuals in Scbangau during night nest building.

Focal	Average amount of raspberries	Median	Range	Number of observations
Beethoven	5	5.5	1-8	4
Indah	5.71	6	1-9	8
Viola	2	2	1-3	2
Ella	5	5	4-6	2
Feb	2.5	2.5	2-3	4
Mozart	2.66	3	1-4	3

Table 3.5: Average amount of nest smacks as well as median and range for thirteen individuals in Tuanan during night nest building.

Focal	Average amount of smacks	Median	Range	Number of observations
Jinak	7.07	5	1-27	97
Juni	13.38	8	1-59	39
Kerry	4.96	3	1-15	27
Mindy	8.25	6	1-33	63
Sumi	2.55	2	1-13	18
Fugit	7.26	6	1-29	15
Henk	6.55	6	1-13	9
Niko	4.14	3	1-12	7
Rambo	8.38	7.5	2-28	8
Wodan	7.5	7.5	1-14	4
Dayak	2.66	3	1-4	6
Gismo	5.5	3.5	2-14	6
Preman	7.16	5	2-20	12

In Tuanan, average number of nesting sounds are significantly higher than average number of nesting sounds in Scbangau (Mann Whitney U Test, $U = 14.50$, $p = 0.032$, $N_1 = 13$, $N_2 = 6$). However, the median of the two populations does not differ significantly (Mann Whitney U Test, $U = 25.50$, $p = 0.231$, $N_1 = 13$, $N_2 = 6$).

3.2. Nesting Sound Correlates

3.2.1. Nest Building Duration

As Merrill (2004) stated in her study, the only feature of nest building that showed any significant relationship to the production of nest raspberries in Suaq Balimbing was the duration of nest building and this was only true for **night** nest building. Since the nesting sounds occur in the late stages of nest building they might be connected to adding extra lining to the nests. Therefore, I checked also for relationship between day and night nest building duration and the production of nesting sounds.

3.2.1.1. Nest Building Duration With and Without Nest Raspberries in Sæbangau

The average time spent building a **day** nest at Scbangau was approximately 2.67 minutes (range of the mean day nest building durations: 1-5 minutes, N = 4 individuals). The average time spent building a **night** nest was approximately 8.53 minutes (range of the mean night nest building durations: 5.88 - 12.75 minutes, N = 6 individuals).

All individuals that were observed building both **day** and **night** nests (N = 4) spent a longer time building **night** nests than **day** nests. However, the sample is rather small and the difference is not significant. But a trend was found towards longer night nest building (Wilcoxon Signed Ranks Test, $Z = -1.826$, $p = 0.068$, N = 4). The sample was too small to compare for age/sex classes.

Figure 3.7 shows the mean **night** nest building duration with and without nest raspberries for different individuals. This could only be done for **night** nests since I do not have data on individuals who built nests both with and without raspberries during the **day**. Moreover, only four individuals built **night** nests both with and without raspberries. Two individuals (Feb and Ella) were observed making nest raspberries during every **night** nest observation and therefore there is no night nest

building duration with raspberries being absent. Because of this, they were left out of the statistical analysis. In **night** nest observations, Viola was the only individual of the four who actually took longer building **night** nests when not making any nest raspberries (Figure 3.7).

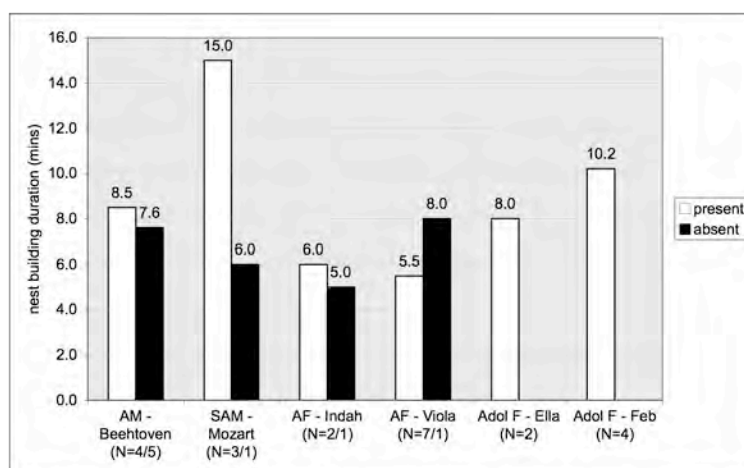


Figure 3.7: Mean night nest building duration (in minutes) for nests where the raspberries were recorded as present or absent for six individuals in Scbangau (AF: adult female, AM: adult male, SAM: subadult male, Adol F: adolescent female; N = number of observed night nest with/without nest raspberries).

Figure 3.8 shows the average time spent building a **night** nest with raspberries present and absent. Average time spent building a **night** nest with raspberries was 8.75 minutes whereas the average time spent building a **night** nest without raspberries was approximately 6.65 minutes (N = 4 individuals). For all individuals combined, mean **night** nest building duration with raspberries present was not significantly different from mean **night** nest building duration with raspberries absent in **night** nests (Wilcoxon signed rank test, $Z = -0.730$, $p = 0.465$). However, the sample size was quite small (N = 4 individuals).

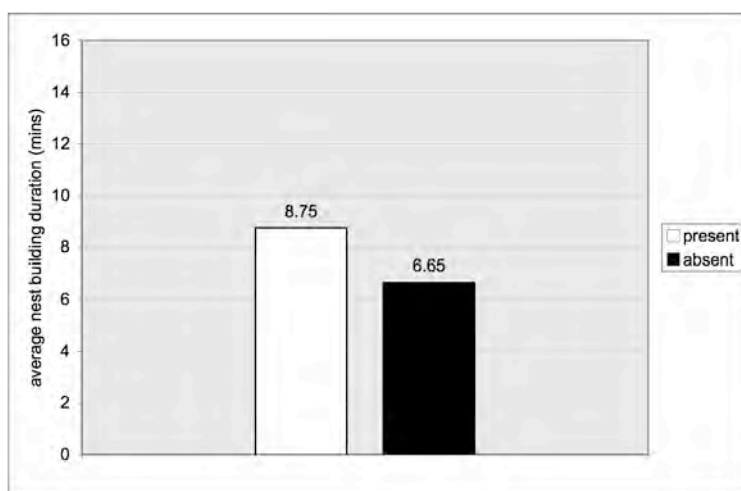


Figure 3.8: Average durations of nest building (in minutes) for night nests when raspberries are present and absent (N = 4 individuals).

3.2.1.2. Nest Building Duration With and Without Nest Smacks in Tuanan

The average time spent building a **day** nest at Tuanan was approximately 2.39 minutes (range of the mean nest building duration: 1.33 – 3.6 minutes, N = 13 individuals). The overall average time spent building a night nest was approximately 7.27 minutes (range of the mean nest building duration: 5.5 – 9.58 minutes, N = 13 individuals). Nest building durations are significantly longer for **night** nests than for **day** nests (Wilcoxon Signed Ranks Test, $Z = -3.180$, $p < 0.001$, N = 13).

Figure 3.9 shows the mean **night** nest building duration in minutes for 13 individuals when nest smacks were recorded as present or absent. Except for the subadult male Dayak, all individuals spent longer building **night** nests with nest smacks than they did building nests without nest smacks. The adult flanged male Niko was not observed making nests without nest smacks and therefore, his data is not considered in this statistical analysis.

