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Nesting behaviour of the great apes

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Introduction

Nesting behaviour of the great apes is considered to be night-time behaviour, and it has been widely studied of apes in the wild with focus on preferred tree species, heights of the nests, and nest group sizes. There are also several different theories on why this behaviour occurs.

In this thesis, different theories behind nest building behaviour will be discussed as well as nesting behaviour in captive settings as this is rarely studied and may have implications for the welfare of captive apes.

The chimpanzee, the gorilla, the bonobo and the orangutan all use nests as sleeping platforms during the night. Sleep and nesting is closely related. Day nests are sometimes built to rest, eat and groom in, but night-nests are more complex and the apes use more energy and time building night-nests.

There is no doubt; “nest building forms an integral part of the behavioural repertoire of all wild populations of great apes” (Fruth & Hohmann, 1996). McGrew (2004, p 107, in Lock, 2011) described it as “…..the most solid of norms” in their daily activity budgets.

Without any guidance from other apes, an individual ape will try to build a nest or a nest-like structure; early analyses could prove that there is a genetic component to nest construction. It is also clear that young apes that are more exposed to nest building adults are much more efficient nest constructors and they also build stronger nests. This supports the theory that

primates make conscious decisions about the nest building. Some researchers have even suggested that the knowledge and technological skills that great apes possess about nest building may be a precursor to tool use; both of these skills require sophisticated cognition and thinking (Yoshida, 2012).

There are four main hypotheses behind this behaviour which will be discussed in this thesis:

- Anti-predation
- Increased thermoregulation and shelter
- Increased comfort ability and quality of sleep
- Anti-pathogen

There are variations in nesting behaviour between species, age-classes and sex. Together with some aspects of the social factors in nest building some of these variations will also be mentioned.

Nest building also occur in captive settings if suitable material is offered. Examples of captive apes showing nest building behaviour: the majority of a group of laboratory housed chimpanzees tried to build nests for sleeping in when they were offered some material (Bernstein, 1962). Gorillas and orangutans in captivity were also observed to attempt to build nests when they were offered materials suitable for nest construction (Bernstein, 1969), (Lock, 2011).

Adding nesting materials could enhance natural behaviour in apes kept in zoos and other captive settings. It could also improve the quality of life for these animals as it will allow species-typical behaviour, and it may also increase the quality of sleep and rest, allowing a large bodied animal to sleep comfortable.

Sleep-the importance of it

Sleep is a vulnerable state for animals as it compromises the ability to detect predators and it is time consuming (Campbell & Tobler 1984; Hornyak et al. 1991; Lima et al. 2005). A human spend around eight of twenty-four hours sleeping while chimpanzees spend around 8.8 hours (Stanley, 2005; Videan, 2006b). The great apes are all diurnal which means that they

are active during the day and sleeping throughout the night. It is necessary and advantageous for the great apes to sleep. During the sleep the apes get rest and restore their ability to learn, memorise and function normally both mentally and physically. Sleep also allows the body to heal; this is marked by growth and repair of the immune system and the nervous systems and also in muscles and bones (Savage & West 2007; Siegel 2005, 2008). In sleep, the body temperature decreases as well as the metabolic rate and so sleep also helps in conserving energy (Webb 1975).

In mammals sleep consist of a non-rapid- (NREM) and rapid eye movement sleep (REM). NREM consists four stages: in stage one the sleep is light and drowsy, while its more deep and slow waved in stage three and four (Stanly, 2005; Lock, 2011). In the last part of the night the REM sleep increases and it is now the predominant type of sleep.

"Sleep architecture, the distribution of slow-wave sleep stages in the beginning and REM sleep towards the end of the sleep period, is suggested to reflect an evolutionary trade-off between the benefits of sleep versus risk of predation (Lima et al. 2005). Great ape nest building may be a solution to this trade-off allowing a large-bodied primate to have relaxed sleeping postures and greater REM sleep" (Stewart, 2011).

Chimpanzees in captive settings have been reported to sleep most of the night on their right or left side compared to supine position (Videan, 2006b). On the other hand Stewart (2011) found that wild living chimpanzees almost only slept in supine posture and that they found this position soon after building the night nest. Maybe the supine position is more comfortable in the wild due to the cup shape of arboreal nests (Stewart, 2011) whereas in captive settings the apes use different nesting material to build nests on a flat support structure (Videan, 2006).

As we can understand a good night sleep is rather important for the great apes, and this may have been one of the reasons why nesting behaviour evolved.

Survey of literature

Why build nests?

Constructing nests is a daily habit among all the great ape species for sleeping during the night or resting during the day (Fruth & Hohman, 1996). Nests are believed to increase the comfort when sleeping (Anderson, 2000), improve thermoregulation (Fruth & Hohman, 1996) as well as to provide protection from predators and pathogens.

"The pattern of nest construction across all great apes typically follows a standardised sequence – selection of sleep site, construction of the nest foundation (by bending, breaking and weaving branches in a criss-cross pattern), constructing the nest rim (by bending smaller twigs in an approximately circular shape around the circumference), and finally lining the nest by picking and adding softer twigs and leaves (Fruth & Hohmann 1996)" (Lock 2011).

I. The theory of anti-predation

Most primates live in trees and are said to be arboreal species, but even the more terrestrial species such as the chimpanzee choose to sleep at elevated heights in trees during the night.

The body sizes of the great apes are variable according to species, age and sex, but all the great apes may be considered to have a relatively large body size and the fact that they also have low densities (Hayward et al. 2006a) limits the number of possible predators (Zuberbuhler and Jenny, 2002). In addition to this most of the great apes are distributed within closed forest habitats (Lehmann and Dunbar, 2009). Altogether this means that the great apes are thought to be at low risk of predation.

Despite this, the most important theory behind nest building among the great apes is still the avoidance of predators. If we consider their long life time, their slow maturation to reproductive age and long intervals between births, even low rates of predation could have significant impact on the great apes (Stewart and Pruetz, 2011).

Leopards and lions are able to prey on great apes but they are not the most preferred prey. Lions prefer preys that are in the range of 190-550 kg (Hayward and Kerley, 2005). But there are always exceptions. In Mahale Mountains National park the deaths of four chimpanzees were caused by lions over a period of four months. Hair and bone from chimpanzees were found in lion faeces during this time (Tsukahara, 1993).

Leopards prefer preys that are 10-40 kg, with the most preferred weight of 23 kg. Chimpanzees are within this range and especially juveniles and females (Hayward et al. 2006a). In this analysis both gorillas and chimpanzees are taken by leopards according to their abundance.

Juveniles and females frequently build their nests higher up in the trees than adult males do. This may be due to their increased vulnerability.

Gorillas are different compared to the other great apes; they often build ground nests (Schaller, 1963; Remis, 1993; personal observations). Maybe this is due to lack of trees that can support their large body size or the low risk of predation on these large apes. Juvenile gorillas however, tend to nest arboreally, and sometimes adults and silverbacks do too. The low proportion of ground nests built by young gorillas indicates their vulnerability to predators (Yamagiwa, 20009).

Nesting at elevated heights in trees makes the great apes more inaccessible to potential predators and many primates sleep toward the terminal ends of branches as this could help them detect danger early and permit escape (Anderson, 2000).

II. The theory of nesting and comfortable sleep

As I already mentioned all the great apes are of relatively big size in adulthood. The importance of sleep has also been discussed. Nests may contribute in providing these large bodied animals to rest horizontally and more comfortably and this may in turn improve the quality of sleep. REM sleep is accompanied by loss of muscle tone and so requires a horizontal platform and recumbent posture (Stewart & Pruetz, 2013). Nesting may also provide fewer disturbances from environmental factors like cold wind, wet ground etc.

Some authors even suggests that the ability to sleep more comfortable and safely may have had an influence on the type and quality of sleep, increasing the energy available the next day

which could have enabled cognitive evolution in hominids (Baldwin et al. 1981; Fruth & Hohmann 1996).

One should also keep in mind that great apes are active during the daytime, and their vision is not adapted to darkness. The nest may provide a feeling of security when resting and sleeping in the heights of trees, and one can imagine that it is more comfortable to sleep in a safely build nest than on a simple branch of the tree where falling down could be a risk factor (Baldwin et al.1981).

The nests consist of branches and leaves, and the softer leaves are put on top which may provide a softer and warmer "bed" for these heavy animals. Bonobos (Fruth & Hohmann 1993) were proven to prefer nesting at canopy heights, where there was increased amount of more flexible and softer twigs and leaves, which may have facilitated the construction of a more comfortable nest. Stewart et al. (2007) reported that chimpanzee nests that contained additional material (leaves, twigs and branches) were more comfortable in the central area, where most of the body weight is distributed. Ghiglieri (1984) reported that chimpanzees often pulled „padding material" from up to four surrounding trees and added them to the nest (Lock, 2011).

All these findings indicate that the great apes favour to rest and sleep in as comfortable nests as possible and the anti-predatory theory is not the only important theory behind nesting behaviour.

III. Theory of nesting for better thermoregulation and protection from hoarse weather

Another hypothesis for nesting behaviour is that it may have a function in thermoregulation (Fruth & Hohmann, 1996). Sleeping in nests could help to achieve both heat loss and uptake. This would depend on the climatic conditions. The advantage of this is a reduction of metabolic costs of physical thermoregulation (Kosheleff and Anderson 2009). It is assumed that arboreal nesting provides some protection from rain, cold winds, wet ground and other hoarse weather condition.

Sleeping in a nest may give insulation from low ambient temperatures during the night (McGrew, 2004). In 2011 F.A.Stewart carried out an empirical study with a human subject, this study provided support for the insulation function of arboreal nests at a location with low temperatures during the night. Her study was aimed at chimpanzees. Further on Stewart found that nest variation on two different sites (Issa and Fongoli) revealed nests to be thicker in cooler conditions and to use more broken branches 1-3 cm in diameter and break support in conditions with higher humidity. This may reflect greater insulation of nest. In Fongoli, Stewarts results supported her hypothesis that nests with greater structural support are made in conditions with increased wind.

Another study proved that western gorillas at Mondika typically sleeps on the ground, but when rainfall increased and temperatures decreased they more often made nests (Mehlman and Doran, 2002). One can assume this was to seek protection from rough weather and to stay warmer when resting and sleeping.

Chimpanzees at Assirik, Senegal, built their nests higher up in the trees and more open to the sky during the wet season, maybe this was to avoid dripping vegetation and giving them increased exposure to morning sunshine (Baldwin et al. 1981).

IV. Anti-pathogen

Another theory or hypothesis for the nest building behaviour of the great apes is the avoidance of disease vectors like the mosquitoes. By sleeping up in the trees, mosquitoes and other pathogen may be avoided (McGrew, 2004).
There are approximately 400 parasite species infecting primates and around 30 % of these are transmitted by arthropods (Pedersen et al, 2005. Stewart 2011).
Viruses and helminthes are sometimes also transmitted by vectors although protozoa are most common. Examples are malaria, Plasmodium sp.