Figure 3.10 shows the mean **day** nest building duration in minutes for 13 individuals when nest smacks were recorded as present or absent. Except for the subadult male Preman, all individuals spent longer building day nests with nest smacks present than

they did when smacks were absent. Only seven individuals were considered for the statistical analysis that built day nests both with and without smacks.

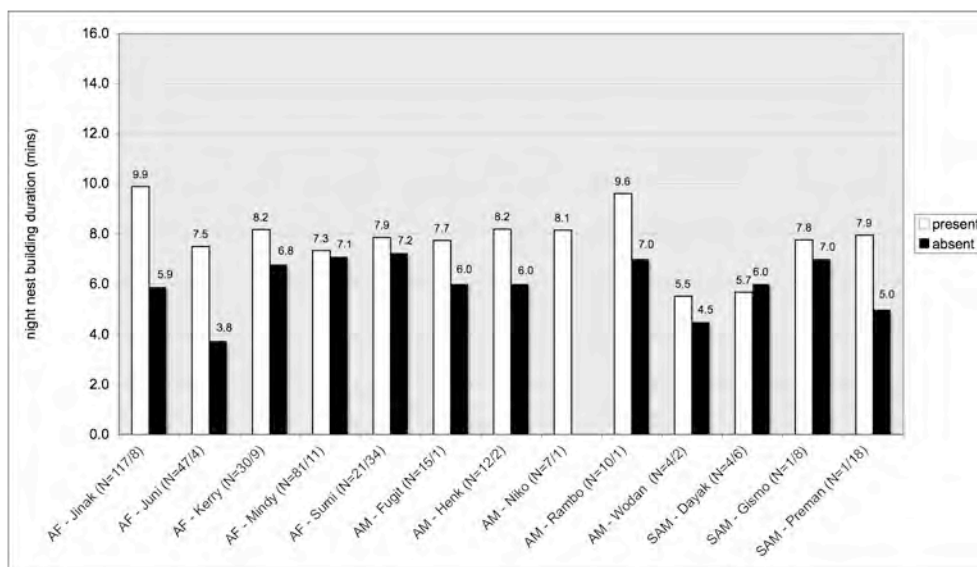


Figure 3.9: Mean durations of night nest building (in minutes) for 13 individuals in Tuanan for nests where nest smacks were recorded as present or absent (AF: adult female, AM: adult male, SAM: subadult male; N = number of nest observations with/without nest smacks).

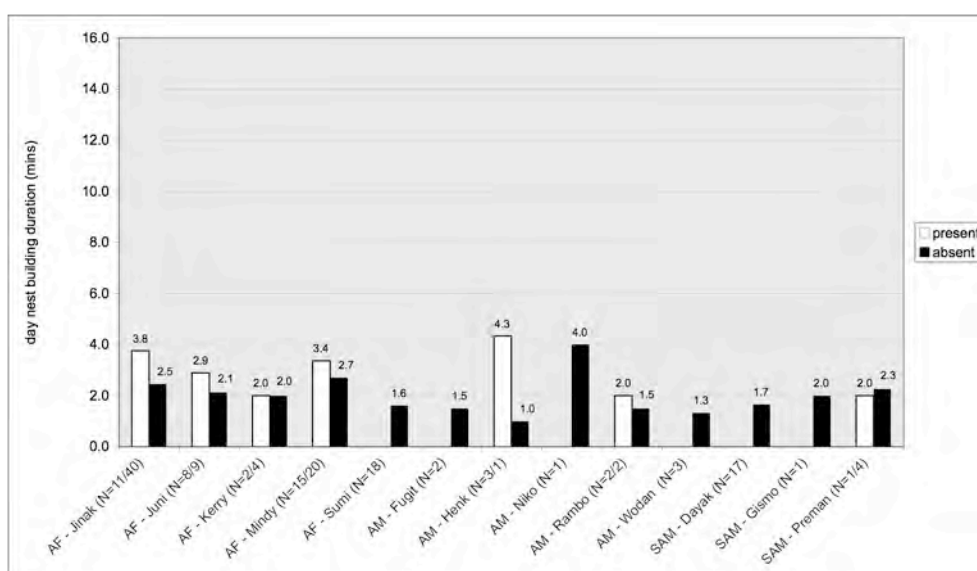


Figure 3.10: Mean durations of day nest building (in minutes) for 13 individuals in Tuanan for nests where nest smacks were recorded as present or absent (AF: adult female, AM: adult male, SAM: subadult male; N = number of nest observations with/without nest smacks).

Figure 3.11 shows the average duration of nest building for **day** and **night** nests with nest smacks present and absent for all individuals combined. The building durations of **night** nests with nest smacks present are significantly longer than building durations of **night** nest with nest smacks absent (Wilcoxon Signed Ranks Test, $Z = -2.903$, $p = 0.004$, $N = 12$). Building durations for **day** nest with nest smacks are also significantly longer than for nest without nest smacks (Wilcoxon Signed Ranks Test, $Z = -1.992$, $p = 0.046$, $N = 7$).

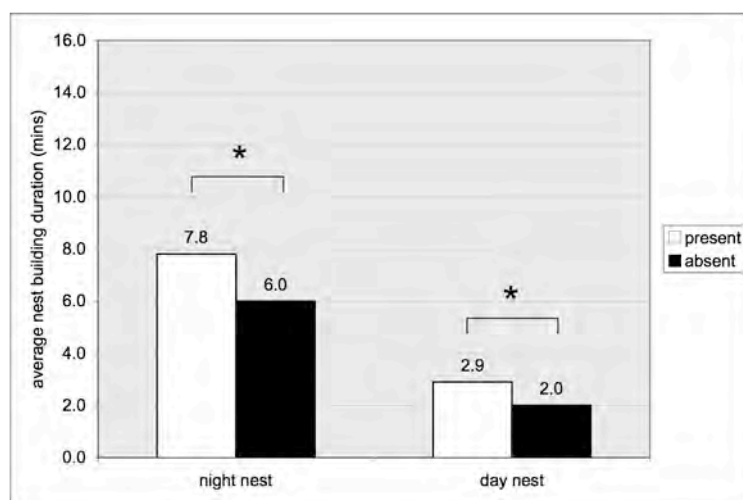


Figure 3.11: Average durations of nest building for night and day nests when nest smacks are present and absent. Durations of nest building are significantly longer for nests with smacks than for nests without smacks (Wilcoxon Signed Ranks Test, $Z = -2.903$, $p = 0.004$, $N = 12$ for night nests, $Z = -1.992$, $p = 0.046$, $N = 7$ for day nests).

Table 3.6 and Figure 3.12 show the mean nest building durations for each age/sex class for **night** nests when nest smacks were recorded either as present or absent. Durations of **night** nest building within each class (average durations for each individual were averaged among age/sex classes) were compared when nest smacks were present or absent. There was not enough data on **day** nests to compare age/sex classes. Differences in building duration between age/sex classes were not significantly different neither with nest smacks present (Kruskal-Wallis Test, $H = 0.721$, $P = 0.697$, $N = 13$) nor with nest smacks absent (Kruskal-Wallis Test, $H = 0.340$, $P = 0.844$, $N = 12$).