During Fiona.A.Stewarts (2011) study on chimpanzees she slept both on the ground and in nests in trees made by chimpanzees. She counted the number of bites and compared the different results of her experiment. She found that she was bitten by insects etc. more frequently during ground than in nest and the number of bites per hour was also fewer when

she slept in nest. Mosquitoes were the main irritant, but she also observed that she got bitten by tsetse flies and ants.

“The hypothesis that arboreal nest sleep reduces bites from possible vectors was supported with an order of magnitude more bites received on the ground “(Stewart 2011).

In contrast to this Koops et al. (2012) found no difference in mosquito density at different heights in Guinea. Maybe it is the freshly broken branches of nests that chemically deter biting insects and results in fewer bites? (Stewart, 2011). Some bird species are also known to select aromatic nesting material to reduce nest bacterial load (Starlings, Gwinner, Berger, 2005) or repel insects (Lafuma et al., 2001), (Stewart, 2011).

It may seem like mosquitoes affects sleeping habits in several primates. For example, in New World monkeys, the use of dense vegetation as well as tree holes as resting and sleeping sites has been thought to decrease the exposure of Anopheles mosquitoes and thus reduce the malarial infection rates (Heymann & Nunn, 2005).

Another example is that the orangutans in Borneo chose to make nests of tree with mosquito-repelling properties in periods with a lot of mosquitoes (Largo et al. 2009). The orangutans were also observed carrying pieces of these tree species as covers for other nests.

Some social aspects of nesting

In 1996 Fruth and Hohmann found that clusters of nests built at the same time and in the same area by gorillas, bonobos and chimpanzees indicated that nest building is an inherently social activity (Lock, 2011). Generally one can say that free living apes sleep socially. This was, however, not true for orangutans (Rayadin &Saitoh, 2009) even though some adult males have been observed to sleep in the very same nesting tree as a female-infant pair and a juvenile (Schaller, 1961).

There are variations within species of the great apes concerning the social aspects of sleeping. Gorillas tend to nest and sleep in the same group as during the day. Medium-sized mountain gorillas and juveniles often nest closer to each other compared with other age/sex classes in

the very same group. These medium sized gorillas (females and non-silverback males) usually nested 1,5 meters from each other, less than 1 meter from juvenile, but 4 meters from silverback males (Schaller, 1965).

In contrast bonobos often form larger nesting groups (Fruth & Hohman, 1996). A study have proved that daytime groups of bonobos consisted of a maximum number of 9, and during the night this number increased to 24 individuals in a nesting group (Mulavwa et al. 2010). Bonobos of lower ranking have been reported to sleep in the periphery of the nesting group (Fruth & Hohmann, 1996).

On the other hand, chimpanzee daytime groups usually decrease into smaller groups for night-nesting. Observations have indicated a number of 2 and 4 nests per group within a single tree or trees standing close to each other (Baldwin et al. 1981), (Lock, 2011). Among chimpanzees females and juveniles nest close to each other while the mature males nests further away from the group (Goodall, 1968). Two adult male brothers have been reported to build and share the same nest, they were observed sleeping in close contact to each other during the night (Riss & Goodall, 1976).

There are several theories behind the social aspects of sleeping patterns in the great apes. Some of them form smaller groups during the night while others prefer to nest more isolated,

like the orangutans, and some form larger nesting groups. It could be that they simply nest closer to individuals they prefer or are related to, or it may have some practical aspects, like earlier detection of predators for example.

Terrestrial nesting

All the great apes build nests; the chimpanzee, the bonobo, the orang-utans, and the gorilla. They do it every day, sometimes more than once. They prefer different nesting sites, heights and materials etc. but there are only one major difference; the gorilla frequently nests on the ground rather than up in trees, they are said to be terrestrial nest builders. They sometimes even sleep on the bare ground without any nest (Scaller, 1963; Remis, 1993). The other species build nests in trees, so called arboreal nesting.

There are two possible explanations for this phenomenon in gorillas; there may be a lack of trees strong enough to support their large and heavy body (Remis, 1995) or the predation pressure is so minimal that they simply don't need the protection that arboreal nesting may provide (Yamagiwa, 2001). When this is said there are always exceptions from the rules. Young gorillas often build nests in trees and occasionally also adult males sleep in a tree nest.

But why would a huge ape build a nest on the ground? One reason could be that a nest, even on the ground will insulate the gorilla's body from damp ground and in this way increase the comfort and hence increase the quality of sleep and maybe also reduce skin irritation and

exposure to parasites. Another theory could be that the ape might find it easier and quicker to build a comfortable nest on the ground than in a tree.

Studies have proved that there are sex differences in gorillas nest construction. Female gorillas build nests in trees more frequently and higher up than silverbacks do (Mehlman & Doran, 2002 , Tutin et al. 1995). Furthermore silverbacks nests on the ground more frequently than non-silverbacks (Mehlman and Doran, 2002; Remis, 1993). This could indicate that more vulnerable gorillas prefer to make tree nests for the sake of protection during the night.

Yamagiwa (2001) studied the nesting of the gorillas. He found that in any type of vegetation, immatures built the highest nests and the proportion of ground nests built by immatures was significantly lower than those by adults. This could be due to their smaller size and hence it could be easier for immatures to find nesting places and materials in trees. It may also point to the fact that young animals are always more vulnerable to predators and ground nesting is not as safe as arboreal nesting.

One should also consider that there are local variations in the proportion of ground nests across different populations of gorillas. In the forest of Virunga, the highest proportion of ground nests was found; 97,1%. In this area shrubs and herbaceous vegetation used for nesting material are found abundantly on the ground (Schaller, 1963). On the other hand, in the tropical forest of Petit Loango where terrestrial herbaceous vegetation is sparse only 7,3% of the nests were on the ground (Furuichi et al.,1997; Yamagiwa, 2001).

Western gorillas sleep on bare-earth nests approximately 45% of time, constructed ground nests 35% of time, and arboreal nests 20% of time (Mehlman & Doran; Remis, 1993).

Another interesting study focuses on the influence the presence or absence of a silverback male has on ground nesting in a gorilla population; Yamagiwa (2001) compared the proportions of ground nests built by both adults and immatures during three different periods: before the death of their leader, after the leader had died, and after the new leader male joined. He found that the mean proportion of ground nests for adults as well as immatures decreased after the death of the leader. When the new leader arrived this proportion increased again, but this was not completely true for the immatures;

"After the new silverback joined the group, the immatures still showed a lower proportion than that before the original silverbacks death, although adults recovered the previous level of ground nest building. The immatures may have avoided the new male and not rely on his protector ability as they did with the previous leader" (Yamagiwa, 2001). This implicates the importance of the leader male as a protector. The gorillas seem to nest more frequently in trees in case of compromised security.

A study on ground nesting carried out by Kathelijne Koops, William C. McGrew, Tetsuro Matsuzawa, and Leslie A. Knapp (2012) is the first one to prove that not only gorillas build night nests on the ground. They provided evidence of widespread ground nesting in a population of chimpanzees, which are usually arboreal nest builders. In this case, it was clear that males tended to sleep in ground nests more frequently than females.

Activities and nest locations

Stewart (2011) observed a few day nests in her study of chimpanzees, as her collection of data focussed on night nests. Fruth and Hohman (1993) found that bonobos used day nests for grooming and playing as well as for resting. They also noticed that these day nests were used to create a personal space, so the bonobos actually used day nesting as a social tool (Fruth & Hohman, 1993). In Stewarts (2011) study on chimpanzees she concluded that nests were used more or less only for resting, but she found food in and under several night nests; this could indicate that some chimpanzees went to their nests with food or they fed during the night and returned to their nests with food. Stewart also saw young individuals play with old nests, but she could not report any social interaction in a night nest. Pruetz (2008) on the other hand observed that day nests were used for social play, grooming and a place for mothers to leave their infants in for a while.

Great apes might spend as much as one half of their lives in nests. Wild living apes have areas they prefer to nest in, and they have also been observed to prefer specific trees for sleeping in (Goodall, 1986; Sept, 1992). A study from Tanzania found that chimpanzee nests were distributed non-randomly, with the highest number of nests on sloped areas (Hernandez, 2009). In Guinea-Bissau, 92 % of 287 nests were found in oil-palm trees, this may indicate a preference for oil-palm trees (Sousa et al. 2011). Some ape species, like the bonobo and the

chimpanzee, re-use nest locations over generations (Fruth & Hohmann, 1994). These nest sites may have abundance of food resources (Goodall, 1986), vegetation they prefer (Furuichi & Hashimoto, 2004), the right type of forest (Baldwin et al. 1981) and low predation risk (Pruetz et al. 2008).

Studies of captive apes have also shown that some nesting locations are habitually used, seemingly because these sites are preferred to sleep in (Lock, 2011).

Age and sex differences

Sex differences

In a study by F.A.Stewart (2011) she found that nest building in chimpanzees differed between the sexes. She found that females built nests in larger trees than males and they also spent longer time building the nests. Female nests were also shorter in diameter; they were more circular and also thicker than the nests built by males. In addition to this she found that females used more lining, leaves, material of greater diameter and they selected support branches for their nest more carefully than males did. This suggests that females include a greater number of larger branches than males.

Bonobo females were reported to build higher in trees and earlier than males (Fruth, 1995). This was believed to be due to the fact that both Pan species compete for access to females in oestrus (Gerloff et al.1999; Wroblewski et al. 2009) (Stewart, 2011). Female bonobos retire earlier in the evening than males (Fruth & Hohmann, 1993).

In Stewarts (2011) study, male chimpanzees tended to concentrate their nests around and under females in oestrus. Males may chose nest sites beneath females to prevent other males access to females.

Female chimpanzees have been reported to build day nests more frequently than males in more than one study (Brownlow et al, 2001; Hiraiwa-Hasegawa, 1989). Male orangutans and male gorillas do not construct night nests as often as female of the same species (Fruth & Hohmann, 1996).

In Bornean orangutans adult males made their nests at lower sites than orangutans in other age-sex classes. Female orangutans with infants often built nests near the main stem where the tree crown most probably would cover them (Rayadin & Saitoh, 2009). Adult orangutan males with larger nest size were reported to reuse their nests more frequently than females. 29,3 % of orangutans reused their nests in the study carried out by Rayadin and Saitoh (2009). Reusing of nests is more common in orangutans; only 13,8 % in chimpanzees (Plumptre & Reynolds, 1997) 4,1 % in gorillas (Iwata & Ando, 2007) and bnobos 0,2 % (Fruth & Hohman, 1996). There could be several reasons for this variation; habitat, access to nesting materials, food availability and the number of suitable nesting sites.

It seems like females more over invest more energy and time in nest building, maybe because they most of their lives have offspring dependent on them and so they have to build bigger and safer nests for two individuals.