Table 3.6: Mean durations of night nest building (in minutes) for each age/sex class at Tuanan when nest smacks were present or absent (AF: adult female, AM: adult male, SAM: subadult male).

age/sex class	Nest building duration (in minutes)		N (individuals)
	Nest smacks present	Nest smacks absent	
AF	8.15	6.15	5
AM	7.75	5.88	4
SAM	7.12	6.00	3

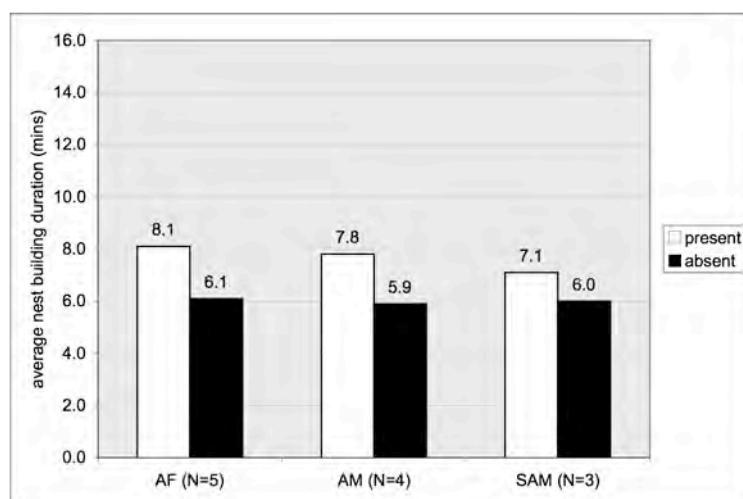


Figure 3.12: Average durations of night nest building for each age/sex class at Tuanan when nest smacks were present or absent (AF: adult females, AM: adult males, SAM: subadult male; N = individuals)

3.2.1.3. Nest Building Duration With and Without Nesting Sounds Compared Between Tuanan and Sæbangu

In Scbangu, animals on average spent more time building **night** nests than in Tuanan (8.53 minutes and 7.27 minutes respectively). However, the difference is not significant (Mann Whitney U Test, $U = 26.00$, $p = 0.254$, $N_1 = 13$, $N_2 = 6$). In Suaq Balimbing, average time to spend building a **night** nest was approximately 8.5 minutes (range 2-15 minutes, $N = 83$ nest building observations).

Merrill's (2004) comparison of females with more than four observation days in Suaq Balimbing and Ketambe showed that Ketambe females spent significantly less time

building their **night** nests (6.9 minutes) than Suaq Balimbing females (9.2 minutes). In Tuanan, adult females (N = 5) spent in average 7.43 minutes building their **night** nests.

In Scbangau, focal animals spent about the same time building their **day** nests as in Tuanan (2.67 minutes and 2.39 minutes respectively). The difference is not significant (Mann Whitney U Test, $U = 26.00$, $p = 1.000$, $N_1 = 12$, $N_2 = 5$). The overall average time spent building a day nest at Suaq Balimbing was approximately 2.7 minutes (range 1-8 minutes, N = 137 nest building observations; Merrill 2004).

Merrill's findings for Suaq and Ketambe showed that the observed females spent about the same time building their **day** nest (2.5 minutes and 2.7 minutes respectively). The difference was not significant (Merrill 2004). In Tuanan, adult females (N=5) spent approximately 2.32 minutes building a **day** nest.

Findings compared between Tuanan (N = 12 individuals) and Scbangau (N = 4 individuals), reveal no significant difference in duration of **night** nest building between the sites when nesting sounds were present (Mann Whitney U Test, $U = 23.50$, $P = 0.952$, $N_1 = 12$, $N_2 = 4$) respectively absent (Mann Whitney U Test, $U = 16.00$, $P = 0.328$, $N_1 = 12$, $N_2 = 4$). **Day** nests are not compared between sites because there is not enough data for focal animals in Scbangau about when raspberries were recorded as present or absent.

3.2.2. Pillow and Lining

As already mentioned, nesting sounds occur in the late stages of nest building and therefore they might be connected with adding extra lining to the nests (Merrill 2004, C. van Schaik, pers. com., pers. obs.). Therefore, I checked not only for duration of nest building (see also 3.1.2), but also for the relationship between the presence of nesting sounds and the building of a pillow or an inner lining with smaller twigs in **night** nests (definitions Table 1.1). For both activities – to build a pillow or an inner lining – individuals break off smaller twigs and put them into the bottom of the nest.

3.2.2.1. *Pillow and Lining in Tuanan*

In Tuanan, a total of 383 **night** nests were considered where both information on the presence and absence of nest smacks as well as information on the presence and absence of building a pillow and/or a lining was available. In 77.3% (N = 296) of all observations, focal animals built a pillow and/or a lining accompanied nest smacks (Table 3.7, Figure 3.13). In 12% (N = 46) of all observations, focal animals built a pillow and/or a lining but did not perform nest smacks. The occurrence of nest smacks is significantly associated with the building of a pillow in **night** nests (Chi-Square Test, $X^2 = 24.393$, $df = 1$, $p < 0.001$).

Table 3.7: Observed frequencies of nest smacks and pillows/lining occurring during **night** nest building events in Tuanan for 13 individuals (total N=383 observed **night** nest building events).

	Nest smack present	Nest smack absent
Pillow/Lining present	296 (77.3%)	46 (12.0%)
Pillow/Lining absent	23 (6.0%)	18(4.7%)

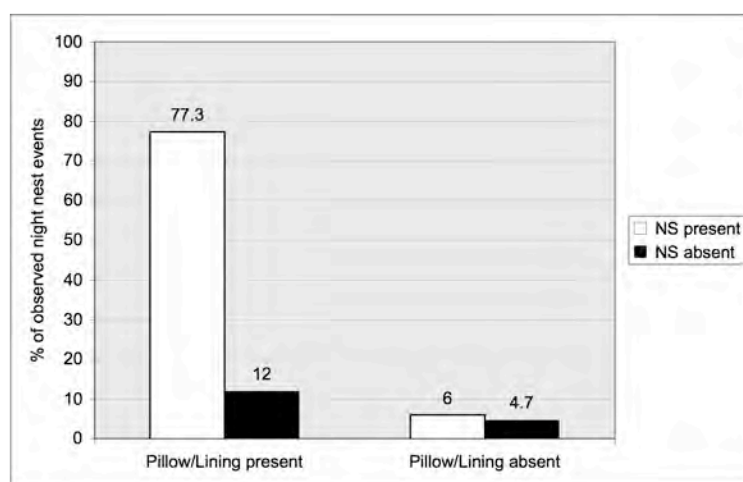


Figure 3.13: Frequencies of observed night nest events with information about building a pillow/lining and the presence and absence of nest smacks in Tuanan (total N = 383 night nest observations).

Figure 3.14 shows the relation between the average frequency of making nest smacks while building a **night** nest and the average frequency of making a pillow while building a **night** nest for the thirteen observed focal animals. There was no significant relation to be found (Spearman Rank Order Correlation, $r_s = 0.306$, $p = 0.310$, $N = 13$). However, Figure 3.15 shows the result if data on the female Sumi is left out. She is an outlier and does not very often make nest smacks while building a night nest (17.6% of all observed night nest events) but she does quite often build a pillow (75.9% of all observed night nest events). When leaving out Sumi, there is a significant relation that a higher nest smack frequency correlates positively with higher frequency of building pillows (Spearman Rank Order Correlation, $r_s = 0.593$, $p = 0.042$, $N = 12$).