Age differences

The nest building of the great apes is known to be a learned behavior. This was determined by comparing the skills of wild-born chimpanzees and chimpanzees born in captivity (Bernstein 1967; Videan 2006a). Many captive individuals gather materials for the night, but only individuals with more experience construct complex nests to sleep in, so the disposition to build nests may be innate (Bernstein 1967; Videan 2006a).

In 1995 Fruth analysed the nesting of bonobos and found that when age increased the duration of construction decreased and the duration of use increased. She also found that immatures and juvenile bonobos practice nest building in daytime before they start to construct nests for night. She concluded that their skills improved over time (Stewart, 2011).

Infants of orangutans and gorillas start to build their own night nests a bit earlier (between 3 and 4 years of age) than chimpanzees and bonobos (Fruth & Hohmann, 1996).

Another feature of immatures, analyzed by Stewart (2011), is that immature chimpanzee males built nests higher up in the trees than adult males did, and also more peripherally from the trunk of the tree. They also used more constructed support branches, but the complexity of the nest building was lower than for mature males. The nests of immature female chimpanzees were found to be quite identical to that of their mothers (Stewart, 2011).

In a study of Bornean orangutans by Rayadin and Saitoh (2009) they demonstrated that the mature orangutans with larger body size made larger nests than immatures. The individuals with smallest body size also made the smallest nests and the largest males made the largest nests. This has also been observed in gorillas, were nest size was smaller for young gorillas than for adults (Groves & Sabater Pi, 1985). Immature orangutans with smaller nests usually made their nests higher up in the trees compared to adult individuals and larger orangutans built larger nests at more stable sites, which are easier to find at lower heights. As young animals are more at risk of predation, it may be safer for them to sleep at elevated sites, and branches at the end of trees are able to support their small size nests. Adults with a higher body weight need nest locations that are able to provide increased support for a big nest and a big body size (Rayadin &Saitoh, 2009).

Nesting in captive settings

The great apes will show nest building behaviour both in the wild and in captive settings if they have the possibility (Berle et al. 1995; Bernstein 1962, 1969; Goodall 1962, 1968; MacKinnon 1974; Videan 2006a).

The provision of suitable nesting materials has proven to encourage this species-typical and natural behaviour among great apes in captivity; both in laboratory and zoo-housed animals. There are several studies showing this fact; Berle 1995, Bernstein 1962, Hill 2004, Lukas 2003, Videan, 2006.

Louise C. Lock (2011) studied captive chimpanzees and she presented data from a nation-wide survey of zoos and safari parks holding at least 3 different species of great apes, and she also made direct observations/video recordings of two captive chimpanzee groups. Her research has proved that nesting behaviour is an important factor in the welfare of captive apes;

«The series of studies in this thesis show that multiple aspects of nesting in captive chimpanzees mirror those of their free-living counterparts. Survey data indicated that captive chimpanzees construct both elevated and, less frequently, terrestrial nests, in keeping with reports of free-ranging chimpanzees (e.g., Goodall 1962; Koops et al. 2007) » (Lock, 2011).

Lock (2011) also found variations in frequency and duration of nest building between sexes of the captive chimpanzees she studied. Females usually spent longer time nest building and they also constructed nests more frequently than males. This also reflects the habit among wild living populations.

As I mentioned earlier chimpanzees in the wild tend to separate into smaller groups when forming nesting groups for the night compared to the larger daytime parties. Lock (2011) found that the chimpanzees she studied in captivity formed nesting groups that contained similar numbers of individuals to those of wild populations.

Lock (2011) also managed to provide the information that the motor patterns used in nest building, like gathering materials and arranging them around the body, were quite similar in captive (Bernstein, 1962; Morimura & Mori, 2010) and wild living chimpanzees (Goodall, 1962; Nissen, 1931).

During the research, Lock (2011) discovered that the majority of her survey respondents gave combinations of materials to their captive apes. Her data also revealed that softer nest materials were chosen over others, and this resulted in higher rates of nest building, even in apes that seldom built night nests. Maybe the urge for physical comfort was the reason of this phenomenon and if this is the case the hypothesis of nest building for increased comfort when sleeping is supported.

In 2001 a study on nest building in captive gorillas were published in the “International Journal of Primatology”. This study presented that gorillas frequently built night nests in an indoor holding facility. They put hay around their bodies, tucked it under themselves and

fluffed it around their heads and bodies to create a nest. All the gorillas had access to nesting materials in Zoo Atlanta and they all performed some nesting behavior.

The gorillas in this study also nested in more elevated sites in cold weather and used more time on the floor in warmer conditions. According to Mehlman and Doran (2002) these findings could be directly related to wild gorillas, who also built more nests in cold weather compared to warm weather (Lukas et al. 2003).

The nest building behavior is not deficient in gorillas born in captivity. The 3 year olds gorillas at Zoo Atlanta usually nested with their mothers, but they engaged in nest-building anyway. These observations might suggest that the behavior will advance by time until the gorillas start nesting on their own (Lukas et al. 2003).

At the end of her study, Lock (2011) gave some recommendations for sleeping and nesting structures for captive apes;

"As the majority of captive apes (survey data; these data) will regularly build nests, enough material should be provided that individuals who choose to build a nest can do so. If possible, extra materials should be provided to allow lining of the nests, and to ensure that nests can be amended, thus encouraging natural nest building patterns and improving comfort. To accommodate both arboreal and ground nesting, a mixture of elevated, mid-level, and floor substrates that can be used by all individuals should be provided. These would also reflect the age- and sex-class differences in preferred nesting heights of wild apes. Having a range of nesting locations/ separate sleeping rooms would permit alternative nesting opportunities in cases of nest abandonment (documented here) and nest usurping (reported here and in survey data) " (Lock, 2011).