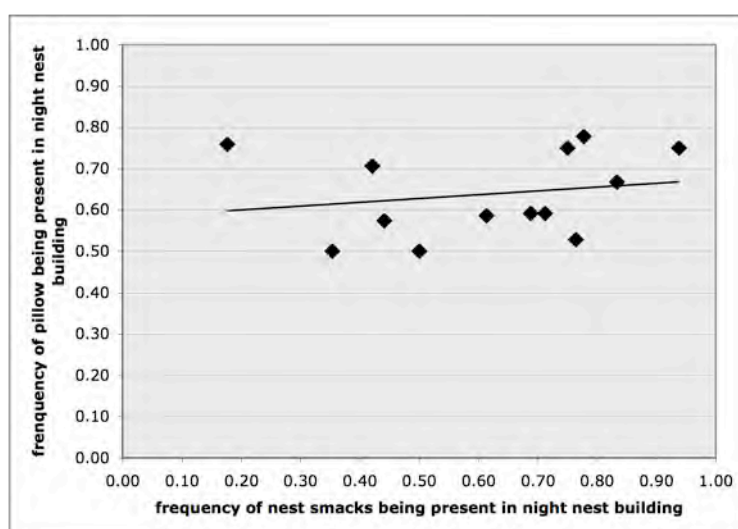


Figure 3.14: The average frequency of nest smacks being present in night nest building in relation to the average frequency of pillow building being present in night nest building for 13 individuals in Tuanan.

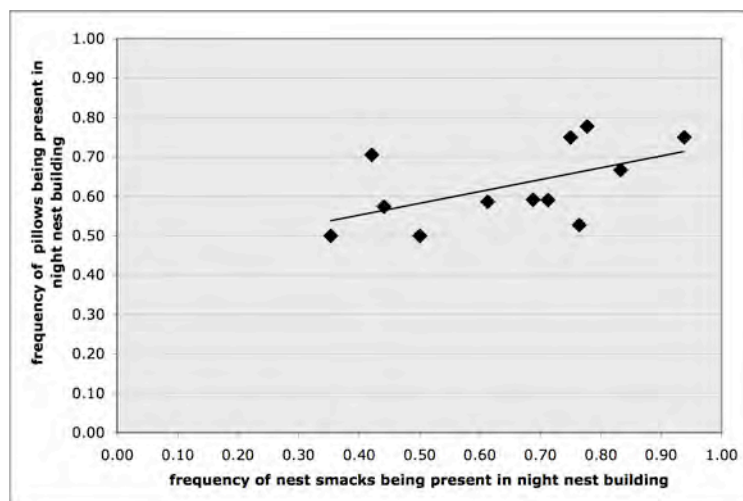


Figure 3.15: The average frequency of nest smacks being present in night nest building in relation to the average frequency of pillow building being present in night nest building for 12 individuals in Tuanan (without the adult female Sumi). There is a significant correlation (Spearman Rank Order Correlation, $r_s = 0.593$, $p = 0.042$, $N = 12$).

3.2.2.2. *Pillow and Lining in Sæbangu*

Unfortunately, there is not enough data to do statistical analysis for Scbangu on both the presence and absence of raspberries AND the presence and absence of making a pillow or an inner lining.

Of all nest with information on building a pillow and/or lining AND information on presence or absence of nesting sounds ($N = 25$), focal animals built night nests with a pillow and/or a lining in 94.4%. Of all nests with pillow and/or lining focal animals performed nest smacks in 73.9% ($N = 17$). Nesting sounds were absent in 26.1% ($N = 8$) of night nests with pillow and/or lining.

3.2.3. Rebuilt Nests in Tuanan and Sæbangu

In Scbangu, in two occasions (6.1%, total $N = 33$ **night** nest observations) focal animals (Feb and Indah) were observed rebuilding an old **night** nest. In both cases of rebuilding an old **night** nest, focal animals were performing raspberries.

In Tuanan, in 20.6% (N = 81 observations) of all observed **day** nest events, nests were not newly built but an old one was rebuilt. Only 7.4% (N = 77) of the **night** nests were rebuilt.

Of all rebuilt **day** nests (total N = 81 observed events), in only 1.2 % (N = 8) of all cases, focal animals performed nest smacks. In 42% (N = 32) of the observed events they were not making nest smacks while rebuilding an old **day** nest.

Of all rebuilt **night** nests (total N = 77 observed events), focal animals performed nest smacks while rebuilding an old **night** nest in 39% (N = 30) of the observed events. In 24.7% (N = 19) focal animals were rebuilding an old **night** nest without making nest smacks.

3.2.4. Associations During Nest Building Events in Tuanan and Sæbangu

In Sæbangu, focal animals were in association with another independent individual only during three nest-building events (9.3 %) of a total of 31 **night** nest observations. In two of these cases, the focal animal building a nest was observed making raspberries. In a total of eight **day** nest observations, animals building a nest were in social association with another orang-utan in two cases. However, they did not perform nest raspberries (dependent infants were not counted as associations).

In Tuanan, in a total of 312 **day** nest building observations, there was a social association during 63 nest building events (20.2%). Of all observed social associations during **day** nest building (N = 63), in 30.2% of the cases focal animals made nest smacks. In a total of 635 **night** nest observations, the focal animal was in association with another individual in 23.4% (N = 153) of the night nest building events.

To look for a statistical relationship between social association and the performance of nesting sounds I only considered **night** nests with information regarding social association as well as regarding the presence or absence of nest smacks (pooled for all

individuals, $N = 453$ nest events). In 84.3% ($N = 91$) of all social associations during night nest building, individuals made nest smacks. They did not make nest smacks in 15.7% of the events. The total of observed nests, including the ones with and without social association, focal animals made nest smacks while being in a social association in 20.1%. No significant difference arises whether there is a party during night nest building regarding presence and absence of nest smacks (Chi-Square Test, $X^2 = 0.159$, $df = 1$, $p = 0.690$, $N = 453$ night nests). Table 3.8 and Figure 3.15 show the amount and percentages of observed night nests where focal animals were in a social association while building nests and whether individuals made nest smacks while building the nest.

Table 3.8: Observed frequencies of nest smacks and social associations occurring during night nest building in Tuanan for 13 individuals (total $N = 453$ observed night nest building events).

	Nest smack present	Nest smack absent
Social association present	91 (20.1%)	17 (3.8 %)
Social association absent	283 (62.5%)	62 (13.6%)

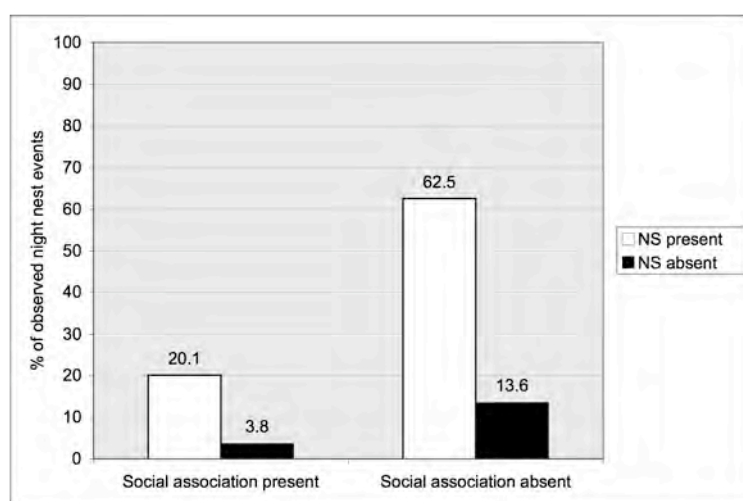


Figure 3.15: Frequencies of observed night nests with information about social associations while building nests and the presence and absence of nest smacks in Tuanan ($N =$ total 453 night nest observations).

3.2.5. Kamunda Feeding in Tuanan

Animals might associate smacking sounds while nesting with feeding behaviour as they handle branches the way they would do while eating. Moreover, while feeding, they sometimes also produce smacks. Since smacking sounds while eating leaves from the Kamunda plant (*Leucomphalos callicarpus*) sound similar to the nest smacks, individuals might make these sounds because they associate the handling of branches and twig biting with their feeding behaviour (C. van Schaik, pers. com; see also 3.2.2.1). Therefore, time of feeding on Kamunda (of the total feeding time in each animal) were calculated to compare with the average frequencies of the occurrence of nest smacks while building nests (Figure 3.16). However, this correlation was not significant (Spearman Rank Order Correlation, $r_s = 0.195$, $p = 0.523$, $N = 13$), therefore allowing to reject this hypothesis.

Sumi is an adult female who does not often make nest smacks (17.6%) and therefore she might not eat or have much Kamunda in her diet. But she eats Kamunda as much as other individuals (4%). For example, the male Fugit also eats Kamunda about 4% of his total feeding time, but makes nest smacks while building a nest in 93.8% of all observed night nest events. The adult male Henk spends the least time feeding on Kamunda (2.7%); however, he still makes nest smacks in 75% of observed night nest events. Also, focal animals that were never observed performing nest smacks (Cipto, Ekko and Ucok) eat Kamunda. In Tuanan, all observed individuals eat Kamunda (M. van Noordwijk, pers. com.). Thus, this closer look still confirms the earlier conclusion.

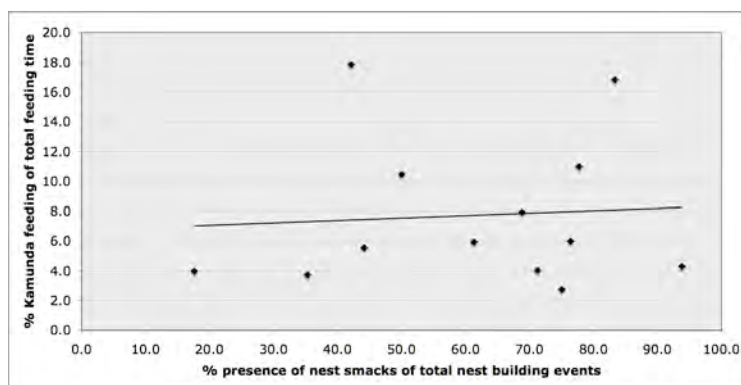


Figure 3.16: The average rate of nest smacks being present in night nest building (in %) in relation to the average rate of Kamunda feeding time (in % of total feeding time) in 13 individuals in Tuanan.

3.3. Playback Experiment

3.3.1. Immediate Reactions

Reactions to the playback experiment revealed that animals in general are reacting neither to the bird nor to the smacking sound. Mostly, individuals ignored the sound source. Mindy was the only focal showing a strong reaction towards the smacking sound. She stopped feeding immediately when hearing the first smacking sound and turned around, staring towards the sound source. She even moved a few meters down and closer towards it. None of the other animals ever showed such a strong reaction. Also, none of the focal animals ever vocalised to either the bird sound or the smacking sound (e.g. by making kiss-squeaks or a long call). Moreover, infants never went into body contact with their mothers, nor did the mother pay special attention to them (e.g. by emitting a throat scrape; A. Naso, pers. com.). No individual immediately travelled away from the source. Moving was always related to feeding (except for Mindy's smacking experiment, see above). If moving occurred, it was most of the time only a few meters within the same tree to grab fruits or leaves from another branch. Otherwise, if the focal went further, it was travelling to another feeding patch and feeding was continued there. Reactions for all the focal animals are listed in Table 3.9. This obvious lack of visible or audible reaction obviates the need for a quantitative comparison with the control condition.

Table 3.9: Reactions of six focal animals to either bird sound (B) or nest smacks (NS) in the experiment (voc: vocalization, cling: body contact with mother).

Focal	B/NS	Immediate Reaction on 3 sounds	Reaction during 10 minutes	Moving	Voc	Infant
Mindy	B	stopped feeding, did not turn around	continued feeding	after 3 mins moved to next feeding patch (15m) in opposite direction of sound source	none	Milo never cling during 10 mins of experiment
Mindy	NS	turned around on 1st smack, stopped feeding, looked towards sound source	continued looking towards sound source, sitting, scratching in-between, started feeding again after 10 mins	moved down about 5 m 2 mins after start, sitting again and looking towards sound source	none	Milo never cling during 10 mins of experiment, playing
Juni	B	looked up quickly after 1st sound, did not turn around	continued feeding in opposite direction of sound source	no moving	none	-
Juni	NS	did not turn around, feeding	continued feeding, after 1 min turned around to eat from another branch in direction of sound source	no moving	none	-
Fugit	B	did not turn around, feeding	continued feeding	no moving	none	-
Fugit	NS	turned around after 3rd smack	stopped feeding for about 30 sec, continued feeding	moved 2m in opposite direction of sound source and continues feeding after 4 mins	none	-
Nanio	B	turned slightly around on 3rd sound, looked towards sound source	lay on a branch on its back, facing upwards in the sky, scratching in-between	after 6 mins moved 10 m away in opposite direction of sound source	none	-
Nanio	NS	stopped feeding on 1st sound, continued feeding after 2nd sound	continued feeding	after 3 mins moved 2m up and continues feeding	none	-
Kerry	B	did not turn around, feeding	continued feeding	no moving	none	Kondor about 3m above
Kerry	NS	stopped feeding on 1st sound, turned around on the 2nd, continuously chewing	turned back again to opposite side of sound source and continued feeding	no moving	none	Kondor never cling
Jinak	B	due to time problems this experiment could not be conducted				
Jinak	NS	did not turn around, stopped feeding for about 10 sec on the 1st sound, then continued feeding	continued feeding	no moving	none	Jerry never cling during 10 mins of experiment

In order to analyse reactions, sector A (closest to the speaker; for setup see 2.3) was considered and comparison was drawn between the reaction to the bird sound and the reaction to the smacking sound. Data was taken during 10 minutes every 30 seconds. Reactions that occurred regarding the bird experiment were compared to the ones regarding the smacking experiment for the duration of 10, 5 and 2.5 minutes to find out whether there is a difference in the immediate reactions. Since Jinak's bird experiment could not be conducted due to time problems, she was not considered in the statistical analysis; however, her reaction to the bird sound is still listed in Table 3.9.