"Sleeping areas should include elevated structures and substrate-covered flooring and the elevated sleeping sites need to be stable and firm. Sleeping locations should allow optimal distance from other individuals" (Lock 2011).

Soft materials that were easy to manipulate were preferred and these types of materials should be given to the great apes to encourage the construction of nests.

“At least two different materials should be presented at the same time to encourage species-typical nest-lining behaviour” (Lock, 2011).

Enrichment for captive non-human primates

We should know the natural behavior and physiology of species when keeping it in captivity. It is important to develop a satisfying enrichment program to meet a species behavioral, physical, social, cognitive, and psychological need.

Environmental enrichment devices

Environmental enrichment devices are objects that can be manipulated by the animal. Natural environmental enrichment devices can be large and small branches of trees, wood wool, hay and other plants. The plants/trees/flowers should be harmless to the animal and it should be kept clean to prevent bacterial growth. Artificial devices such as balls, tires, rubber toys and puzzle boxes can also be useful (Lutz & Novak, 2005).

Habitat Enrichment

The design and size of habitat is crucial for providing enrichment for captive animals. Different substrates, levels and complexities should be available in the captive habitat. It should be possible for the animals to reach and change platforms. Tiers and ropes should be provided as well as nesting areas, suitable feed/water sites and crevices for environmental enrichment devices and food hiding for enrichment.

Sensory enrichment

Sensory enrichment is made to address the animals senses; smell, vision, touch, hearing and taste. It should also enhance species-typical response, territorial, reproductive or hunting behaviors. Materials of different textures like straws, wood or paper can provide tactile stimuli. Environmental enrichment devices of different colors that can be moved by wind/water can provide visual stimuli, as well as the sight of other animals. Mirrors and video presentations are also examples of visual stimuli.

Food enrichment

There are many ways to present food to captive animals. Feeding, hunting, foraging behaviors and problem solving strategies can be enhanced by a variety of ways to provide food. The food may be served fresh, frozen, hard, smooth or even buried in the habitat.

Social groupings

The knowledge of how the animals in a given specie feed in the wild should be taken into consideration when feeding captive animals. Social groupings should reflect those in wild living animals to facilitate feeding, grooming, social and territorial behaviors.

Behavioral conditioning

Training to maintain learned behavior or to learn new behaviors. Animals often voluntarily take part of this kind of stimulation. It should be based on rewarding positive and wanted behavior, rather than punishing unwanted actions. This may increase the intellectual focus of an animal (Maple & Stine, 1982).

Nesting as environmental enrichment in captivity

As discussed earlier in this thesis, sleep quality and duration is important for the health of mammals in several ways; repair the tissues of the body, control thermoregulation and regulate the immune system (Walker, 2008) as well as to allow the animals to function both mentally and physical. Deprivation of sleep can result in depression, memory impairment (Killgore et al. 2008) and increased blood pressure (Banks & Dinges, 2007).

Therefore it is crucial for captive apes to have a safe and sound place to rest and sleep during the night which can offer comfort and warmth.

Nest building is species-typical behavior that can easily be accommodated in captive settings. It can encourage natural behavior, permit better thermoregulation and help activating great apes in zoos and laboratory holdings. It is also believed to increase the feeling of security and physical comfort, which in turn may influence the welfare of the animals.

"Welfare should be assessed in terms of what individual species have evolved to be able to cope with" (Barnard & Hurst, 1996).

It is know that animals in captivity sometimes show abnormal behavior which does not occur in the wild. Examples are regurgitation and re-ingestion in gorillas (Akers & Schildkraut, 1985; Lukas, 1999) and stereotyped body rocking in chimpanzees (Pazol & Bloomsmith, 1993) (Hosey, 2004). Self-mutilation in laboratory-housed primates has been reported to be a major problem (Chamove et al., 1984), although this behavior is rarely seen in zoos (Hosey & Skyner, in preparation). Abnormal behavior should be prevented from occurring, and there are several ways to improve the life quality of animals in captivity.

British legislation requires that zoo enclosures:

"…should be equipped in accordance with the needs of the animals with bedding materials, branch work, burrows, nesting boxes, pools, substrates and vegetation and other enrichment materials designed to aid and encourage normal behaviour patterns and minimise any abnormal behaviour" (Secretary of State‟ s Standards of Modern Zoo Practice 2004, Chapter 4) (Lock, 2011).

Animals in the wild also face stressors, and the welfare of free-living primates may also be compromised at times (Hosey, 2005). Over the years, humans have destroyed large areas of the natural habitat of several primate species. This affects the nature negatively and the welfare of the animals in such areas is a concern (Kirkwood et al., 1994; Sainsbury et al. 1995).

It is important to understand how variables in captive settings can have implications on the welfare of the apes.

"Environmental enrichment is a concept which describes how the environments of captive animals can be changed for the benefit of the inhabitants. Behavioral opportunities that may arise or increase as a result of environmental enrichment can be appropriately described as behavioral enrichment."

-D.J. Shepherdson

It is obvious that all personnel working with great apes in captivity should be educated about nesting behavior, and they should provide a suitable amount of materials that can be used for the construction of nests. Documents and polices that set care and housing standards for apes should always include that nesting materials are necessary (Lukas et al. 2001).

Knowing that nest building is a species-typical and natural behavior of all great apes makes it clear that all captive apes should be given the opportunity to perform this behavior. All facilities that keep apes in captive environments should be aware that two different bedding substrates may encourage nest building (Nissen, 1931), (Lock, 2011).