For none of the mentioned time periods was there any significant difference in looking in direction of sector A (towards sound source) between the bird experiment (control experiment) and the smacking experiment. However, for the time periods of 5 and 2.5 minutes there is a trend towards longer looking in the direction of sector A in the smacking experiment (Wilcoxon Signed Ranks Test, $Z = -0.944$, $p = 0.345$ for 10 minutes, $Z = -1.826$, $p = 0.068$ for 5 minutes, $Z = -1.841$, $p = 0.066$ for 2.5 minutes, $N=5$). A larger sample could reveal more accurate results. Figure 3.17 shows the average frequencies of looking in direction of sector A during time periods of 10, 5 and 2.5 minutes in the smacking and the bird experiment (for all focal animals combined, $N = 5$).

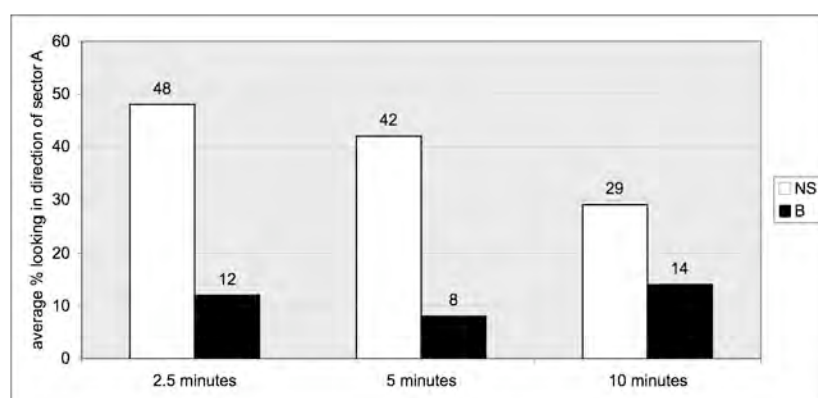


Figure 3.17: Average frequencies of looking (%) in direction of Sector A (closest to the speaker) for all focal animals ($N = 5$) in the playback experiment during 10 minutes, 5 minutes and 2.5 minutes in the nest smack experiment (NS) and the bird experiment (B, control).

3.3.2. Delayed Reactions

3.3.2.1. *Distance Travelled After the Experiment*

Further statistical analysis was done solely with four of the focal animals. Data of the adolescent male Nanio was left out. Nanio was building his nest soon after the bird experiment (6 minutes, about 20 meters away). However, when he heard noises from other orang-utans (Mindy, Milo) close by, he left his nest, travelled away, and built another night nest later on (100 minutes after the experiment start) and farther away, outside of the regular grid system. Due to this disturbance, this data was not considered.

As already mentioned, no focal immediately moved away from or clearly towards the sound source. Moving during the 10 minutes of data taking was related to moving to another feeding patch. For a broader view, distances between the place of the experiment and place of night nest building were measured on the regular maps that are taken daily on the focal animal's travel activity. Distances between the place of experiment and the place of night nest building ranged between about 5 meters (Kerry, smacking experiment) and 125 meters (Juni, bird experiment). Figure 3.18 shows the average distance travelled after the experiment's start until the place of nest building for the smacking and the bird experiment. Distance travelled after the smacking experiment was not significantly shorter than distance travelled after the bird experiment (Wilcoxon Signed Ranks Test, $Z = -1.604$, $p = 0.109$, $N = 4$).

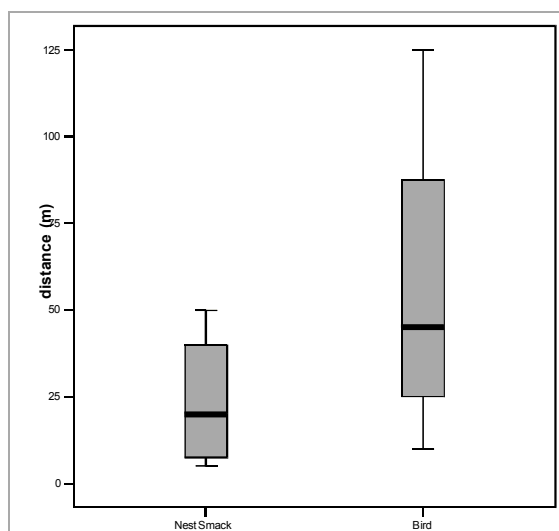


Figure 3.18: Average distance travelled (N = 4 individuals) after the experiment start until the place of nest building for the smacking experiment (NS) and the bird experiment (B) (median and range are indicated).

3.3.2.2. Nesting Time After the Experiment

Also, time between the start of the experiment and the time of night nest building was analysed. I calculated the amount of minutes between the start of the experiment and the start of night nest building and again compared results obtained from the smacking and the bird experiment (Figure 3.19). Once more, there was no significant difference (Wilcoxon Signed Ranks Test, $Z = -1.095$, $p = 0.273$, $N = 4$). However, since the experiment did not start at the same time for each focal (as early as 14:11 for Juni's bird experiment and as late as 15:27 for Mindy's bird experiment) it is hard to say whether nesting time is a delayed reaction on the experiment or whether it depends on other factors. Such other factors may be for example the amount of food an animal had already eaten during the day and food availability or also weather conditions or even territoriality that may play a role in time and place of nest building.

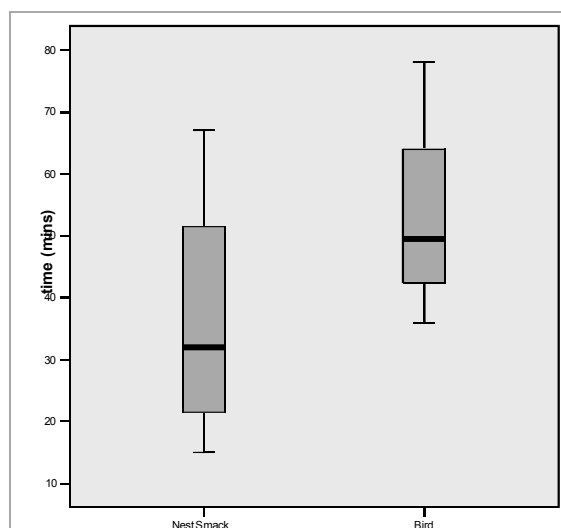


Figure 3.19: Average minutes (N = 4 individuals) between the start of the experiment and the start of the nest building process in the smacking experiment (NS) and the bird experiment (B) (median and range are indicated).

Therefore, to get another perspective, time of nest building between the two experiments was compared. However, this is probably a very individualized aspect of each focal animal's life and daily activity budget. There was a trend towards earlier nest building after the smacking experiment compared to the bird (control) experiment (Wilcoxon Signed Ranks Test, $Z = -1.826$, $p = 0.068$, $N = 4$).

I also compared nest building time after the smacking experiment to the regular average nesting time of each individual. There was no significant difference but there was a trend towards earlier nest building time after the smacking experiment compared to average nest building time (Wilcoxon Signed Ranks Test, $Z = -1.841$, $p = 0.066$, $N = 4$). However, comparing nest building time after the bird experiment to the average nest building time also revealed a trend towards earlier nest building after the bird experiment than average nesting time (Wilcoxon Signed Ranks Test, $Z = -1.826$, $p = 0.068$, $N = 4$).