Discussion

The aim of this thesis was to highlight some different aspects of nesting behaviour of the great apes, looking particularly on the theories behind nest building to get a better understanding of why this behaviour occurs and why it is important to give captive apes the possibility to nest.

Anti-predation

Chimpanzees has been proven to build nests higher (more elevated) in areas with high risk of predation. Average nest height of chimpanzees is between 10-20 meters (Fruth & Hohmann, 1994), but in the Tai forest, were there is high risk of predation, nests were found 23 meters above the ground. In Zaire chimpanzees were reported to escape to the tallest trees that could provide a good view of humans nearby, maybe to detect threats earlier (Kortland, 1992).

Were leopards and lions are more common, the median height of chimpanzee nests are usually higher (Baldwin et al. 1981) and they also nest closer together and avoid the more open nest sites compared to populations that are in less risk of predators (Stewart, 2011).

Terrestrial nest building has been performed more frequently by the arboreal chimpanzees in areas where the predation pressure is low (Maughan & Stanford, 2001). Nests are built more peripherally within trees where there are high presence of predators (Stewart, 2011). This supports the hypothesis that arboreal nest construction is a behaviour related to predation pressure.

There are several factors that influence nest site selection in great apes. The risk of predation is probably one of them according to most researches. Hypotheses for natural behaviour can always be discussed and it is hard to decide what is correct;

“Predation pressure in Nimba was low or absent. Current tree-nesting may reflect a recent extermination of large ground predators. The observed preference for bigger and taller trees could reflect a strategy to reduce accessibility from ground predators. However, chimpanzees nested mostly in the middle layer of the tree crown and thus did not maximize nest height. Further, preference for a low first branch increased, rather than reduced, accessibility to the nest tree. The chimpanzees increased their functional nest height, possibly by orienting nests in the direction of the slope, but the height difference was small and unlikely to be functional. Also, chimpanzees showed no preference for either more or less isolated tree canopies. In

sum, our findings provide no support for the antipredation hypothesis. We cannot exclude the possibility that arboreal nests functioned (partly) as an antipredator strategy in the past, but current tree-nesting does not reflect predator avoidance adaptations" (Koops et al. 2012).

A question to be asked is; what about captive apes? They also build elevated nests for sleeping in and they are in no risk of predation. I believe that arboreal nesting is one of the most species-typical behaviour of many primates and that nesting at elevated sites provides a safe and sound place to retire for the night, whether it is in the wild or in a zoo. The feeling of being secure while resting is crucial for good quality sleep, which is important. Captive apes may experience stress from their environments and from humans, and so the possibility to escape to elevated heights to construct a comfortable nest may be important to their welfare.

In most studies it is found that predation pressure has an influence on the nest building of the great apes. I don't think it is the only supported hypothesis behind this behaviour but I find it likely that it is one of the greatest reasons why nesting behaviour occurs.

If the numbers of predators that can be a threat for the great apes decreases in the future, maybe terrestrial nesting will become more frequent. This is only a thought and I believe that only time will show.

Nesting for more comfortable sleep

"It turns out that orangutans follow a similar pattern of construction for all their nests. After choosing a horizontal branch or branches to build the nest on, the apes bend particular branches inwards and weave them together. Smaller, broken branches are then layered on top of this basic structure and woven into a sort of "mattress." Then, leafy branches are added as a lining. Finally, depending on the individual and the nest, roofs or leafy pillows are sometimes added" (Yoshida, 2012).

Several researchers have collected data on how additional material, like leafy twigs, are put on top of the nests to perhaps increase the comfort (Bolwig, 1959; Ghiglieri, 1984; Goodall, 1962).

Why would a great ape add soft material to sleep on if not for the comfort of it? Well, I have no answer to that, but it is quite obvious that a soft nest constructed of natural materials can provide support for a big bodied non-human primate.

The nest will allow them to sleep in horizontal position and it may incease the quality of sleep, which in turn may be important to maintain healthy, both mentally and physically. The largest specie of the greatest ape is the gorilla, and even though they often sleep on the ground they sleep in nests on the ground. This is probably not to avoid predators, but it supports the theory of nest building for comfortable resting.

Another fact is that apes tend to seek protection from hoarse weather conditions in arboreal nests. In the wet rainy season gorillas nest more frequently in trees compared to the dry season. An arboreal nest is potentially warmer, drier and less exposed to wind than a ground nest. This also supports the hypotheses of nesting behaviour to facilitate comfort and high quality rest.

Captive apes tend to choose softer materials for the construction of night nests (Lock, 2011), and this may also indicate that they prefer comfortable night nests. It may be painful for a heavy primate to sleep on a hard structure without any softer covering.

Thermoregulation

The theory of thermoregulation as a reason for nesting behaviour has been supported by several studies. During the night, the body temperature of the apes will decrease and a nest may help maintain a higher body temperature. It has been shown that chimpanzees build nests higher up in the trees in humid conditions, like the wet season (Koops et al. 2012).

Nest height variation across seasons; i.e. they nest higher in the wet season, supports the theory that apes nest to get protection from environmentally disturbances like wind and humid condition.

Gorillas have also been observed to nest in trees more frequently in the wet season (Tutin et al. 1995). This may be to keep warmer during the night and avoid sleeping on the wet, cold ground.