Since this might be a seasonal effect, I also compared nest building time after both experiments to the "seasonal" average nesting time of each individual (seven regular nesting times before or after the experiments were averaged). There was no

significant difference but there was a trend towards earlier nest building time after the smacking experiment compared to average “seasonal” nest building time (Wilcoxon Signed Ranks Test, $Z = -1.826$, $p = 0.068$, $N = 4$). Moreover, comparing nest building time after the bird experiment to the average “seasonal” nest building time revealed a trend towards later nest building after the bird experiment than average “seasonal” nesting time (Wilcoxon Signed Ranks Test, $Z = -1.826$, $p = 0.068$, $N = 4$).

4. Discussion

The aim of this study was to examine the sounds that orang-utans make while building their nests. I collected data in the two ecologically similar sites Tuanan and Scbangau (Central Kalimantan, Indonesia, Figure 2.1). Since nesting sounds have never been described acoustically yet, sound recordings were collected in Tuanan and Scbangau and then entered into the computer in order to analyse their acoustic features. Merrill (2004) gave closer attention to the occurrence and function of nesting sounds in Suaq Balimbing (Sumatra) by looking at several nesting sound correlates. She also confirmed the complete absence of nesting sounds in Ketambe (Sumatra). Her results provide a basis for a comparison with the results from Tuanan and Scbangau. In Tuanan, I additionally conducted a playback experiment in order to gain more information on possible functions of nesting sounds.

4.1. *Nesting Sounds in Tuanan and SUBangau*

4.1.1. Description and Sound Analysis

Nesting sounds from Tuanan and Scbangau sound very different to the human ear. Nest smacks in Tuanan resemble a smacking sound whereas so called nest raspberries in Scbangau resemble a spluttering sound. Nesting sounds in both sites occur in the context of nest building (pers. obs.).

Sound analysis with Raven 1.2 (Charif et al., 2004) shows that the smacks have their average maximum frequency at approximately 1206 Hertz, whereas raspberries have their average maximum frequency at approximately 296 Hertz. Smacks are louder than raspberries, but compared to other orang-utan vocalisations, such as long calls, these sounds are very faint. Long calls are audible up to 1500 meters in the forest (MacKinnon, 1974). The smacking or spluttering sound is also weaker than the bending and breaking of branches while building a nest (pers. obs.). Therefore, animals probably recognize other animals building their nest more by hearing branch bending and breaking than by hearing the faint nesting sounds. In comparison, the

loud-calls of bonobos around nest building time are audible over long distances and function to alert others (Merrill & White, 1996). Therefore, nesting sounds probably are not long-distance communication signals, although they may be signals for short-distance communication.

4.1.2. Distribution Patterns

All well-habituated individuals in Tuanan and Scbangau make nesting sounds. Only some unhabituated individuals (that were also kiss-squeaking toward observers at a high rate) never performed nesting sounds so far. In Gorillas, a very soft “purr” sound is described not in a nesting context but when animals are utterly relaxed (Schaller, 1963). This may indicate that also nesting sounds are only made by habituated and relaxed animals that feel comfortable and secure to build their nests in the presence of human observers. However, in Tuanan, also some unhabituated individuals were observed making nesting sounds. Even though the two females Desy and Inul were followed only rarely and they still kiss-squeaked at observers at a high rate, they still made nest smacks when building their night nests (see Table 3.2). However, this sound may still serve as a calming signal for the nest-building animal itself or to reinforce its intention to build a nest. Alternatively, stressed animals may not build nests at all or only quick nests that lack additional lining, pillows or twig biting. Hence, because nesting sounds are associated to building a pillow or a lining, they also do not perform nesting sounds.

According to the cultural definition of Whiten (1999), a variant is considered cultural if it is customary (shown by most or all relevant individuals) or habitual (shown at least by several relevant individuals) at least one site but is absent in at least one other ecologically similar site. Nesting sounds could also be a cultural variant of the orang-utans’ behaviour repertoire (Merrill, 2004; van Schaik et al., 2003a; van Schaik et al. 2006). All observed, well-habituated animals made nesting sounds throughout all age/sex classes in both populations and in addition, even infants made such sounds while trying to build a nest. Results from the analysis show that nest smacks are well distributed in the Tuanan population and reach a customary level, whereas raspberries

are absent. In the Scbangau population, nest raspberries are shown on a customary level. Only two observed individuals, who both were mainly observed making raspberries very seldom, also made nest smacks or something similar to a smacking sound. Moreover, in Suaq Balimbing, the customary level of raspberries is confirmed as is the complete absence of any nesting sounds in Ketambe (Merrill, 2004; van Schaik et. al., 2003). Table 4.1 gives an overview on the occurrence of nesting sounds in four different research sites in Sumatra and Kalimantan.

Table 4.1: The occurrence of nesting sounds (smacks or raspberries) at four different sites: Ketambe (Sumatra), Suaq Balimbing (Sumatra), Tuanan (Kalimantan) and Scbangau (Kalimantan). Categories are defined as followed: C = customary, H = habitual, R = rare, P = present at unknown frequency, E = absent for clear ecological reasons, A = absent without clear ecological reasons (data for Sumatra from Merrill, 2004; with the permission of C. van Schaik).

Sound	Site			
	Ketambe (Sumatra)	Suaq Balimbing (Sumatra)	Tuanan (Kalimantan)	Subangau (Kalimantan)
Nest smack	A	A	C	R
Nest raspberry	A	C	A	C

4.2. Nesting Sound Correlates

4.2.1. Nest Building Duration and Nest Additions

In both populations, nesting sounds are more common in night nests than in day nests. In Scbangau as well as in Tuanan night nest building takes more time than day nest building. This supports the thesis that animals make these sounds in the later stage of nest building where they build pillows, pad the inner lining, and/or do the twig biting, which is again related to adding loose twigs to the nest. In contrast to night nests, day nests are of simpler construction and often miss additional lining with loose twigs. Also in Suaq Balimbing, animals spent longer building night than day nests and nest raspberries were more common in night than in day nests (Merrill, 2004).

In Tuanan, individuals spent significantly more time building day and night nests when nesting sounds were present than when nesting sounds were absent, whereas this was only confirmed for night nests in Suaq Balimbing (Merrill, 2004). In Tuanan, there are no differences between age/sex classes. In Scbangau, these results could not be statistically confirmed due to a small data sample. These results again support the hypothesis that nesting sounds occur in the late stage of nest building and are related to adding extra lining and loose twigs to the nest. Comparison between Ketambe females and Suaq females showed that in Ketambe, where animals do not perform nesting sounds, females spend less time building their nests (Merrill, 2004). Interestingly, animals in Ketambe also lack twig biting or the additional lining and pillow construction in the nest (van Schaik et al., 2003a).

Analysis showed that the production of nesting sounds in Tuanan is associated with the building of a pillow or an extra lining with loose branches. Due to a small sample size, this could again not be statistically confirmed for Scbangau. In Tuanan, one individual is an outlier. The female Sumi makes nest smacks rarely (in 17.6% of all observed nesting events). However, she builds a pillow quite often (in 75.9% of all observed nesting events). Sumi sometimes living in highly disturbed areas and observers cannot follow her closely. Therefore, she might perform nesting sounds more often but they cannot be tracked down (M. van Noordwijk, pers. com.).