Stewart (2011) discovered that in warm and dry weather conditions, chimpanzees used fewer branches, less support and be thinner and less elaborate in such environmental conditions. This also supports the theory of better thermoregulation: thinner nests may increase heat loss in warm weather.
I believe that thermoregulation is one of the main functions of nests building. Different studies have proven that ecological factors such as rainfall will have an impact on nesting among apes. If you could choose; would you sleep on the cold, wet ground or on an elevated safe sleeping platform of soft leaves and twigs? I think that sleeping in a nest will help keep apes warm and comfy during the night, as well as it can enhance heat loss if necessary.

Anti-pathoghen

Mosquitoes, other insects and parasites may be disturbing for the great apes and they can also be vectors of various pathogens. Fleas and lice can easily accumulate in nests and this may be a good reason to build a new nest every night instead of reusing old nests.

Orangutans carrying with them trees with mosquito repellent properties to use in nests are interesting and further research should be done to understand this better.

Arboreal nesting could help decrease bites from insects living on the ground and some freshly broken trees may help deter insects.

All in all I don't think this is the main function of nesting, but nesting behaviour is probably multifactorial and the avoidance of pathogens is likely to be one of the functions of a nest.

Stewart experienced less bites from insects sleeping arboreal in a chimpanzee nest than she did on the ground, and this may indicate that arboreal nesting decreases the disturbance from mosquitoes and other insects. On the other hand, chimpanzees build nests in trees even in areas and periods of very low mosquito density and no obvious link between nesting patterns and mosquito density has been proven (Koops et al. 2012).

Age and sex differences

Juvenile great apes nests with their mothers up to a certain age. They might engage in nest building during the day and they have also been observed playing with nests, but they don't construct their own night nests before they are 3-6 years old.

The ability to construct nests increases with age (Fruth, 1995). Young apes have to practice their nest building skills to be able to make good and safe nests as adults. The time used to build a nest decreases with age, maybe because they become more and more skilled.

Young individuals are more vulnerable and this seems to reflect their choice of sleeping sites; immatures tend to build nests higher and further away from the tree trunk. This could be to avoid predators or simply because the thinner branches peripherally are easier to manipulate for small apes. Another theory is that big apes can't find materials strong enough to support them at such elevated heights.

As one would expect, immatures of lower body weight build smaller nests than adult apes. Less support is needed for a small individual compared to that of a big one. I think its interesting how young apes learn to be efficient nest builders.

Female apes have been reported to spend more time on nest building than males. It may be because an infant is dependent on her, and so her nest should provide space, safety and comfort for her and her offspring. However, Stewart found that two chimpanzee females without infants constructed nests that were similar to the other females (Stewart, 2011).

In addition to this, adult females tend to nest higher than males. This could indicate that the males have a role in protecting the females by nesting lower and more exposed to predators. It could also be due to the fact that there is less risk for predation at elevated heights.

Nesting in captivity

Looking at the fact that nesting is a natural behaviour and one of the most species-typical behaviour of the great apes, it is important to educate care takers about this in zoos and other captive settings were great apes are kept.

Providing correct and adequate amount of nesting material is easy to manage and it can help prevent unwanted and abnormal behaviour. Another important argument to give great apes the opportunity to nest in captive settings is that it may increase the quality of sleep as it provides comfort, warmth and a safe place to rest a big body.

The construction of a nest is also a healthy way to activate the apes as it is a natural behaviour. If apes are not given the opportunity to build nests it could have negative influence on the welfare in captive settings.

I see little reason not to give captive apes the possibility to perform nest building. It should be required by law in all countries that natural and species-typical behaviour should be encouraged in case of all captive animals. Elevated sleeping platforms and appropriate nesting materials can increase the welfare for captive apes and this fact should not be neglected.

“Sleeping areas should be large enough to accommodate communal sleeping, especially with reference to bonobos, gorillas, and to a lesser extent, chimpanzees, that are known to sleep socially in the wild. Sleeping areas could also incorporate several different rooms, as individual apes may prefer specific areas for nesting and sleep. Further, these areas should feature both elevated structures for nest construction, but should also incorporate floor coverings and substrate in their design, given the relatively high prevalence of ground nesting. In keeping with the data reported here, a combination of nesting materials should be presented to allow individual preferences to be expressed” (Lock, 2011).

In her study, Lock found that most facilities were they kept great apes gave them the opportunity to make night nests. This is probably not true for all zoos etc around the world, and effort should be made to increase the knowledge about nesting behaviour in great apes and the importance of it.

Summary and conclusions

While studying different literature about nesting behaviour I found that most researchers agree that this is an important specie-typical behaviour, and the great apes will build nests both in the wild and in captive settings.

This behaviour have probably several functions: it may help to avoid predators, it may give increased comfort and quality of sleep, it may facilitate better thermoregulation and it may be to avoid insects and vectors of pathogens. There might be other reasons and functions to build nest that human still haven't understood yet. The social aspects of nesting may be more meaningful than we think and further research is needed on this topic.

Captive apes need to be given the opportunity to perform nest building activity, as this can increase the welfare of the animals as well as to allow them to perform their natural behaviour. Great apes may spend up to one half of their lifetime in nests. Being aware of this I think nest and sleep sites should be carefully considered. Nesting materials can be used as environmental enrichment for captive non-human primates.

Variations among species, populations, and age and sex classes do occur but the fact is that great apes tend to sleep in nests, and therefore they should have the possibility to do so also in captivity. In the wild they have preferred areas for nesting and they choose specific tree species. This should be taken into consideration when keeping great apes captive.

I believe that better understanding of nesting behaviour can contribute to a better welfare for captive apes, and it should be encouraged in all zoos and similar facilities were non-human primates are kept in captivity.

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