Nesting sounds are also performed when individuals do not build a new nest but rebuild an old nest by improving it with twigs and branches. This again supports the fact that nesting sounds occur in the late stages of nest building where loose twigs are added to the nest. This adding of extra lining may improve the orang-utan's sleep by providing the potential for more relaxed and comfortable sleeping postures (Fruth & Hohmann, 1996).

In Merrill's study (2004), raspberries did not show any relationship to nest position or distance to the top of the nest tree. Nest raspberries do not appear to have any function related to nest exposure and probably do not have anything to do with the tree structure (Merrill, 2004).

In all experiments there was no vocal reaction at all. In Mitani's long call experiment, some males immediately "kiss-squeaked" when they heard long calls but most of them were never observed to vocalize following long calls under normal conditions (Mitani, 1985). In the present playback experiment, there was no vocalisation such as kiss squeaks, which could be the case if the animal feels uncomfortable or threatened (MacKinnon, 1974). Also, in experiments with mother-infant pairs the child never went in body contact with its mother, neither after the smacking nor after the bird song. Also, the mother never made a throat scrape (A. Naso, pers. com.). Therefore, they probably have not recognized the smacking as source of threat or danger and they probably have not felt uncomfortable.

4.3.2. Possible Function as a Communication Signal

As a communication signal, nesting sounds may have different functions such as distance regulation or announcing that the sender is bedding down and it is time for building the nest. However, as we have seen, most animals do not build their nest while a conspecific is around. Associations with other conspecifics are rare. Orang-utan are semi-solitary animals (Rijksen, 1978). Therefore, most of the time there is no receiver for this signal. Moreover, the sounds are really faint and are often not audible due to rain or branch breaking during the nest building process (pers. obs.).

When the nesting sounds should announce that a sender is bedding down, then the sounds should be made ahead or at the beginning of the nest building process. However, personal observations showed that no individual ever made sounds before starting to build its nest. Most of the time, nesting sounds were made towards the of the nest building process and results showed that sounds are associated with the lining of the nest with loose twigs in the late stages of the nest building event (this study; Merrill, 2004). However, in Kinabatangan (Borneo, Malaysia), animals make nesting sounds just before the nest building process starts (van Schaik et al., 2003a).

Nesting sounds could be used as a communication signal to indicate that an individual builds its nest in this spot. The signal-receiving individual is then moving away and

builds its nest somewhere else. However, distance between nesting associations may also depend on the relationship between the animals. Animals did not move away instantly after hearing the sounds. Sometimes they moved a few meters but this seemed to be more in order to find another feeding spot. Delayed reactions in terms of distance travelled after the experiment did not significantly differ between the two stimuli. Also the only flanged male that participated in the experiment obviously did not feel disturbed. Due to territory defence, it could have been that he showed a stronger reaction when he is realising an unexpected conspecific is around. He could have the intention to find out who is present since flanged males usually behave antagonistically towards each other (Mitani, 1985).

A possible communication function could be that animals announce that they go to bed and induce others to do the same (synchrony effect). Animals then should start to build their nest earlier after the smacking experiment than after the control experiment. However, there was no clear indication of this thesis since amount of minutes between the start of the experiment and the actual nest building process did not differ after the two different stimuli. Only considering the nesting times but not the start of the experiment, shows a tendency towards earlier nest building time after the smack. However, the start of the experiment was sometimes over one hour earlier. Nest building time compared to the average nesting time (over the whole data collecting period) did not indicate a difference between the two stimuli. However, for the “seasonal” nesting time (within the time period of the experiment) there was trend towards earlier nesting after the smacking experiment compared to the “seasonal” nesting time. Moreover, there was also a trend towards later nest building after the bird experiment compared to the “seasonal” nesting time. However, nesting time may depend on many other factors such as food, weather, season, activity, etc. In this case, may be a larger sample size could yield some more accurate results.

Animals showed no significant differences in reaction to the playback stimuli. Most likely seems the possibility that this signal induces other orang-utans to build their nest, too. However, this signal seems to have no major function. Since there is a lack of associated social or adaptive function for this behaviour it might be a candidate for a cultural variant.

4.3.3. Problems Conducting the Playback Experiment

It is quite difficult to analyse the experiment properly since there were many problems, which are listed as follows. However, there are also some suggestions for improvements. Therefore, I see this experiment as some kind of a pilot study playback experiment, which could be worked out more intensely and be done with more individuals.

- 1) There was only a very small sample size ($N = 5$ and $N = 4$, depending on the analysis) and not enough time to do more experiments. Moreover, due to time limitation, the experiment was only done in Tuanan and only nest smacks were used but no raspberries.
- 2) No video recording of the experiment was done since no camera was working at this time period and on the other hand there were not enough persons to assist with taking footage.
- 3) Other experiments were taking place in the same time period such as the tiger experiment as well as the long call experiment and had to be considered in time planning and choice of focal animals. Experiments could only be conducted in the dryer season and this is also why so many experiments had to take place in the same time period.
- 4) Weather conditions were important since the experiment could not be done when it was raining or very windy because of the sensitive equipment and the audibility of the playback stimuli.
- 5) Limited access to computer and also energy limitations (the generator was only working in the evenings) made it difficult to digitalize and prepare sound for the experiment.

4.3.4. Possible Improvements of the Playback Experiment

To improve the experiment it would be very helpful to have a personal assistant who could fully concentrate on the experiment and could help with videotaping. Recording the reactions would be very helpful to better analyze it and to look at it later on again.

of lianas (*Stenochlaea palustris*). However, a correlation between feeding sounds and nesting sounds was not analysed (Merrill, 2004; C. van Schaik, pers. com.). Therefore, the occurrence and composition of plants that are associated with smacking or spluttering could be analysed more closely in the different habitats. Another interesting aspect to consider may be the behaviour of infant orang-utans. To exclude ecological reasons one may look at whether infants in Tuanan perform nest smacks before they eat leaves from the Kamunda plant.

This study as well as Merrill's observations (2004) showed that nesting sounds are correlated with the padding and the lining of the nest with loose twigs. However, neither observations and analyses nor the playback experiment revealed an adaptive or social function. They are not likely to be a communication signal (this study; Merrill, 2004). Their lack of an adaptive function indicates that nesting sounds are not likely to be innovated and maintained by individuals trying to solve adaptive problems and thus ecological explanations for variations are not plausible (Merrill, 2004). Despite the fact that animals do not nest in social associations very often and that social associations are not directly correlated to the performance of nesting sounds, they still have regular social contact to conspecifics. This behaviour might be a by-product of copying the behaviour of other orang-utans that act as role models. Therefore, as imitating nesting sounds is not a complex task, variants of nesting sounds are likely to be spread through social transmission.

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- In Tuanan, focal animals make similar smacking sounds while eating leaves from the Kamunda plant (*L. callicarpus*). However, ecological associations with feeding behaviour could be rejected so far.
 - In the playback experiment, immediate reactions in terms of turning around towards the sound source tend to result in stronger response to the smacking than to the bird sound (control). Delayed reactions in the playback experiment did not clearly support a communicative function as a distance regulation signal or nesting time regulation signal.

7. References

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